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**“Hunting between the air and the water:
the Australasian gannet
(*Morus serrator*)”**

A thesis presented in partial fulfilment of the requirements for
the degree of Doctor of Philosophy in Ecology
at Massey University, Auckland, New Zealand

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DEDICATION

To my mother Lidia Capuska

To the memory of my father, Emilio Machovsky

To the best possible family I could ever dream of



To my FRIENDS... even some widespread around the world,
you are always in my heart

FRONTISPIECE



Australasian gannets (*Morus serrator*) are highly specialised amphibious predators capable of coping with the optical and physiological demands of rapidly transitioning between the air and water interface. Photo cover of Proceedings of the Royal Society B: Biological Sciences 2012, 279 (1745), courtesy of David Raubenheimer.

ABSTRACT

Australasian gannets (*Morus serrator*) are the second rarest member of the seabird group Sulidae. Among the three species of gannets worldwide, they are the only species that regularly breeds in southeastern Australia and New Zealand. Like all gannets, *M. serrator* face considerable challenges in foraging, relying on sparsely and patchily distributed pelagic prey, which move in a 3D environment. Whereas most predators are specialise hunters in one media, gannets have to hunt within a complex air-water interface. The aim of the present thesis is to examine the hunting strategies of Australasian gannets, with particular emphasis on how these birds use both aerial and aquatic adaptations to locate and capture prey.

The acquisition of information concerning food sources was analysed using GPS data loggers, field observations and high resolution video footage. I tested the hypothesis that gannets obtain information of food resources from their partners using bill fencing as referential signals analogous to the waggle dance in honeybees (*Apis mellifera*) (Chapter 2). Results did not support this hypothesis but suggested that Australasian gannets use a combination of strategies, probably including memory that facilitates their return to locations where prey was previously captured (Chapter 3) and local enhancement to locate active feeding sites (Chapter 2).

The impact of intraspecific competition for local resources was studied between large (Cape Kidnappers, 7,300 breeding pairs) and small (Farewell Spit, 3,900 breeding pairs) colonies in New Zealand using GPS data loggers (Chapter 3). Results indicated that gannets from the larger colony invested more in foraging (greater foraging times and foraging distances). This is consistent with previous studies of other gannet species, suggesting that *M. serrator* experience intraspecific competition for food when living in large colonies.

Pelagic prey are able to evade predation by descending to depths beyond the reach of diving birds. Among the adaptations evolved by gannets for dealing with this challenge is plunge-diving, where the bird uses gravity in the aerial phase of the hunt to gain speed and momentum for descending into the water column. I conducted a fine scaled analysis using videography of the aerial and aquatic phases of this highly specialised hunting strategy. Analysis of the aerial phase (Chapter 4) showed that the initiation of plunge dives are synchronised among members of foraging groups,

suggesting a form of group-level behaviour in which gannets might benefit from the sensory experiences (prey detection) of conspecifics. The analysis also showed that gannets adapt the aerial phase of their dives in presence vs. absence of heterospecific predators. In the aquatic phase (Chapter 5), gannets perform short and shallow V-shaped dives and long and deep U-shaped dives in pursuit of pelagic fish and squid. My findings revealed that gannets adjusted their dive shape in relation to the depth of their prey rather than prey type, as previously hypothesised. Although the maximum number of prey captured per dive by the gannets was higher than previously reported, reaching up to five fish in a single U-shaped dive, the results presented herein suggest that the two dive profiles were equally profitable.

To examine the role of underwater vision in prey capture, I used underwater video footage, photokeratometry and infrared video photorefractometry (Chapter 6). Analysis of video footage confirmed that there are two distinct phases in the underwater component of plunge dives in Australasian gannets, an initial phase in which the bird is propelled through the water column by the momentum of the plunge (M phase) and a phase in which it is actively propelled by wing flapping (WF phase). The highest prey capture rate was observed during the WF phase, a result that suggests the use of vision in underwater prey pursuit. I therefore used photokeratometry and video photorefractometry to test whether gannets are able to adapt optically in the transition from aerial to aquatic media. My measurements showed that underwater visual accommodation in the gannets was attained within 2 - 3 frames (80 - 120 ms) of submergence, a remarkably short timescale in relation to the optics of most vertebrate eyes.

The preceding chapters demonstrate some highly effective behavioural and sensory capacities used by gannets in foraging. In Chapter 7 I demonstrate evidence of fatal injuries due to collision between conspecifics in plunge-diving Australasian and Cape gannets (*M. capensis*). The analysis also revealed a case of attempted underwater kleptoparasitism, in which a diving bird targeted a previously captured fish in the beak of another gannet. This novel observation suggests a further challenge for hunting gannets, namely to retain prey following the capture.

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It's been a big journey....yes indeed. In the mid-1980s I remember reading an interview of some famous person and they were asking him about his favourite things and particularly about his dreams. Mimicking the interview, I wrote down my favourite things (I remember there were 2 or 3) and the list of dreams I had at that point in time. Believe it or not, one of those was to become a "marine biologist". Here I am 25 years later writing the last pages of my PhD thesis. A lot of water has passed under the bridge... I lost my hair in the process... and to my own amazement, I now speak and write in a different language and I am immersed in a different culture. Nothing can express the joy and pride I feel being able to tick the last dream of that list: 'Become a doctor in science'

"Dreams are not negotiable...they are little treasures in your soul... don't waste them, just enjoy the adventure of making them real."

Gabriel E. Machovsky-Capuska

Zig Ziglar said, "Success occurs when opportunity meets preparation." The success of the achievement of this dream reflects the support of several people. Special thanks to Karen and Sabrina Machovsky, Cristina Negri, Laura Plana and Lilia Sevillano for their hours invested in the development of my bilingual skills. Many thanks to Adrian Voycovich and family, Dr. Simon Thrush, Dr. Judi Hewitt, Dr. Drew Lohrer and the members of the Benthic Ecology Group at NIWA-Hamilton for the opportunity to work with all of you during my early years in New Zealand.

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LIST OF ABBREVIATIONS

Chapter 1

kg	Kilograms
cm	Centimetres
ca.	Approximately
S	South
e.g.	For example
3D	Three dimensional

Chapter 2

E	East
BF	Bill fencing
GPS	Global Positioning System
g	Grams
s	Seconds
h	Hours
mm	Millimetres
CK	Cape Kidnappers
Km	Kilometres
m	Meters
MDC	Maximum distance from the colony
FPL	Foraging path length
TAC	Time away from the colony
S	Speed
CT	Couple time
BF/CT	Bill fencing/ Couple time ratio
BT	Bill touches
C	Pearson correlation coefficient
P	Statistic p value
2D	Two dimensional
DD	Direct departure

LC	Landing near conspecific
S	Splashdown
ICH	Information Centre Hypothesis
GMC	Gabriel Machovsky-Capuska
INS	Institute of Natural Sciences

Chapter 3

FS	Farewell Spit
FT	Flying time
RT	Resting time
SD	Standard deviation
vs.	Versus
SW	southwest
NE	northeast
M	Male
F	Female

Chapter 4

ms	Milliseconds
----	--------------

Chapter 5

MSFA	Multi-species-feeding-associations
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Chapter 6

M	Momentum phase of the dive
WF	Wing flapping phase of the dive
D	Defocus measure in dioptres
IR	Infra-Red
F	Dioptric power of a cornea
E	Eccentricity of the light source
A	Distance of the camera to the eye
DF	Dark fraction in the pupil and
R	Pupil radius

LED	Light Emitting Diode
CCD	Charge-Coupled Device camera
p	Pages

Chapter 7

G-G	Gannets colliding with gannets
G-SWH	Gannets colliding with sharks, whales and/or humans
G2M	Gannet found floating dead in the water on the 2 nd May
G17M	Gannet found floating dead in the water on the 17 th May

Chapter 8

UV	Ultraviolet
----	-------------

GLOSSARY

Emmetropia: the situation where parallel rays are focused exactly on the retina and vision is perfect (Chapter 6, Zadnik et al. 2004)

Fundus: the portion of the interior of the eyeball around the posterior pole, visible through the ophthalmoscope (Chapter 6, Jones et al. 2007)

Hyperopia: also called far sightedness, refers to the situation where near objects are seen with difficulty compared to distant objects. Far sightedness is the result of the visual image being focused behind the retina rather than directly on it (Chapter 6, Donahue and Baker 2005).

Local Enhancement: foragers may indirectly locate food patches by observing the foraging behaviour of conspecifics and/or heterospecifics predators (Chapter 2, Thorpe 1963). Once the food source has been located, predators can increase their information on the prey by observing its behaviour as well as that of other predators that are foraging in the area (Chapter 4, Schaller 1963).

Myopia: the state of refraction in which parallel rays of light are brought to focus in front of the retina of a resting eye. Also called near sightedness (Chapter 6, Saw et al. 1996).

Visual accommodation: The ability to focus the eye to see objects sharply at varying distances (Chapter 6, Thewissen and Nummela 2008).

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CHAPTER 1

1. Introduction

1.1 Overview of the challenge of feeding

Nutrition is fundamental to almost all aspects of an animal's existence, including fitness, growth, reproduction, predator avoidance, immune responses, migration, and hibernation and is thus a central aspect of adaptation to the animal's niche (Raubenheimer 2010). It has been suggested that predator performance is affected by the preys' nutrient composition (Mayntz and Toft 2001), with prey items varying considerably in this respect depending on species, foods eaten, season, life style and sex (Jensen et al. 2012). To meet the animal's various needs -for example growth, locomotion, maintenance and rearing offspring- high-quality diets that are nutritionally balanced with respect to these requirements are necessary (Provenza et al. 1997; Raubenheimer and Simpson 1997; Raubenheimer and Simpson 2003). Within their chosen habitat, predators face the problem of locating and capturing foods while avoiding predation and other hazards, challenges that are more extreme for some animals than for others (Raubenheimer 2010). The efficient exploitation of available food is thus a vital requirement (Emlen 1966; MacArthur and Pianka 1966), and consequently foraging strategies to the habitat in which they evolved (O'Brien et al. 1990).

Many vertebrates, including mammals (Poole and Dunstone 1976; Dunstone and Clements 1979; Bastida and Rodriguez 2009), reptiles (Trillmich and Trillmich

1986; Shine et al. 2003), frogs (Christian 1982), fish (Temple et al. 2010) and birds (Oliver 1955; Thewissen and Nummela 2008), forage in different habitats (e.g. terrestrial and aquatic, air and water) and are described as “amphibious foragers”. Among them exists a highly selected group of fish and birds that forage specifically within the air-water interface (Thewissen and Nummela 2008). The need to function in both media, at the sensory and motor levels, imposes major constraints, evolutionary pressures and physiological trade-offs on the individual’s morphology, physiology and sensory systems (Kröger and Katzir 2008). Amphibious predators are confronted with four main problems while searching for food in the air-water interface. First, breathing while in the air and/or underwater represents a difficult task to achieve under foraging circumstances (Kooyman and Ponganis 1997; Heithaus and Frid 2003). Second, there are multiple constraints on sensory capabilities that are linked to the physical characteristics of these two different environments (Denny 1993). Third, mechanical interactions between the animal and its environment represent a fine line between being a highly successful predator and becoming prey. For example locomotion in both media is a highly energetically expensive task which requires specific behavioural and morphological adaptations (Rayner 1986). Fourth, considering that thermal conductivity of water is higher than that of the air, amphibious predators require appropriate insulation to maintain their body temperature (Denny 1993).

Spending 90% of their lives at sea, seabirds are an example of successful amphibious predators that are able to perform sensory and motor tasks in both media. These air-breathing predators feed underwater but also travel through the air, and thus are constrained by an aerial-aquatic trade-off in body design (Schreer and Kovacs 1997; Weise et al. 2010). While in the air, wing morphology and streamlined

body shapes reduce the aerodynamic costs of locomotion (Brewer and Hertel 2007), while reducing drag coefficients and energetic costs while submerged (Kooyman and Ponganis 1997). Although the oxygen stored in the body is depleted underwater through metabolic processes including locomotion (Sato et al. 2007), the total body mass density and buoyancy in birds is mainly affected by the volume of the air trapped in the plumage and the respiratory system (Wilson et al. 1992). However, feathers provide the necessary thermal insulation to fly under cool temperatures and also forage underwater (Rayner 1986). To prolong dive times and increase the proportion of time spent in pursuit of prey (Kato et al. 2006), birds must efficiently control buoyancy resistance for saving energy (Watanuki et al. 2003). Searching for prey requires visual mechanisms to cope with light reflection and refraction, as well as visual accommodation between the air-water interface (Sivak et al. 1977, 1989). Finally, foraging on marine pelagic prey often widely and patchily distributed in space and time (Weimerskirch 2007) can present additional challenges to predatory seabirds. For a predator to be successful raising young, it specifically needs a long-range foraging strategy to locate the food source and an accurate time-budget tactic to allow them to balance self-feeding with offspring-feeding (Weimerskirch et al. 1994). Under these foraging circumstances, the probability of an independent discovery of sufficient food by solitary foragers is likely low. In this heterogeneous environment, social foraging is a highly effective strategy that often depends on social interactions among group members (Couzin et al. 2005), adjustment of foraging movements (Pinaud and Weimerskirch 2005) and also the need of acquire valuable information of the location's quality of food.

1.2 Australasian gannets: “the highly specialised hunter”

Australasian gannets (*Morus serrator*) are the second rarest member of the seabird group Sulidae (Nelson 2005) and the only one of the three species of gannets that breeds in southeastern Australia and New Zealand (Nelson 1978). “Takapu” is the New Zealand Maori name for this sexually monomorphic seabird (Figure 1) that weighs approximately 2.6 kg, with a wingspan of 170-180 cm and an overall length of ca. 84 – 91 cm (Nelson 1978, Machovsky-Capuska et al. 2011b, Chapter 5).

Within New Zealand, gannets are distributed in 26 breeding colonies on the east coast and only 3 on the west coast, spanning a latitudinal range of 34 - 46 °S (Robertson 1992; Stephenson 2005; Schuckard et al. 2012, Appendix 1). With an annually increasing population in New Zealand (ca. 2.3 %, Nelson 2005) Australasian gannets are considered highly successful marine predators able to cope with the challenges of foraging for patchily distributed marine resources.



Figure 1. Australasian gannet starting its foraging trip from Cape Kidnappers colony, New Zealand.

After being replaced on the nest by their partner (Figure 2), the foraging gannet faces the dilemma of where to find food while optimizing time and energetic budgets to their needs and those of their offspring (Hamer et al. 2000; Ropert-Coudert et al. 2004, Chapters 2 and 3, Figure 2). However, there is a lack of information regarding their foraging strategies and the use of personal and social information while searching for food (Chapters 2 and 3, Figure 2). Gannets are known to have a flexible diet, feeding mainly on pelagic prey such as pilchard (*Sardinops* spp.), anchovy (*Engraulis* spp.), jack mackerel (*Trachurus novaezelandiae*) and arrow squid (*Nototodarus* spp., Wingham 1985; Robertson 1992; Schuckard et al. 2012, Appendix 1). These pelagic prey are able to evade predation by descending to depths beyond the reach of diving birds. Among the adaptations that have evolved for dealing with these challenges is plunge-diving (Figure 2). This is a highly specialised foraging technique in which the bird locates prey aerially and then plunges at high speed into the water for subsurface pursuit and capture (Cunningham 1866; Machovsky-Capuska et al. 2011a, b, 2012, Chapters 4, 5, 6 and 7). Feeding events often take place in multi-species feeding associations (MSFA) that involve high densities of foragers including heterospecifics (e.g. other seabirds, dolphins and whales) with different foraging tactics (Clua and Grosvalet 2001; Burgess 2006) and have been suggested to be collectively-organised (Wodzicki and Robertson 1955, Chapter 4). To search and detect prey under the complex optical conditions characteristic of the air-water interface (Lee and Reddish 1981; Machovsky Capuska et al. 2011b, Chapter 5; Machovsky Capuska et al. 2012, Chapter 6) gannets may predict their diving performance (Chapter 5). Once submerged, they either adopt a V-shaped dive profile, in which the bird surfaces immediately after a downward momentum phase that occasionally

includes a short phase of wing flapping, or a U-shaped profile in which the momentum phase is followed by a longer phase of active propulsion using wing beats (Garthe et al. 2000; Ropert-Coudert et al. 2009; Machovsky-Capuska et al. 2011b, Chapter 5).

The aerial detection of prey (Cunningham 1866; Lee and Reddish 1981) as well as the active pursuit of prey underwater is regarded as visually guided (Machovsky-Capuska et al. 2012, Chapter 6, Figure 2). Plummeting into the water is a highly effective strategy, as evidenced by the success of four families of seabirds (Sulidae, Phaethonidae, Laridae and Pelecanidae) that feed in this manner (Nelson 1978; Machovsky-Capuska et al. 2011a, Chapter 7). However, feeding in high-density assemblages can involve fierce competition (Camphuysen and Webb 1999), risk of predation (Heithaus and Frid 2003) and expose gannets to risk of injury or death due to accidental collisions (Machovsky-Capuska et al. 2011a, Chapter 7). Finally, after foraging trips that could exceed several hundred kilometers (Wingham 1985; Chapter 3) gannets need to navigate back to their colonies and distinguish their nest-mates from several hundred sexually monomorphic conspecifics (Oliver 1955; Nelson 1978; Daniel et al. 2007; Matthews et al. 2008; Krull et al. 2012; Figure 2) in a society that exhibits high divorce rates (43%, Ismar et al. 2010). The majority of the arrivals into the colony involve an aerial call and a head-wagging response from their nesting partners that subsequently leads to a sustained bout of bill clashing called the “bill fencing ceremony” (Figure 2). This is assumed to consolidate the pair bond (Nelson 1978, Chapter 2) but might involve other functions, such as the exchange of foraging information (Chapter 2).



Figure 2. Decision-making process during the foraging journey of Australasian gannets: 1) Re-encounter with the appropriate partner in the “bill fencing ceremony”; 2) From the periphery of the colony, decide where to forage; 3) Searching for food; 4) Plunge-diving events; 5) Pursuit and capture of underwater prey; 6) Finding their nests at Cape Kidnappers colony. Photo 1 courtesy of David Raubenheimer and Photo 5 courtesy of Danny Boulton.

1.3 Thesis structure and objectives

The primary aim of the present thesis is to understand how Australasian gannets forage between the air and water in a complex 3D marine environment. This thesis comprises six research chapters (Chapters 2 to 7) with an introductory and concluding chapter (Chapters 1 and 8, respectively). Each research chapter has been written in a publication format and represents manuscripts that were published or are currently in preparation for submission (journal authorship and authors' contributions are detailed below). This approach inevitably leads to repetition but this has been minimised where possible through cross-referencing among chapters.

The thesis structure is as follows:

Chapter 1 introduces the study and provides an overview of relevant literature available on Australasian gannets' sensory and nutritional ecology. The context of the study and the gaps in the literature that it aims to address are also highlighted.

Chapter 2 explores the possible role of bill fencing in Australasian gannets as a signal to enhance foraging efficiency analogous to the waggle dance in honeybees. Data were collected by G.E. Machovsky-Capuska during fieldwork conducted at Cape Kidnappers' gannetry during the 2008/2009, 2009/2010 and 2010/2011 breeding seasons (Figure 3). Experiments were designed by G.E. Machovsky-Capuska with the assistance of D. Raubenheimer. Data analyses were undertaken by G.E. Machovsky-Capuska with the assistance of D. Raubenheimer, E. Libby and M.E. Hauber. The chapter was written by G.E. Machovsky-Capuska and improved

by edits and suggestions provided by D. Raubenheimer, M.E. Hauber and E. Libby.

This chapter is currently in preparation for submission:

Machovsky-Capuska, G. E., Hauber, M. E., Libby, E., Couzin, I., Wikelski, M., and Raubenheimer, D. Bill fencing in Australasian gannets: is it a signal to enhance foraging efficiency?

Chapter 3 compares foraging behaviour of Australasian gannets between two colonies in New Zealand. Data were collected by G.E. Machovsky-Capuska during fieldwork conducted at Cape Kidnappers' and Farewell Spit gannetries during the 2009/ 2010 and 2010/ 2011 and 2012 austral breeding seasons, respectively (Figure 3). Experiments were designed by G.E. Machovsky-Capuska. Data analyses were undertaken by G.E. Machovsky-Capuska with the assistance of E. Libby. The chapter was written by G.E. Machovsky-Capuska and improved by edits and suggestions provided by D. Raubenheimer, M.E. Hauber, E. Libby, R. Mullers, J. Waas and P. Battley. S. Dwyer assisted with the creation of the maps. This chapter is currently in preparation for submission:

Machovsky-Capuska, G. E., Hauber, M. E., Libby, E., Schuckard, R., Melville, D., Cook, W., Houston, M., and Raubenheimer, D. A comparison of foraging strategies of chick-rearing Australasian gannets at two colonies in New Zealand.

Chapter 4 explores the patterns of synchronisation and collective decisions in plunge-diving Australasian gannets using aerial videography. Aerial video footage used in this chapter was collected from 10 different feeding events in October 2009 and December and January 2012 in the Hauraki Gulf by G.E. Machovsky-Capuska (Figure 3). Data analyses were undertaken by G.E. Machovsky-Capuska with the

assistance of C. Amiot and E. Libby. The chapter was written by G.E. Machovsky-Capuska and improved by edits and suggestions provided by D. Raubenheimer, M.E. Hauber and I. Couzin. This chapter is currently in preparation for submission:

Machovsky-Capuska, G. E., Libby, E., Hauber, M. E., Amiot, C., Couzin, I., and Raubenheimer, D. The temporal dynamics of collectivity: plunge-diving synchrony in conspecific and multi-species feeding assemblages in Australasian gannets (*Morus serrator*).

Chapter 5 describes the diving strategies and foraging effort of Australasian gannets in the Admiralty Bay and Current Basin, Marlborough Sounds, New Zealand (Figure 3). Underwater video footage used in this chapter was collected by my collaborator Robin Vaughn. Research questions were elaborated by G. E. Machovsky-Capuska with the assistance of D. Raubenheimer and data analyses were undertaken by G. E. Machovsky-Capuska. The manuscript for this chapter was written by G. E. Machovsky-Capuska and improved by edits and suggestions provided by D. Raubenheimer, R.L. Vaughn, B. Würsig and G. Katzir. In the present chapter, I have taken the liberty of including additional results related to the diving strategies of Australasian gannets with their comprehensive discussion. This chapter has been published as:

Machovsky-Capuska, G. E., Vaughn, R. L., Würsig, B., Katzir, G., and Raubenheimer, D. (2011). Dive strategies and foraging effort in the Australasian gannet *Morus serrator* revealed by underwater videography. *Marine Ecology Progress Series*, 442, 255-261.

Chapter 6 demonstrates the use of vision by Australasian gannets during active pursuit of prey. Experiments were carried out by G.E. Machovsky-Capuska and G.

Katzir during fieldwork conducted at Cape Kidnappers' gannetry during the 2010/2011 austral breeding season (Figure 3). Underwater video footage used in this chapter was collected by my collaborator Robin Vaughn. Analyses produced by these sensory ecology experiments were done primarily by G. Katzir and H.C. Howland, with input from G.E. Machovsky-Capuska and behavioural analyses were undertaken by G.E. Machovsky-Capuska. The manuscript for this chapter was written by G.E. Machovsky-Capuska and improved by edits and suggestions provided by D. Raubenheimer, G. Katzir, H.C. Howland and M.E. Hauber. This chapter has been published as:

Machovsky-Capuska, G. E., Howland, H. C., Vaughn, R. L., Würsig, B., Raubenheimer, D., Hauber, M. E., and Katzir, G. (2012). Visual accommodation and active pursuit of prey underwater in a plunge-diving bird: the Australasian gannet. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 279, 4118-4125.

Chapter 7 provides evidence of injuries due to accidental collisions between gannets and also reveals the use of underwater kleptoparasitism as an alternative feeding strategy. Australasian gannet carcasses were collected on the Hauraki Gulf by S.L. Dwyer (Figure 3). Post-mortem examinations were undertaken by G.E. Machovsky-Capuska under the supervision of M.R. Alley. The manuscript for this chapter was written by G.E. Machovsky-Capuska and improved by edits and suggestions provided by D. Raubenheimer, K.A. Stockin, and S.L. Dwyer. This chapter has been published as:

Machovsky-Capuska, G. E., Dwyer, S. L., Alley, M. R., Stockin, K. A., and Raubenheimer, D. (2011). Evidence for fatal collisions and kleptoparasitism while plunge diving in gannets. *Ibis*, 153, 631-635.

Chapter 8 summarises the findings of each research chapter, draws general conclusions from the data presented within this thesis and identifies future research priorities.

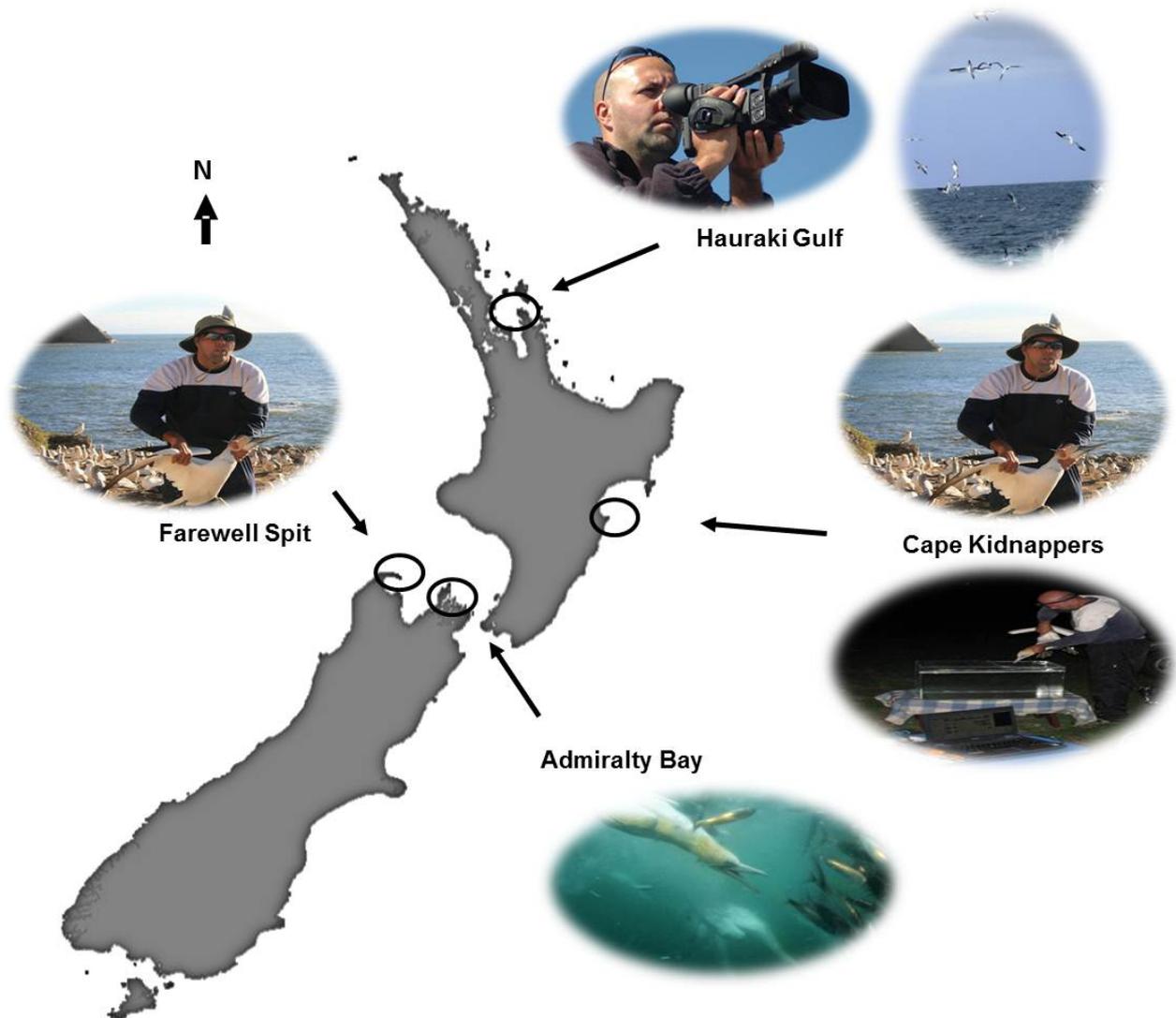


Figure 3. Location of field sites around New Zealand from which data were collected and analysed in the present study. Photos by Danny Boulton and Gabriel Machovsky-Capuska.

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CHAPTER 2

Bill fencing in Australasian gannets: is it a signal to increase foraging efficiency?

2.1 Abstract

Bill fencing is a ritualized behaviour characterised by a sustained bout of bill clashing that takes place between mating partners of Australasian gannet (*Morus serrator*) when they meet at the nest between foraging bouts. Several functions have been suggested for this ritual - including roles in mate choice, pair bond consolidation and mate recognition - but there are little data to discriminate among these hypotheses. Here I propose a new hypothesis for the function of bill fencing, namely that it plays a role in cooperative foraging analogous to the waggle dance of honeybees (*Apis mellifera*), and present an analysis of gannet behaviour at the nest and during foraging to test which hypotheses are best supported. Results are consistent with bill fencing playing a role during courtship and in pair bond consolidation. However, no evidence was found to suggest that it is involved in information exchange regarding the location of foraging resources.

2.2 Introduction

Long-range foraging strategies, as adopted by many seabirds, involve decisions about when to depart, whether to forage solitarily or in groups, and how to acquire information about the locality and quality of food resources. Australasian gannets (*Morus serrator*; hereafter: gannets) congregate in large colonies during the breeding season with members of each pair alternately tending the single progeny and foraging (Nelson 1978; Daniel et al. 2007). If the tending parent leaves the nest unguarded, the egg or chick is highly vulnerable to predation (Stephenson 2005). It is thus strongly in the reproductive interests of both parents (Nelson 1978; Matthews et al. 2008) that their foraging trips are efficient and timed so as not to cross the threshold where the guarding parent abandons the chick to forage. Foraging is, however, challenging, as the pelagic marine foods of gannets are widely and patchily distributed in space and time, often necessitating trips that range over hundreds of kilometers and can span several days (Hamer et al. 2000; Weimerskirch 2007; Machovsky-Capuska et al. 2012, Chapter 3). There is thus a strong potential benefit to breeding pairs cooperating to maximize foraging efficiency, and an effective way of doing so would be for the returning bird to transfer to its mate current information on the nature and whereabouts of resources.

An example of a species that transfers information about foraging in this way is the honeybees (*Apis mellifera*), which signals to nest mates the direction, distance, and quality of foods in a complex ritual known as the “waggle dance” (von Frisch 1967). Three socioecological factors may help to explain the evolution of this unusual form of signaling: i) the highly social conditions in which honeybees live favour the rapid and efficient exchange of information among colony members (King and Cowlshaw 2007); (ii) the honeybees within a colony have a close degree of

genetic relatedness and therefore the evolutionary interests of signaller and receiver are tightly aligned (Hamilton 1963); (iii) the foods for which honeybees forage are typically patchily distributed and quickly exhausted, and in these conditions the timely sharing of information increases foraging efficiency (Beekman and Lew 2008).

Why should equivalent communication signals not have evolved more widely, for example among social vertebrates? We propose that similar languages may be more widespread, but have yet to be decoded. To investigate this, studies are required of other species that fulfil criteria i) – iii) above, and are amenable to the challenges of interpreting coded signals. The Australasian gannet is such a species, because as stated above they are colonial breeders (criterion i), breeding partners have a strong common interest in efficient foraging (criterion ii) and foraging resources are widely and patchily dispersed (criterion iii). We have identified as a candidate for such communication a behaviour known as “bill fencing”, a sustained bout of bill clashing and facial contact that takes place almost invariably in the critical period separating the return of one parent to the nest and the departure of the other (Nelson 1978, Machovsky-Capuska et al. 2009, Figure 1).



Figure 1. Australasian gannets bill fencing. Photo by David Raubenheimer.

Several functions have previously been suggested for bill fencing. As it takes place extensively during the pre-reproductive period of pair formation, one possibility is that it plays a role in mate choice (Meseth 1975; Nelson 1978). Mate choice cannot, however, be the only function of bill fencing, because it continues to be a prominent part of the behavioural repertoire beyond the period of pair bond formation, throughout the breeding season. Another possibility is that bill fencing is used by gannets on re-establishing contact between foraging trips to recognize their partners (Nelson 1978). Other possibilities are that gannets use bill fencing to i)

continually consolidate the pair bond and ii) to acquire information to aid decisions as how much to invest in reproduction and whether to stay or divorce. The latter predicts that divorce rates should be fairly high (Wachtmeister 2001), as indeed they are among Australasian gannets (in the order of 43%, Ismar et al. 2010). Finally, bill fencing might have evolved as a means for birds to manipulate their partners into increasing their investment in reproduction (Wachtmeister 2001).

Beer (1977) concluded that “much of what is regarded as display behaviour, however, is recognized as such before there is a clear understanding of its communication function”. In an endeavour to help clarify the situation, in the work reported in this chapter I combined behavioural observations, video footage collection and data from GPS data loggers in an attempt to test which functional hypotheses for bill fencing in gannets are best supported by the data.

2.3 Material and Methods

2.3.1 Study Area

The study was conducted between September and March 2009 - 2011 on the Beach colony of Cape Kidnappers gannetry (CK), New Zealand (39° 38' 48" S, 177° 05' 36" E). Cape Kidnappers has 4 gannetries and the population of Australasian gannets is around 7300 breeding pairs (Stephenson 2005, Ismar et al. 2010). The Beach colony is located at sea level. This study was conducted under permits of Massey University Animal Ethics committee (09/76) and New Zealand Department of Conservation (ECHB-23237-RES).

2.3.2 Nest identification and pair changeover

Forty three nests sites in the periphery of the Beach colony were randomly chosen and individually marked with permanent markers following Stephenson (2005). Both adults in the nest site were individually banded on separate legs for better identification and feathers were collected for sex identification following Daniel et al (2007). Individual arrivals and departures among marked nests were systematically monitored every half hour from dawn to dusk. The length of time the couple spent together during nest changeover and bill fencing (BF) ceremonies were recorded following Müller-Schwarze and Müller-Schwarze (1980). For comparisons between breeding stages, I separated the season into 3 biologically-defined periods: courtship, incubation and chick provisioning. Data were initially tested using Levene's test for homoscedasticity and Shapiro-Wilk's test for normality and then medians were compared using Kruskal Wallis test (Zar 1996). In addition, departing time and time away from the colony were estimated for all the pairs from nests that BF was subsequently recorded. BF ceremonies were categorized as: 1) upon arrival of the first adult observed (bird A) and 2) upon arrival of the second adult (bird B) of the same pair tested in 1). Bird A and B were named on their arrival on the nest rather than through sex identification. The relationship between duration of BF ceremonies and nest absence were tested using Levene's test for homoscedasticity and Shapiro-Wilk's test for normality and then using Pearson's or Kendall's rho correlations for parametric and non-parametric data, respectively (Zar 1996). For statistical comparisons data were tested using *PASW Statistics* version 18. Data are reported as medians \pm standard deviation. Statistical significance was defined as $p < 0.05$.

2.3.3 GPS deployment and video footage collection

Both breeding adult gannets from the same nest were equipped with GPS data loggers (e-obs, Germany) weighing 35 g, 2% of the adult body weight (Nelson 1978). Data providing position (latitude, longitude, and altitude), speed and time were recorded at 1 s intervals. The data loggers were attached using Tesa tape to the 4 central tail feathers as in Hamer et al. (2000; Figure 2). Nests selected were the same as used in the nest identification and pair changeover analysis. The first bird in a pair observed to be departing from the nest was captured immediately after adopting the sky pointing posture (Nelson 1978), then released after the data logger was fitted (approximately 10 minutes as in Grémillet et al. 2004). The second bird in the pair was captured the following day while nesting, at a time predicted to be within a range of 1 – 5 h prior to the arrival of its partner. This estimate was based on Machovsky-Capuska et al. (2012) suggesting that in this colony the average duration of foraging trips is approximately 24 h. In all cases human interference during nest changeover was avoided.

Upon arrival of the first gannet tracked with the GPS data logger, high resolution video footage of the BF ceremony during nest changeover was recorded using a Canon XH A1S handycam with 20 mm zoom. After observing the adults feeding their chicks, the recently arrived bird was captured and the data loggers and tape strips completely removed. Following Machovsky Capuska et al. (2009, Appendix 3), behavioural components of BF ceremonies were analyzed frame by frame using Adobe Premiere Pro CS4. Considering the problems of accurately extracting angles from 2D video footage I decided to use the number of bill touches during bill fencing ceremonies for behavioural comparisons.



Figure 2. GPS deployment in a chick-rearing adult Australasian gannet. A) and B) Gannets were captured at the periphery of the colony, using a shepherd's hook, and then restrained by hand; C) GPS data loggers (e-obs, Germany) inside of a waterproof housing weighing 35 g; D) The data loggers were attached with Tesa tape to the 4 central tail feathers; E) To aid in their rapid identification, gannets with attached transmitters were marked on their chest using Sharpie markers®. F) After banding and attachment of the GPS the gannet was immediately released at the colony edge nearest its capture site.

Following Grémillet et al. (2004), the recorded GPS trips were analyzed to determine distance travelled, speed, and time away from the colony. To make comparisons with the dance of the honeybees, following von Frisch (1967), relationships between bill touches during BF ceremonies and data collected from GPS data loggers were tested using Pearson's correlations. Since the flight paths of gannets were not direct and involved a combination of foraging sites, I calculated the time-weighted average location to represent the final destination. For each gannet pair from which BF was recorded, I computed the average angle between their final destinations to quantify the difference in their bearing angle from the colony. Being coastal colonies, the gannets at both study sites did not have a full range of 360 degrees available for oceanic foraging trips. To statistically test whether gannets leaving the colony on the same day tend to travel in similar directions, I randomized the day assignments of gannets 100,000 times as part of a permutation test. For each set of day assignments, a permuted group, the average angle between directions was calculated to build a null distribution. This permutation method uses the actual ranges of directions gannets travel at each colony and thus corrects for biases due to geographic constraint. For statistical comparisons data from the GPS units were analyzed using MATLAB 2009. Statistical significance was defined as $p < 0.05$.

2.3.4 Departures and behaviours of gannets from the colony

During the 2009-2010 and 2010-2011 austral breeding seasons (between September and March), population-level departures were observed every hour from dawn to dusk at CK gannetry. Scans were made systematically at 30 s intervals to record the departure time and behaviour of breeding gannets at the colony, using 10

x 50 reticulated binoculars from a cliff 40 m above the colony (Waltz 1982). Since the colony is located at the base of a 60 m cliff, scans allowed a complete 180° view up to a 1 km range of the colony, which was subdivided for the purposes of initial data collection into four sectors of 45°. Following Burger (1997), departure behaviours were recorded as: i) direct departure (DD), ii) landing near conspecific (LC) and iii) splashdown (S). In addition, departing behaviours were also related to plunge-diving conspecific foraging activity (Machovsky-Capuska et al. 2011, Chapter 4). When plunge-diving gannets were visible from the colony, focal birds were followed with binoculars from the colony until they reached the feeding event and the behaviour was classified as a direct departure. Frequencies of direct departure behaviours and prey visibility were compared using χ^2 and Z-tests (Zar 1996). An increase of direct departures when feeding activity was visible from the colony was considered to reflect the use of local enhancement by the departing bird (Buckley 1997; Grünbaum and Veit 2003; Bellier et al. 2005).

2.4 Results

2.4.1 Exchange of foraging information

I succeeded in deploying GPS data loggers in both partners of a nesting pair and filming BF during the nest changeover for the same pairs in 6 couples out of 35 (17%) attempts, this amounting to approximately 600 h of effort. The major challenge was to predict the arrival time of foraging gannets at the colony, in order to film the BF at changeover.

The chick-rearing gannets ($n = 12$) were found to forage distances of 63.24 km (± 25.88 km), with total foraging path lengths of 310.94 km (± 132.17 km) and

foraging trip durations of 27.35 h (\pm 8.95 h). During foraging trips, gannets travelled an average speed of 11.58 km h⁻¹ (\pm 3.96 km h⁻¹, Table 1).

Table 1. Bill fencing ceremony characteristics and foraging parameters for six breeding couples of Australasian gannets fitted with GPS data loggers. Bird A= first arrival adult and Bird B=second arrival adult. MDC: Maximum distance from the colony (km); FPL: Foraging path length (km); TAC: Time away from the colony (h); S: Speed (km h⁻¹); BF: Bill fencing; D: Duration; CT: Couple time (s); BF/CT: Bill fencing/ Couple time ratio; BT: Bill touches

Code	Bird A					BF				Bird B				
	Sex	MDC	FPL	TAC	S	D	CT	BF/CT	BT	Sex	MDC	FPL	TAC	S
BF1	F	45.45	267.02	23.40	11.41	15.64	156.36	10.00	30	M	94.21	530.90	37.73	14.07
BF2	M	63.46	389.16	34.73	11.21	31.92	760.80	4.20	10	F	76.09	177.83	25.84	6.88
BF3	M	76.64	301.03	46.24	6.51	15.14	466.68	3.24	7	F	68.13	393.28	27.16	14.48
BF4	M	19.80	220.54	24.99	8.82	14.52	55.00	26.40	7	F	69.68	553.09	25.61	21.59
BF5	F	63.44	239.75	23.08	10.39	56.24	277.80	20.24	22	M	44.53	192.65	16.58	11.62
BF6	F	27.58	152.02	13.35	11.39	39.90	60.68	65.75	32	M	109.88	314.00	29.53	10.63

The analysis of foraging trips ($n = 12$) collected from GPS data loggers showed a negative correlation between time spent away from the colony by Bird A (the first of the pair that we observed departing) and the speed travelled by Bird B (Table 2). The analysis of the video footage of the BF ceremonies collected in relation to the GPS data loggers revealed a significant negative correlation between the duration of bill fencing and the period of absence of the departing bird (Table 2). No other correlations between distance travelled, time away from the colony, speed, BF duration, bill touches and the length of time the couple spent together during nest changeovers were observed (Table 2). Further, the distribution of the bearing of foraging trips in the GPS deployments assembled from 100,000 permutations (see Methods) revealed that the average angular difference between directions of gannets in BF pairs was not significantly less than random pairs ($p > 0.05$, Figure 3).

Table 2. Correlation coefficients between times of absence from the nest, speed during the trip, flight distance, bill fencing duration, bill touches and couple duration for different breeding adults of Australasian gannets fitted with GPS data loggers (n = 12). Bird A= first arrival adult and Bird B=second arrival adult. MDC: Maximum distance from the colony (km); FPL: Foraging path length (km); TAC: Time away from the colony (h); S: Speed (km h⁻¹); Bf: Bill fencing; CT: Couple time (s); BT: Bill touches; C: Pearson correlation coefficient and bold: statistically significant ($p < 0.05$), two tailed.

	Bird B												
	BFD		CT		BT		MDC		TAC		S		
	C	P	C	P	C	P	C	P	C	P	C	P	
Bird A													
MDC	0.60	0.21	0.32	0.83	-0.30	0.57	-0.37	0.47	0.10	0.85	-0.71	0.12	
FPL	-0.46	0.36	0.16	0.76	-0.39	0.45	-0.10	0.85	0.45	0.37	-0.73	0.10	
TAC	-0.40	0.43	0.57	0.23	-0.76	0.08	0.19	0.72	0.64	0.17	-0.90	0.01	
S	-0.25	0.64	-0.25	0.63	0.14	0.79	-0.27	0.60	0.05	0.93	-0.18	0.73	
Bird B													
MDC	-0.28	0.59	-0.31	0.55	0.55	0.25							
FPL	-0.77	0.07	-0.28	0.60	-0.12	0.82							
TAC	-0.91	0.01	0.24	0.64	-0.43	0.40							
S	0.54	0.27	-0.65	0.16	0.62	0.19							
CT	0.06	0.92											
BT	0.40	0.44											

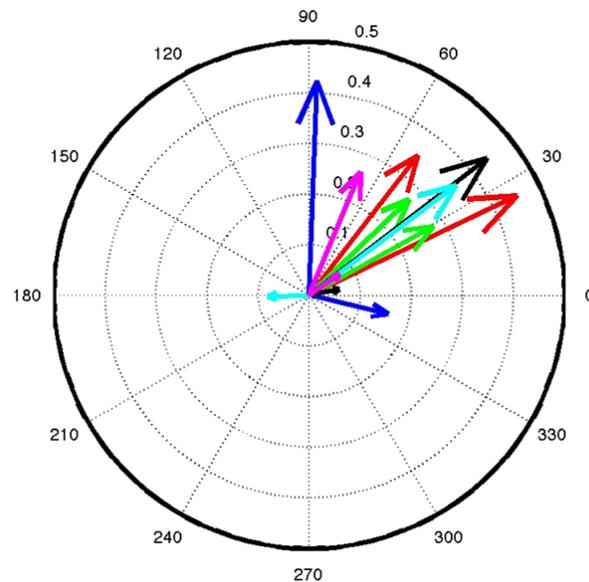


Figure 3. Average bearing angle of flight directions from foraging paths of Australasian gannet adults. Each colour represents bearing of adults from the same nest.

Eighty per cent ($n = 1640$) of breeding gannets departing from CK colony landed in the water near conspecifics forming water rafts from 50 - 70 m from the colony, whereas 19% ($n = 390$) departed directly for foraging sites ($\chi^2 = 721.27$; $df = 1$; $p < 0.0001$, Figure 4). When plunge-diving conspecific foraging activity or food sources were not visible from the colony, the majority of departures were made by solitary gannets ($\chi^2 = 57.04$; $df = 3$; $p < 0.0001$, Figure 4). However, when plunge-diving conspecific foraging activity was observed within 500 m of the colony, DD (60%, $n = 191$) were higher than LC (30%, $n = 95$, Figure 4). This frequency of DD is significantly higher than when plunge-diving conspecific foraging activity or food sources were not seen near the colony (19%, $n = 361$, $Z = 15.43$, $p < 0.0001$), suggesting the use of local enhancement by foraging gannets. Thus, the number of departed birds was also larger when associated plunge-diving conspecific foraging activity was observed nearby the colony ($\chi^2 = 135.40$; $df = 3$; $p < 0.0001$, Figure 4).

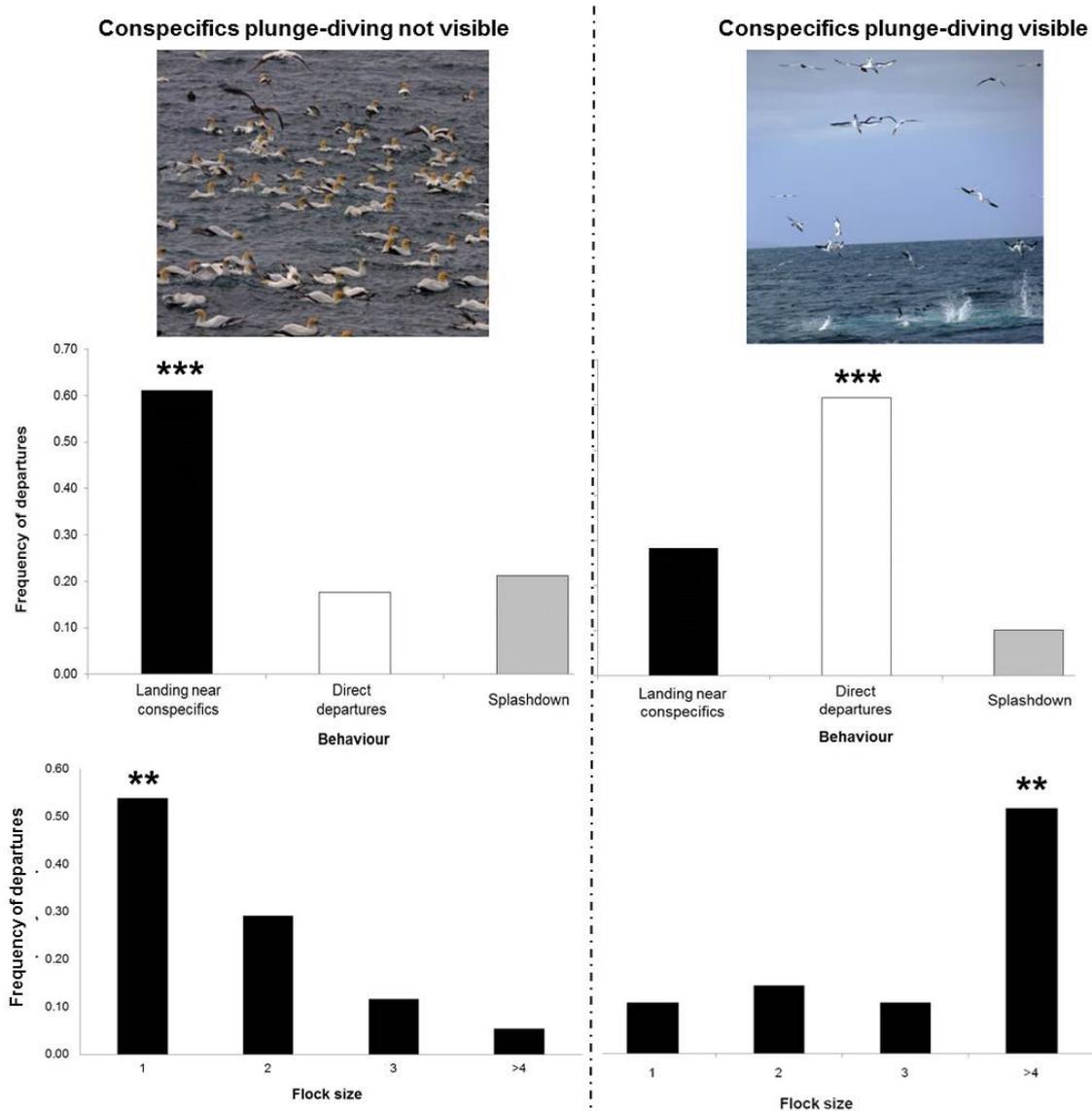


Figure 4. Frequency of departures and flock size of breeding Australasian gannets. Departing behaviours from the colony when associated plunge-diving conspecific foraging activity was not visible from the colony and when associated plunge-diving conspecific foraging activity was visible nearby. *** represents statistically significant results ($p < 0.0001$).

2.4.2 Courtship and pair bond consolidation

From a total of 203 nest changeovers recorded from the marked nests, mean BF ceremony duration was 32.74 ± 29.01 s and mean couple time spent was $213.30 \pm$

216.02 s. BF ceremonies were longer during courtship period with a median of 59.58 \pm 49.07 s (range 11.44 - 172.00 s) than in incubation (43.00 \pm 24.56 s, range 19.94 - 122.00 s) and chick rearing (19.66 \pm 13.72 s, range 4.90 – 99.50 s) (Kruskal Wallis, $h = 56.768$; $df = 2$; $p < 0.001$), whereas couple time was longer during courtship season with a median of 243.00 \pm 398.77 s (range 62.00 - 1889.00 s) than in incubation (128.50 \pm 97.71 s, range 63.00 - 471.00 s) and chick rearing (141.00 \pm 152.69 s, range 20.00 – 1007.00 s) (Kruskal Wallis, $h = 17.682$; $df = 2$; $p < 0.001$). The proportion of BF time in relation to couple time was longer during the incubation season with a median of 32.02 \pm 15.41 s (range 10.93 - 57.97 s) than in courtship (22.01 \pm 17.69 s, range 1.13 - 59.07 s) and chick rearing (16.59 \pm 16.06 s, range 1.08 – 73.32 s) (Kruskal Wallis, $h = 14.935$; $df = 2$; $p < 0.001$) (Figure 5 A).

In the behavioural analysis from the marked nests, I found a significant positive correlation between the duration of the foraging trip and the duration of the subsequent bill fencing bout (Pearson, $r = 0.343$, $p < 0.001$, two-tailed, Figure 5 B). As previously detected in the analysis of the data from GPS loggers, there was also a significant negative correlation between the duration of bill fencing and the period of absence of the departing bird (Kendall's rho, $r = -0.224$, $p < 0.05$, two-tailed). However, no correlation was observed in the analysis of the nest absence duration between adults from the couple (Pearson, $r = -0.098$, $p = 0.53$, two-tailed).

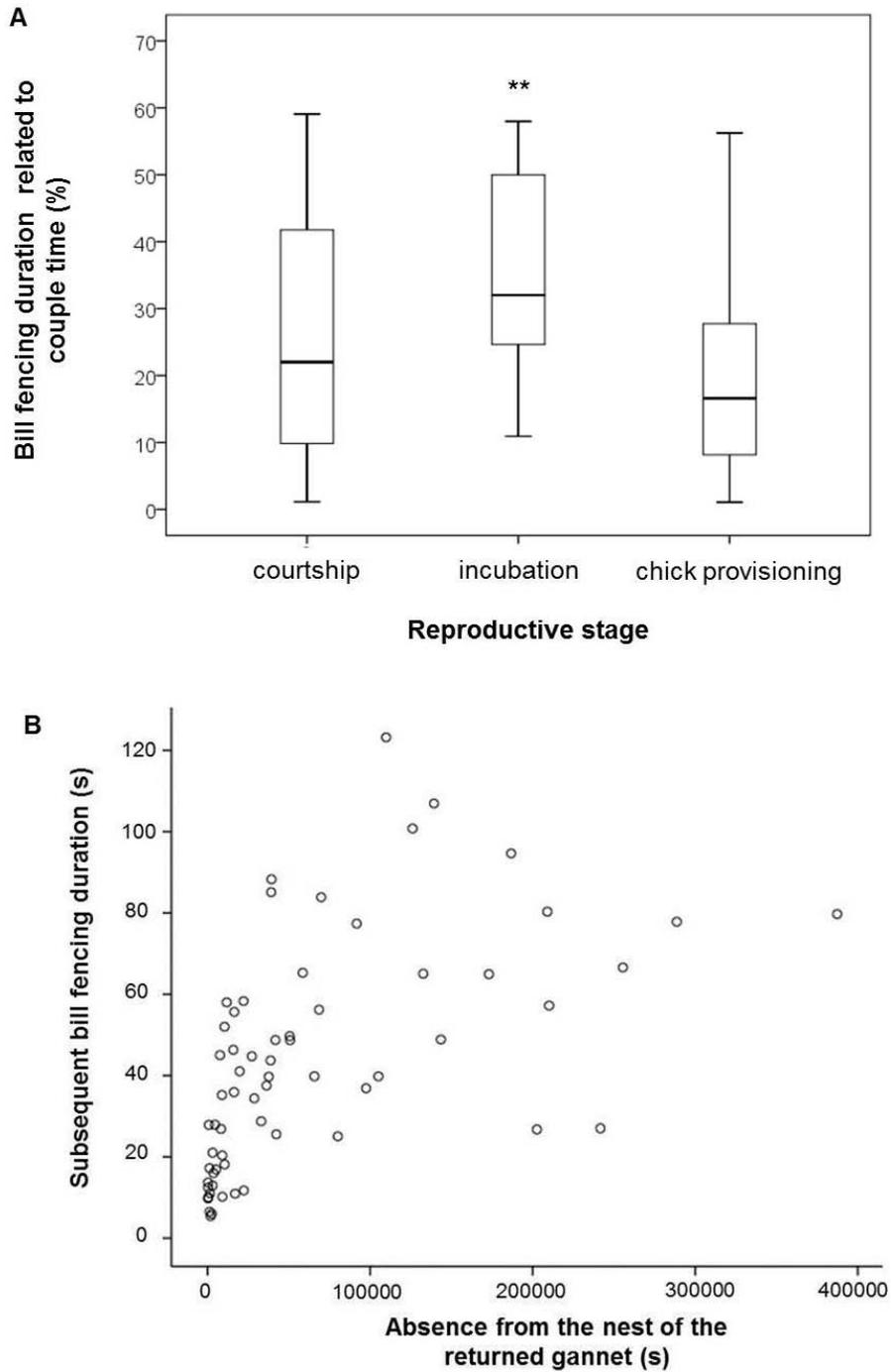


Figure 5. Bill fencing duration related to: A) couple time spent during different breeding stages. ** Statistically significant ($p < 0.001$) and B) absence from the nest of the recently returned bird.

2.4.3 Mate recognition

The analysis of landing behaviours ($n = 786$) showed that gannets started BF with their partner upon arrival on the nest in the majority of the cases (80%, $n = 629$), whereas 20% ($n = 157$) landed near the wrong partner and did not BF ($\chi^2 = 278.66$; $df = 2$; $p < 0.0001$). The majority of the BF ceremonies recorded (84.5 %, $n = 512$) started with an aerial call from the arriving bird and a head-wagging movement response from the nesting partner ($\chi^2 = 248.05$; $df = 2$; $p < 0.0001$).

2.5 Discussion

Beer (1977) noted that “there is at least the possibility that some animals use one kind of communication behaviour to communicate more than one kind of message”. In gannets, bill fencing has been described as one of the finest displays in the bird world (Nelson 1978). Although it has been suggested to serve as a courtship display (Cunningham 1886; Townsend 1920), mate recognition (Meseth 1975), pair bond consolidation (Nelson 1978) and exchange of foraging information (present study), its function remains unclear. The present analysis provides no evidence that bill fencing plays a role in exchange of foraging information or mate recognition in gannets. It does, however, implicate bill fencing in courtship and pair bond consolidation.

2.5.1 Exchange of foraging information

Widely and patchily distributed food resources present considerable challenges to predators. Species with successful biparental care must have parents that balance their reproductive investment against that of their partner (Trivers 1972). Information transfer between conspecifics, whether through deliberate or incidental signals, may

increase the chances of finding food (Bradbury and Vehrencamp 1998). Indeed, in the “waggle dance of honeybees”, von Frisch (1967) observed that the dancer signals to closely related nest mates the direction, distance, and quality of foods. Among seabirds, Cape gannets (*M. capensis*) are well known to increase their reproductive effort via increasing nest attendance and the frequency of foraging trips when needed (Bijleveld and Mullers 2009).

How do gannet partners know how much to invest in parental care? Results on the duration of bill fencing ceremonies in relation to distance, duration and angle of bearing of foraging trips did not provide evidence for the exchange of foraging information between partners analogous to the waggle dance in honeybees. However, considering that bill fencing ceremonies started upon the return to the nest from foraging, a possible foraging role of these ceremonies could be the assessment of the nutritional state of the returned bird. This would enable the departing bird to limit the duration of its foraging trip to a period that does not exceed the threshold for the returned bird to leave on its subsequent trip. Further studies are needed to test this.

Colonies have also been suggested to act as centers for transfer of information (ICH) (Ward and Zahavi 1973) and gannet colonies, in particular, have been suggested as candidates to test this hypothesis (Mock et al. 1988; Richner and Heeb 1995). The ICH predicts that naïve birds would leave the colony following successful birds directly for foraging, to maximize the probability that information about the moving and patchy food source is current. I found, however, that 80% of the birds did not head directly to the feeding grounds when plunge-diving conspecific foraging activity or food sources were not seen from the colony, but stopped near the colony in a water raft or by itself before departing for foraging. These results support

previous findings on common murrelets (*Uria aalge*) gathering near the colony prior to departing for foraging (Burger 1997) and they provide a functional explanation for observations on gannets forming and joining water rafts before heading out to sea to feed (Weimerskirch et al. 2010). Burger (1997) suggested that seabirds in water rafts would be better positioned to detect incoming conspecifics than from within the colony itself, but observational evidence for this is limited to Guanay cormorants (*Phalacrocorax bougainvillii*) (Weimerskirch et al. 2010).

Acquiring information from cues and signals of foraging conspecifics is widespread among seabirds in a process called local enhancement (Thorpe 1963). When plunge-diving conspecific foraging activity and food sources were observed from the colony within a range of 200 to 700 m, direct departures (DD) were significantly increased than when food was not visible nearby, supporting the claim that gannets use local enhancement while foraging as previously suggested in other gannet species (Nelson 1978; Grémillet et al. 2004). Foraging in this way, gannets have access to more accurate information and can make better-informed decisions by observing and following group mates (King and Cowlshaw 2007; Conradt 2011). In addition, I have also observed an increase in the flock size that may be related to the advantages of collective/synchronized diving pattern while foraging (Chapter 4). Although among birds an increase in the flock size has been related to a higher feeding success (Fernández-Juricic et al. 2004), in gannets this remains untested.

2.5.2 Courtship and pair bond consolidation

Several species, among them birds, are known to have an extensive period of courtship with the opposite sex that continues far beyond the act of pair formation (Huxley 1923; Andersson 1994). A variety of signals and behaviours are believed to

be used during these sexual interactions for assessing partner quality (Townsend 1920; Wachtmeister and Enquist 2000). My data indicated that bill fencing occurred during the main breeding stages with the longest ceremonies observed during courtship periods and the shortest in the chick provisioning stages. These results clearly suggest that bill fencing could be used as tool for mate assessment during courtship, as suggested by Nelson (1978). My findings also revealed that the duration of bill fencing in regards to the time the couple spent together during changeovers was slightly lower than in courtship stage. These results suggest that gannets extend the quality assessment of their partners into the chick provisioning period.

Within monogamous bird species a large variation in the degree of mate retention over consecutive breeding seasons exists (Rowley 1983; Choudhury 1995). Individuals should keep the same mate only when the benefit of mate retention in terms of lifetime reproductive success exceeds the benefits of all other pairing options, whereas divorce is expected when the cost of keeping the same mate exceeds the cost of mate-switching (Cézilly et al. 2000). With high divorce rates (43% in gannets, Ismar et al. 2010), incubation was suggested to be the most crucial pair bonding stage between breeding partners (Müller-Schwarze and Müller-Schwarze 1980; Cézilly and Johnson 1995). Displays and ceremonies are well known to play an important role in pair bond consolidation (Armstrong 1965; Beer 1977). Results presented here, showed the highest proportion of bill fencing ceremonies in relation to couple time during the incubation stage. This is consistent with the idea that breeding gannets use these ceremonies to strengthen their pair bond during the time the couple spent together.

2.5.3 Mate recognition

Successful social organization of colonies in seabirds depends on the capacity for mutual recognition at some distance, at least between mates, parents and young and also neighbours (Thorpe 1968). Gannets have individual calls that enable them to be individually recognized (White and White 1970; White et al. 1970; Miner-Williams 2008; Krull et al. 2012). My present finding that nesting birds respond with a head-wagging movement to their partner's aerial calls is consistent with the suggestions of White (1971). However, in my study, a minor percentage of successful landings and mate recognition occurred without an aerial call from the arrival bird suggesting that visual identification may also play an important role in this process (White 1971; Miner-Williams 2008; Ismar 2010). All this evidence suggests that mate recognition occurs during the landing process that subsequently leads to the initiation of bill fencing ceremonies (Figure 6).

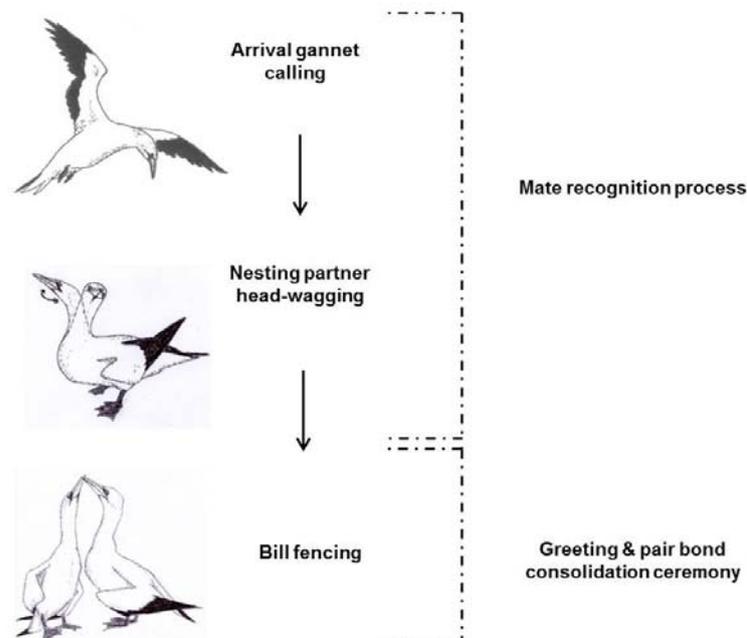


Figure 6. Mate recognition in the Australasian gannet based on landing behaviour and bill fencing efficacy. Illustrations by Laura van Zonneveld.

In conclusion, although the present results provided no support for the hypothesis that bill fencing involves the exchange of foraging information regarding the location of foods analogous to that in honeybees, further studies are needed to test for a possible role as a) an integrator for coordinating the periods of absence from the nest with the foraging success and nutritional states of the partners and b) as a possible predictor of divorce between nesting pairs. In addition, the role of water rafts as information transfer of foraging gannets' compass bearing needs further exploration. The data do, however, support a role for bill fencing during courtship and pair bond consolidation.

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CHAPTER 3

Variable foraging patterns in chick-rearing Australasian gannets from New Zealand

3.1 Abstract

Patchily distributed marine pelagic prey can present considerable challenges to predatory seabirds, including gannets. In this study I used GPS data loggers to examine the behaviour of chick-rearing Australasian gannets (*Morus serrator*) during foraging trips from two colonies in New Zealand which differ markedly in several biological and oceanographic respects. My goal was to test the extent to which gannet foraging strategies vary across disparate habitats, and determine whether the observed differences are consistent with predictions derived from studies of other gannet species. Gannets from the Cape Kidnappers (7,300 breeding pairs) travelled further distances from the colony (222.6 km) over longer periods of time (141.7 h) than the gannets from Farewell Spit (3,900 breeding pairs). Flexible foraging strategies between colonies and foraging site fidelity observed at these two sites may be shaped by the influence of food availability, oceanographic conditions and intraspecific competition as previously described for Northern (*M. bassanus*) and Cape gannets (*M. capensis*).

3.2 Introduction

Marine pelagic resources of predatory seabirds can present considerable challenges because the prey is often widely and patchily distributed in space and time (Weimerskirch 2007). This may result in foraging trips that range over hundreds of kilometres and span several days (Hamer et al. 2000; Rayner et al. 2010). In such circumstances, breeding pairs need effective long-range foraging strategies to locate the food source and accurate time-budgeting to balance self-feeding, offspring-feeding, and the foraging requirements of the partner tending the nest (Weimerskirch et al. 1994; Ropert-Coudert et al. 2004).

The three species of gannets (*Morus* spp.) are highly successful predators well known to cope with the demands of foraging in the complex marine environment (Nelson 2005). Remarkably, whereas the population of Cape gannets (*M. capensis*) decreased in the 20th century, the Northern (*M. bassanus*) and Australasian gannet populations have both increased (Bunce 2001; Nelson 2005; Crawford et al. 2007; Schuckard et al. 2012, Appendix 1). While depletion of food sources due to intensive fisheries is suggested to be the main cause of the decline in the Cape gannet population (Crawford et al. 2007), the Northern gannet population increase has been related to low pressure from fisheries on food sources, prey availability and flexible foraging strategies (Hamer et al. 2001, 2007; Garthe et al. 2007; Montevecchi et al. 2009). Although Australasian gannets have been considered to be the Southern hemisphere form of the Northern gannet, the two species seem to occupy different breeding and foraging niches (Stephenson 2005).

Australasian gannets (hereafter: gannets) breed exclusively in southeastern Australia and New Zealand (Nelson 1978) and, despite the recent positive population trends, the species remains the second rarest member of the seabird group Sulidae

(Nelson 2005). Within New Zealand, gannets are distributed among 26 breeding colonies on the East coast and only 3 on the West coast, spanning a latitudinal range of 34°S - 46°S (Nelson 2005). Gannets are known to have a flexible diet, feeding mainly on pelagic prey such as pilchard (*Sardinops* spp.), anchovy (*Engraulis* spp.), jack mackerel (*Trachurus novaezelandiae*) and arrow squid (*Nototodarus* spp.) (Robertson 1992; Schuckard et al. 2012, Appendix 1). These highly successful marine predators have been reported to travel an average feeding range of 268 km (Wingham 1985) with reliable foraging success (72% feeding success per attempt, Machovsky-Capuska et al. 2011a, Chapter 5).

Here I report a study in which GPS data loggers were used to examine and compare the behaviour of chick-rearing gannets during foraging trips in two Australasian gannet colonies in New Zealand, the Cape Kidnappers (7,300 breeding pairs) and Farewell Spit (3,900 breeding pairs) colonies. In particular, I seek to a) gain a better understanding of gannets foraging strategies and b) define the main foraging areas in which gannets feed in the two regions. As proposed by Hamer (2000) and Garthe (2007) for the Northern gannet and by Ropert-Coudert et al. (2004) and Mullers and Navarro (2010), I predict that gannets will show flexible foraging strategies in relation to food availability.

3.3 Material and Methods

3.3.1 Study Area

The study was conducted during the chick-rearing periods from 2009 to 2011 on the Beach Colony of Cape Kidnappers gannetry (CK), North Island, New Zealand (39° 38' S, 177° 05' E) and in 2012 at Farewell Spit gannetry (FS), which is located at the

northern end of the South Island of New Zealand (40°33' S 173°01' E). CK has a population of around 7,300 breeding pairs (Nelson 2005, Ismar et al. 2010), whereas FS gannetry has a population estimated at 3,900 breeding pairs (Schuckard et al. 2012, Appendix 1). This study was conducted under permits of Massey University Animal Ethics committee (09/76) and New Zealand Department of Conservation (ECHB-23237-RES).

3.3.2 GPS deployment

Chick-rearing gannets were banded with a ring on their leg (Daniel et al. 2007) and equipped with GPS data loggers (e-obs, Germany) weighing 35 g, 2% of the adult body weight (Nelson 1978). Data related to position (latitude, longitude, and altitude), speed and time were recorded at 15 s intervals. The data loggers were attached with Tesa tape to the 4 central tail feathers as in Hamer et al. (2000, Chapter 2) and feathers were collected for sex identification following Daniel et al. (2007, Chapter 2). Departing birds were captured and fitted with a data logger immediately after they displayed the sky pointing posture (Nelson 1978) and thereafter released. Following Grémillet et al. (2004) the recorded GPS trips were analysed to determine distance travelled, speed, and time away from the colony. Since the flight paths of gannets were not direct and often involved a combination of foraging sites, I calculated the time-weighted average location to represent the intended destination. For each day of deployment, I computed the average bearing angle between their destinations to quantify the difference in their daily bearing from the colony. Being coastal colonies, the gannets at both study sites did not have a full range of 360 degrees available for oceanic foraging trips. To statistically test whether gannets leaving the colony on the same day tend to travel in similar directions, I randomized the day assignments of

gannets 100,000 times as part of a permutation test. For each set of day assignments, a permuted group, I calculated the average angle between directions to build a null distribution. This permutation method uses the actual ranges of directions gannets travel at each colony and thus corrects for biases due to geographic constraint. For statistical comparisons data from the GPS units were analyzed using MATLAB 2009 and *PASW Statistics* version 18. Data were initially tested using Levene's test for homoscedasticity and Shapiro-Wilk's test for normality, and *t*-tests were used for subsequent parametric comparisons (Zar 1996). We report data as means \pm standard deviation. Statistical significance was defined as $p < 0.05$.

3.4 Results

A total of 32 individual foraging trips were recorded (21 from CK and 11 from FS, Figure 1 a, b). During foraging trips gannets spent on average 23.55% (± 7.46) of the time flying at CK and 29.02% (± 21.93) at FS, whereas they rested on the water an average of 75.55% (± 7.40) of the time at CK and 70.08% (± 21.93) at FS. Overall, plunge-diving only accounted for less than 1% of the time budget in both colonies. Of the trips from FS the maximum duration was 27.4 h, the maximum distance from the colony was 93.5 km and the maximum foraging path length was 629.1 km. In contrast, gannets from CK travelled longer distances away from the colony (222.6 km), with longer maximum foraging paths (818.5 km) over longer period of times (141.7 h, Table 1).

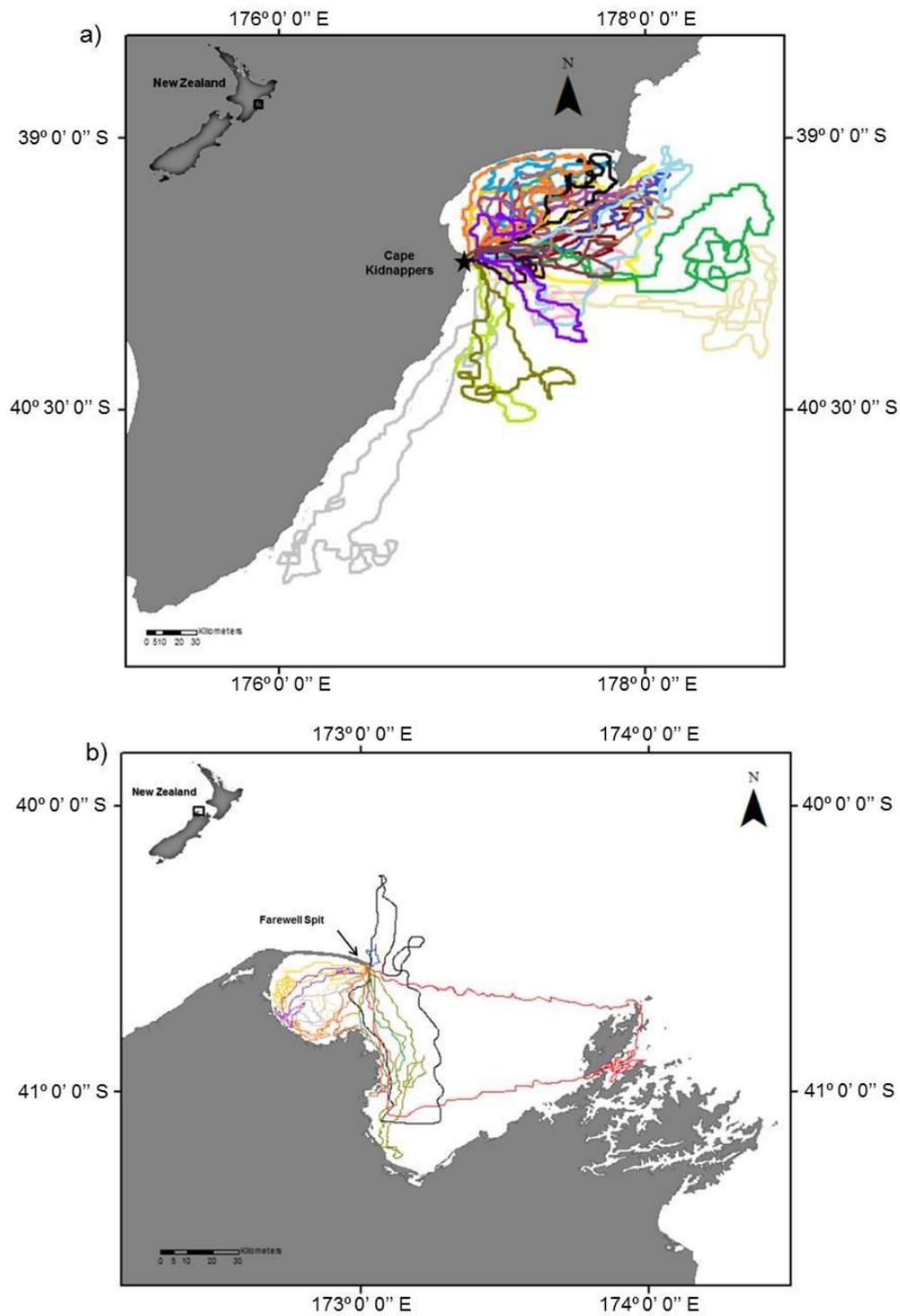


Figure 1. Foraging tracks of chick-rearing gannets fitted with continuous GPS data loggers at: a) Cape Kidnappers (n = 21) and b) Farewell Spit (n = 11) colonies in New Zealand. Individual trips are marked in different colours.

Table 1. Colony characteristics and foraging parameters of gannets breeding at Cape Kidnappers and Farewell Spit. GL= Geographic location; PS= Population size; MDC= Maximum distance away from the colony (km); FTD= Foraging trip duration (h); TFP= Total foraging path (km); FT= Flying time (h); RT= Resting time (h); S= Speed (km h⁻¹). Values are given as mean \pm standard deviation (SD). Bold: Statistically significant (*t*-tests, $p < 0.05$).

Parameter	Cape Kidnappers	Farewell Spit	Statistics	P
GL	East coast (North Island)	West coast (South Island)		
PS	7,300	3,900		
N	21	11		
MDC (km)	71.6 \pm 44.1	40.2 \pm 28.2	2.09	p =0.046
TFP (km)	316.1 \pm 176.5	184.6 \pm 188.9	1.87	p =0.072
FTD (h)	32.8 \pm 26.3	14.7 \pm 10.7	3.34	p =0.003
S (km h ⁻¹)	11.2 \pm 3.9	15.3 \pm 16.1	0.348	p =0.321
FT	6.3 \pm 3.2	4.4 \pm 4.1	-0.99	p =0.332
RT	26.5 \pm 26.3	10.5 \pm 7.7	0.99	p =0.334

The bearing angles of departing birds deployed on the same day at CK ($n = 6$ groups, 18 birds) and FS ($n = 4$ groups, 8 birds) were compared using GPS data loggers. The majority of FS gannets foraged southwest of the colony ($\chi^2 = 7.36$; $df = 2$; $p < 0.05$), while the CK gannets preferred northeast of their colony ($\chi^2 = 13.71$; $df = 2$; $p < 0.001$). A permutation test (see Methods) revealed that the average angle of bearing between gannets deployed on the same day was not significantly less than random pairs ($n = 10$, $p > 0.05$).

GPS data loggers were deployed in two consecutive breeding seasons at the CK colony. A comparison between years showed that the maximum duration of trips was higher in 2010 (141 h in 2010 vs. 48.1 h in 2011), the maximum distance from

the colony was less (94.2 km in 2010 and 222.6 km in 2011) and the maximum foraging path length was less (530.9 km in 2010 and 818.5 km in 2011). These differences, however, were not statistically significant (Table 2).

Table 2. Characteristics of foraging trips made by chick-rearing adult gannets at Cape Kidnappers in 2010 (n = 11) and 2011 (n = 10). MDC= Maximum distance away from the colony (km); FTD= Foraging trip duration (h); TFP= Total foraging path (km); FT=Flying time (h); RT=Resting time (h); S= Speed (km h⁻¹). Values are given as mean ± standard deviation (SD). Statistically significant, *t*-tests, *p* < 0.05.

Parameter	2010	2011	Statistics	P
	Mean ± SD	Mean ± SD		
MDC	55.07 ± 18.68	72.83 ± 59.44	-0.94	0.36
FTD	37.14 ± 35.06	27.83 ± 11.27	0.80	0.43
TFP	255.95 ± 119.92	336.07 ± 207.50	-1.10	0.29
FT	5.67 ± 2.48	6.74 ± 3.92	-0.75	0.46
RT	31.47 ± 35.39	21.09 ± 9.10	0.90	0.38
S	8.46 ± 3.44	11.99 ± 4.58	-2.00	0.06

Similarly, although longer trips were observed in males than in females from both colonies studied, there were no significant differences between sexes (Table 3).

Table 3. Foraging parameters of male (M) and female (F) Australasian gannets breeding at Farewell Spit (M=6 and F=5) and Cape Kidnappers (M=10 and F=11), New Zealand. MDC= Distance away from the colony (km); FTD= Foraging trip duration (hr.); TFP= Total foraging path (km); FT=Flying time (hr.); RT=Resting time; S= Speed (km h⁻¹). Values are given as mean \pm standard deviation (SD). Statistically significant, *t*-tests, $p < 0.05$.

Parameter	Colony	Mean \pm SD		Statistic	P
		Males	Females		
MDC	FS	36.4 \pm 36.6	44.8 \pm 16.2	-0.47	0.65
	CK	78.7 \pm 56.0	49.7 \pm 18.1	-1.60	0.13
FTD	FS	16.4 \pm 12.5	12.7 \pm 6.7	0.32	0.75
	CK	40.1 \pm 36.7	25.9 \pm 8.3	-1.25	0.23
TFP	FS	209.6 \pm 246.9	154.6 \pm 104.9	0.46	0.65
	CK	334.9 \pm 203.9	257.0 \pm 126.0	-1.07	0.30
FT	FS	5.1 \pm 5.5	3.2 \pm 2.4	0.75	0.47
	CK	6.8 \pm 3.9	5.6 \pm 2.4	-0.88	0.39
RT	FS	11.3 \pm 8.7	9.5 \pm 7.1	-0.77	0.46
	CK	33.3 \pm 37.1	20.3 \pm 7.7	-1.14	0.27
S	FS	10.4 \pm 7.4	10.3 \pm 4.4	1.12	0.30
	CK	10.2 \pm 4.3	10.1 \pm 4.5	-0.15	0.99

3.5 Discussion

Seabirds, including gannets, spend most of their life over the ocean foraging in diverse marine environments (Lack 1968). Foraging for patchily distributed foods, breeding gannets are constrained by the increasing energy demands of their offspring (Hamer et al. 2000) and by the risk of injury while diving (Machovsky-Capuska et al. 2011a, Chapter 7). Spatial and temporal fluctuations in prey concentrations create challenges for foraging (Chapters 4, 5, 6 and 7). The present

findings on foraging time budgets and the use of flexible foraging strategies in chick-rearing Australasian gannets are consistent with those reported for Northern and Cape gannets (Hamer et al. 2001; Ropert-Coudert et al. 2004; Garthe et al. 2007). I acknowledge the possible limitation that my data were restricted by the information collected by use of GPS data loggers, whereas previous results were obtained combining GPS data loggers, regurgitations and data in food availability.

The flexible foraging strategies observed in Australasian gannets are likely shaped by food availability and oceanographic conditions as well as intraspecific competition. First, the distribution of food sources due to oceanographic conditions has been suggested to influence individual foraging strategies in gannets (Hamer et al. 2001; Grémillet et al. 2004; Montevecchi et al. 2009). Gannets tagged with GPS data loggers from FS foraged in Golden and Tasman Bays and occasionally within the range of a high primary productive zone, namely Admiralty Bay, Marlborough Sounds (Heath 1985). Gannets from FS feed mainly on pilchard (*Sardinops* spp.) and anchovy (*Engraulis* spp.), (Machovsky-Capuska et al. 2011b, Chapter 5; Schuckard et al. 2012, Appendix 1). Pilchards are reported throughout the year in Golden Bay, Tasman Bay and in the Marlborough Sounds and are often visible as surface schools from October to April when diatoms bloom in nutrient-rich upwelling, coinciding with the gannet breeding season (Baker 1972; Paul et al. 2001). Unique local oceanographic conditions in this area enhance primary productivity and prey abundance may explain the lower foraging investment found in gannets from this colony as compared to their counterparts at CK. Thus, the expansions of the gannet population at FS by an average of 11.5% per annum (Schuckard et al. 2012, Appendix 1) as well as the abundance of large numbers of seabirds and marine mammals in this region reflect the great biomass of food available in the region

(Heath 1985; Markowitz et al. 2004; Vaughn et al. 2007; Merriman et al. 2009). Gannets from CK showed coastal foraging behaviour in areas influenced by East Cape current and the Wairarapa Eddie (Heath 1985). Pilchard, anchovy and saury (*Scomberesox saurus*) have been suggested to be the main prey of breeding gannets at CK (Roberson 1992). The difference between the duration and length of the foraging trips between 2010 and 2011 breeding seasons may be related to delays in the phytoplankton blooms that occur in the region, overlapping with the gannet breeding season and create fluctuations in food availability (Garner 1961; Bradford and Roberts 1978).

Second, colony size has been suggested to increase intraspecific competition on food sources by diffusing them farther away and subsequently augmenting the distance that gannets need to travel for food (Lewis et al. 2001). Northern gannets from larger colonies (ca. 50,000 breeding pairs, Bonaventure Island, Canada) have been reported to travel from the colony to a maximum distance of 225 km with trips that lasted up to 138.5 h, whereas conspecifics from smaller colonies (ca. 10,000 breeding pairs, Funk Island, Canada) have been reported to travel a maximum of 92 km with trips that lasted up to 25 h (Garthe et al. 2007). The present results reveal that gannets from the larger colony (CK) travelled on foraging trips approximately twice the distance travelled by gannets from the smaller colony (FS). This finding is consistent with the theory of Lewis et al. (2001) and Garthe et al. (2007) proposed for Northern gannets, but conflicts with reports for Cape gannets by Lewis et al. (2006). However, interpretation of my results is subject to the caveat that I was unable to collect data from both colonies in the same breeding season, and the sample size was small ($n = 2$) for this comparison. The reduced foraging investment observed at the FS colony could possibly help explain why this population has grown

five times faster than the New Zealand population (11.5% vs. 2.3% per annum, Schuckard et al. 2012, Appendix 1 and Nelson 2005, respectively). Finally, although sex has also been mentioned to influence gannet foraging behaviour (Lewis et al. 2001; Ismar et al. 2010) no differences were observed between males and females in the present study.

As long-lived species, gannets could learn the locations of suitable foraging sites through their lifetime and develop memory-based search strategies (Davoren et al. 2003). The results presented here indicate that gannets forage mainly in specific areas in relation to their respective colonies (SW from the FS colony and NE of CK colony) suggesting a similar site foraging fidelity pattern related to food availability and a combination of memory-based and local enhancement search strategies (Chapter 2) consistent with previous findings in Northern and Cape gannets (Hamer et al. 2001; Grémillet et al. 2004; Lewis et al. 2006). Further studies are needed to gain a better understanding of the relationship between prey availability and foraging strategies as well as the influence of commercial fisheries in gannet foraging areas around New Zealand. For this, a wider range of colonies within New Zealand should be included in the comparison, as in Lewis et al. (2001).

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CHAPTER 4

The temporal dynamics of collectivity: plunge-diving synchrony in conspecific and multi-species feeding assemblages in Australasian gannets

4.1 Abstract

Species that forage in groups often synchronise their behaviour. Synchronised foraging may provide benefits through information transfer about foraging resources, but can also increase competition if resources are limited. To better understand the mechanisms and functions of synchronised foraging strategies, I examined the patterns of synchronisation in plunge-diving Australasian gannets (*Morus serrator*) using aerial videography. From a total of 106 dive initiations, the probability that a gannet's plunge-dive was immediately followed by another conspecific was 60%. When heterospecific predators were present at feeding events, the diving bouts had a longer duration, involved a greater number of gannets plunge-diving in synchrony, and a shorter latency between followers than when gannets were foraging in the absence of other predators. When whales were present in the feeding events the altitude from which gannets commenced the aerial phase of plunge-dives was lower than in the absence of whales. These results offer evidence of plunge-diving synchronisation in gannets, highlight the impact of context (presence vs. absence of heterospecific predators) on the patterns of synchronised diving, and raise the possibility that mimetic behaviour is the mechanism underlying plunge-diving synchronisation.

4.2 Introduction

Information transfer between conspecifics that forage in groups, whether through deliberate signals or incidental cues, may increase the chances of finding food and maximise capture success (Bradbury and Vehrencamp 1998). However, collective foraging also has several costs (Couzin and Krause 2003), including the potentially fierce competition that may result once resources are found (Krause and Ruxton 2002). Studies of social groups of foragers, including honeybees (*Apis mellifera*) (von Frisch 1967; de Vries and Biesmeijer 1998), fishes (Reebs 2000; Couzin et al. 2005), waterfowl (Bailey and Batt 1974; Hutto 1988; Ramseyer et al. 2009), ungulates (Geist 1971; Fischhoff et al. 2007), penguins (Tremblay and Cherel 1999; Takahashi et al. 2004), pelicans (Saino et al. 1995), and primates (Collins 1984; Leca et al. 2003) have shown that groups display a structural order that can only be understood by considering a large number of interactions among group members (Couzin et al. 2002).

An important correlate of collective decision making is the demonstration of synchronised movement, and animal groups may use complex sensory, cognitive, and communication processes to achieve synchronisation (Krause and Ruxton 2002). These processes may involve vocal, chemical or visual signals (Petit et al. 2009), but can also be achieved without communication (Dostálková and Špinka 2007), for instance when animals use the same decision rules to respond to shared environmental cues (Zentall 2001). It has been suggested that synchronisation may be a product of particular types of behaviour (Engel and Lamprecht 1997) or social structures in which specific animals lead groups on the basis of their age, experience or dominance (King and Cowlshaw 2009). In contrast, there are also examples of synchronisation in which any group member can initiate a movement that is

immediately followed by others (Ekman and Askenmo 1984). Such collective decision-making and the resulting synchrony of movements based on initiator-follower interactions are well known in primates (Schaller 1963), particularly in white-faced capuchin monkeys (*Cebus capucinus*) (Leca et al. 2003; Petit et al. 2009). Four predominant factors appear to be involved in the capuchins' collective decision making processes: i) hierarchical interactions (Abbott et al. 2003); ii) patchily distributed food sources (Garber 1989); iii) highly sociable foragers (Milton 2000) and iv) synchronised movements (Boinski and Campbell 1995).

The socio-ecology of Australasian gannets (*Morus serrator*, hereafter: gannets) shares to some extent the four factors involved in the aggregations of white-faced capuchin monkeys. Gannets are long-lived, and display dominance hierarchies in relation to the location of their nests within the colony (Nelson 1978). Foraging is challenging, as the pelagic marine foods of these seabirds are widely and patchily distributed (Hamer et al. 2000; Machovsky-Capuska et al. 2011a, Chapter 7). Gannets are known to gather in high-density assemblages of conspecifics and heterospecifics (e.g. dolphins and whales) to plunge dive for fish and squid (Wodzicki and Robertson 1955; Machovsky-Capuska et al. 2011a, b, Chapter 7 and 5, respectively; Schuckard et al. 2012, Appendix 1). Birds locate prey from the air and then plunge at high speed into the water for pursuit and capture (Cunningham 1866; Machovsky-Capuska et al. 2012, Chapter 6). This behaviour is also challenging, exposing gannets to risk of injury or death due to accidental collisions (Machovsky-Capuska et al. 2011a, Chapter 7). Although diving events have been suggested to be collectively-organised (Wodzicki and Robertson 1955), there is little information on the dynamics of this behaviour in gannets and related seabirds.

The aim of the work reported in the present chapter is to examine the relationships between individual behaviour and group dynamics of Australasian gannets during feeding events. Specifically, I use videography to test for evidence of synchronised diving in Australasian gannets, and compare the group-level and individual patterns of plunge-diving in conspecific vs. heterospecific assemblages of feeding gannets. Although it is difficult in studies of free-ranging plunge divers to definitively disentangle the mechanisms involved in group-level patterns of behaviour, a quantitative analysis of the patterns of behaviour suggested possible mechanisms of dive synchronisation and collective decision-making used by wild gannets, and enabled me to compare these with processes reported in previous studies on the collective decisions in capuchin monkeys.

4.3 Material and Methods

Behavioural analysis was performed using aerial footage of gannet plunge diving in the Hauraki Gulf (36°51' S, 174° 46' E), North Island New Zealand. A total of 40 minutes of high-resolution video footage were collected from 10 different feeding bouts in October 2009 and December and January 2012 using a Canon XH A1S handycam with 20 mm zoom on board *Dolphin Explorer*, a 20 m dolphin tour catamaran at 5 m observer eye-height. Gannets were tracked at a consistent zoom magnification including the horizon to index the individual bird's position to define a horizontal plane (Land 1999). The duration of the aerial phase of a plunge-dive was measured from the instant that the bird initiated a 180 degrees body rotation in the air which was followed by a plunge-dive into the water (Figure 1). We considered two dives to be synchronised if they satisfied both a temporal and spatial criterion. The temporal criterion is that the second (follower) diving bird initiated its dive between the period that the first bird showed the plunge-diving intention (see below and

Figure 2) and hit the water. The spatial criterion is that the birds were within 10m of each other.

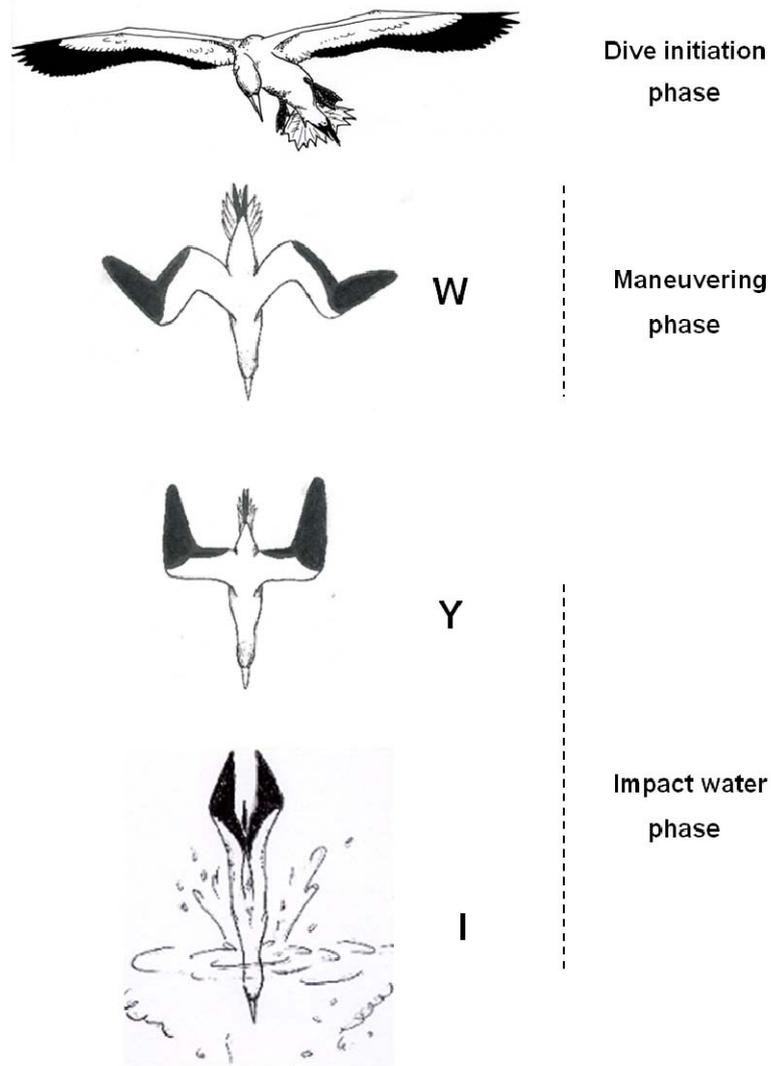


Figure 1. Different wing positions during the aerial phase of a plunge-dive in gannets. Modified from Nelson (1978); illustration by Sonja Clements and Laura van Zonneveld.

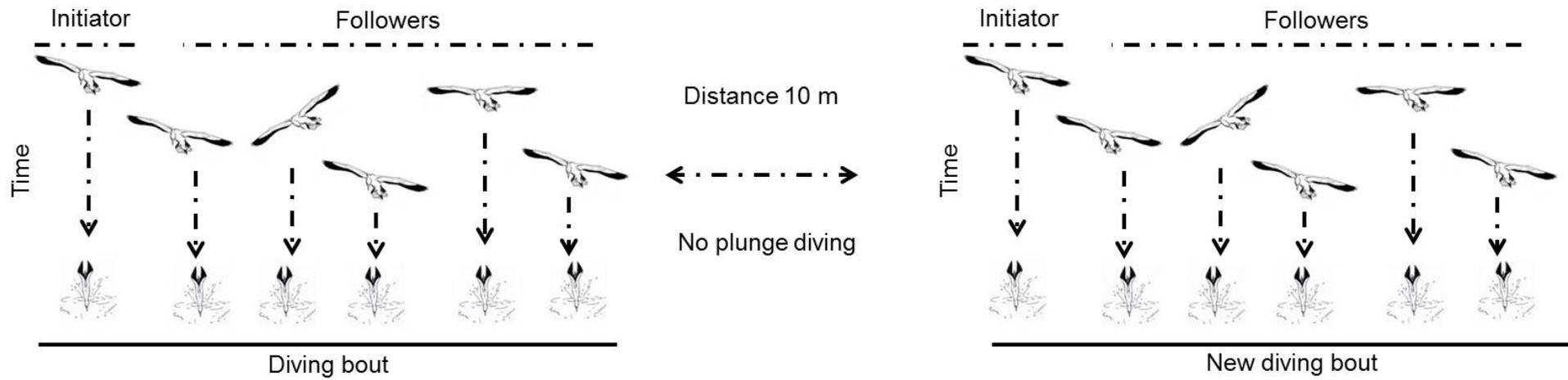


Figure 2. Synchronise plunge-diving in different diving bouts of gannets. Illustration by Laura van Zonneveld.

Following Petit et al. (2009) movements were categorised as either completed or aborted. Any dive that resulted in the gannet entering the water was classified a “completed plunge-dive”, whereas a manoeuvre that was cancelled before hitting the water was considered “aborted”. Within the flock of birds, the first gannet that rotated its body or decreased its height in respect to the water to initiate a free fall, was considered to exhibit an intention to plunge-dive and was considered an “initiator” (Figure 1). Due to difficulties of accurately estimating the altitude from which gannets initiated plunge-dives, dives were assigned to two different height categories: ≤ 4 m and ≥ 5 m. Plunge dive events were quantified in space and time. When the first bird that performed a completed plunge dive was followed after the initiation (e.g. within the synchronisation time) by other conspecifics within 10 m of the initiation’s plunge-dive, the action was classified as “followed initiation”. However, when no bird followed the initiator’s plunge-dive within the synchronisation time, the action was classified as “unfollowed initiation”. Frequencies of followed and unfollowed initiations were compared using χ^2 tests. A plunge-dive was considered a “new initiation” when it occurred outside the synchronisation time of the previous event or more than 10 m away. Following Petit et al. (2009), the latency period represents the time separating an initiator plunge-dive and the plunge-dive of a follower. A survival analysis was used to quantify the time-structure of decision-making in plunge-diving events in gannets, with the latency between followers used as a measure of dive synchronisation.

Gannets were observed to forage either with conspecifics only (n = 5 feeding bouts), or in the presence of other marine predators (n = 5 feeding bouts) such as common dolphins (*Delphinus* spp.) and Bryde’s whales (*Balaenoptera edeni*). I additionally tested whether the presence of these marine predators influenced the

duration of each bout of synchronised diving, and the number of gannets diving synchronously. For the latter, I distinguished between large and small diving groups as those that were larger and smaller than the median group size, respectively. By this criterion large groups consisted of 5 or more gannets, and small groups of fewer than five, and we tested whether the probability of large vs. small diving groups was influenced by the presence of heterospecific predators. Data were initially tested using Levene's test for homoscedasticity, and Shapiro-Wilk's test for normality (Zar 1996). Mann-Whitney and χ^2 tests were used for subsequent non-parametric comparisons (Zar 1996). In addition, I compared the survival function of the first follower latency in the presence/absence of other predators, using Peto and Peto modification of the Breslow's test (Peto and Peto 1972). Although Petit et al (2009) used log rank tests for this comparison here I used the standard Mantel-Haenszel procedure based on Breslow's test because the hazard functions obtained were not parallel.

Video footage was analysed frame by frame using Adobe Premiere Pro CS4. Distance of the different diving bouts was determined using Adobe Photoshop CS4 extended version 11.0.2. A mean length for adult Australasian gannets of 89 cm (Nelson 1978; Chapter 5) was used as a size reference. To determine the statistical significance of the frequencies of followed and unfollowed initiations, I randomly permuted the times of the dives 100,000 times while keeping the dive duration the same. For each random permutation, I recalculated the group size for each initiator and used these counts as statistical validation for the observed data. Tests were performed using *IBM SPSS Statistics* version 19 and *MATLAB* version 2011. Data are reported as medians and ranges. Statistical significance was defined as $p < 0.05$.

4.4 Results

From a total of 10 feeding bouts, median bout duration was 238 s (range 190 – 290 s) and involved a median of 46 dives (range 31 - 92). No significant differences were observed in the duration of feeding bouts in the presence or absence of marine predators (Mann-Whitney, $p = 0.07$) and in the number of dives involved (Mann-Whitney, $p = 1.00$).

A total of 106 initiations over 10 feeding bouts were recorded (median = 6, range 4 – 11 initiations). Over the total number of initiations, the overall probability of a gannet to be followed after an initiation was 60 % ($n = 64$). It was not possible to definitively quantify the proportion of gannets flying in the flock while others were plunge-diving. However, analysis of my data showed that followed initiations involved more than five conspecifics in 53 % of cases (median = 5, range 1 - 43 followers). The distribution of 100,000 permutations of these data revealed an expected random average of 166 out of the 540 dives to be with followers, whereas the observed number of followed initiations was significantly greater than this ($p < 0.0001$). Additionally, the permutation tests confirmed that the observed frequency of groups of five gannets or more was greater than would be expected if the flights were randomly distributed ($p < 0.0001$).

From a total of 540 plunges, 96% ($n = 518$) were completed with a median duration for the aerial phase of the plunge of 1360 ms (range 360 – 3640 ms), and 4% ($n = 22$) were aborted with a median duration of 1000 ms (range 680 – 1280 ms). All the observed aborted dives were terminated while the gannets were in the manoeuvring phase of the plunge (Figure 1). They occurred in no particular order with respect to the initiator and did not lead other followers to abort their dives.

A comparison of the frequency of followed and unfollowed initiations between gannets foraging exclusively in conspecific groups and in the presence of heterospecific marine predators showed no statistical differences ($\chi^2 = 0.213$; $df = 1$; $p > 0.05$). However, the duration of synchronised diving bouts was longer in the presence of heterospecific predators ($n = 21$, median = 6.88 s, range = 1.44 - 14.90 s) than when gannets foraged in conspecific groups ($n = 43$, median = 2.20 s, range = 1.04 - 11.20 s) (Mann-Whitney $U = 295.5$, $Z = -2.75$, $p < 0.05$) (Figure 3).

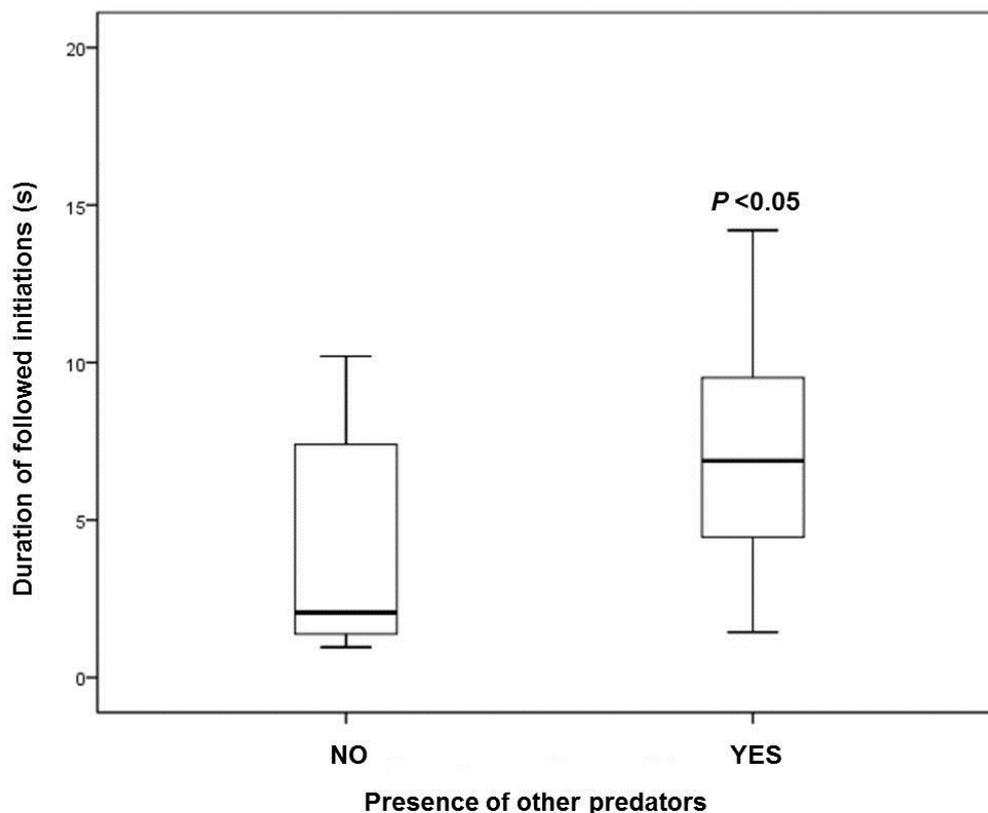


Figure 3. The duration of synchronised dive movements in gannets. Box plots show the median, 25% and 75% quartiles, and error bars represent the standard deviation.

There was a trend for the duration of unfollowed initiations to be longer in the presence of whales and dolphins, but this was not statistically significant (Mann-Whitney $U = 112.0$, $Z = -1.90$, $p = 0.07$). Diving gannets foraging in the absence of heterospecific predators showed a median latency between followers of 1440 ms

(range = 520 – 2080 ms), which was longer than in the presence of heterospecific predators 760 ms (range = 120 – 1680 ms) (Breslow = 10.08, $df = 1$, $p < 0.0001$) (Figure 4).

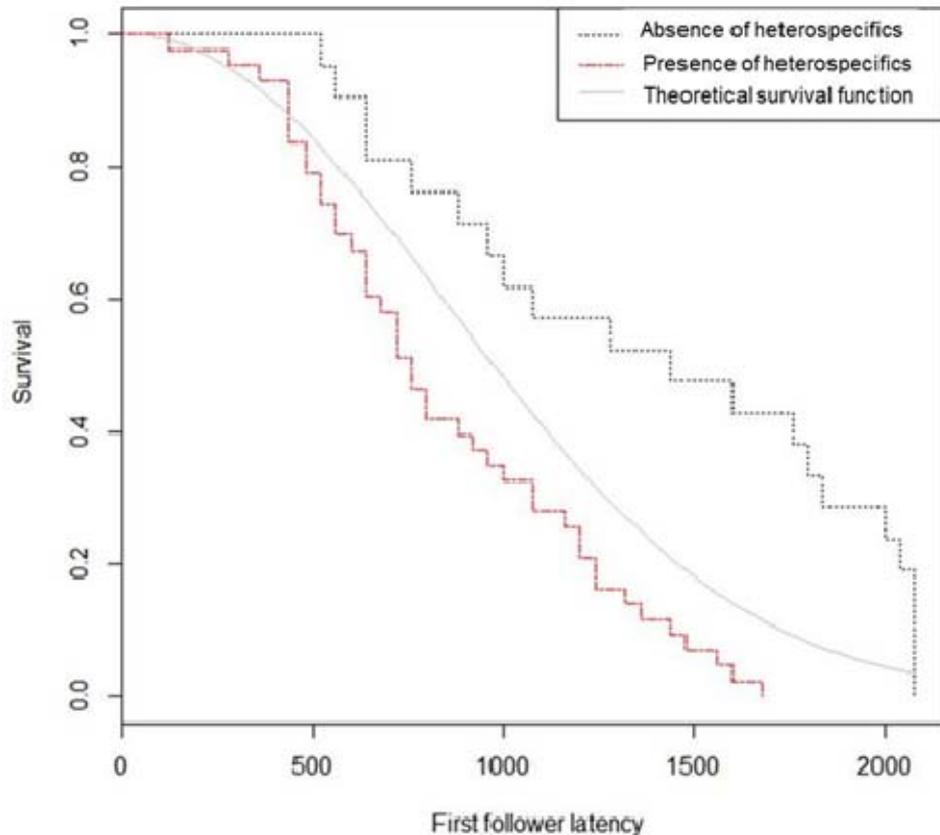


Figure 4. Survival curve of the first follower latency for gannets foraging in the absence (dotted line) and presence (red line) of heterospecific predators. The grey line shows the Theoretical survival function ($\lambda = 1165.50$ ms, $\gamma = 2.09$).

While no significant differences were observed in the frequencies of less than five gannets plunge-diving in synchrony in the presence/absence of heterospecific predators ($\chi^2 = 0.095$; $df = 1$; $p = 0.758$), the diving bouts in the presence of predators that involved more than 5 birds plunge-diving in synchrony was higher than when the gannets foraged in the absence of other predators ($\chi^2 = 18.182$; $df = 1$; $p < 0.0001$) (Figure 5). When whales were present in the feeding events, the

altitude from which gannets commenced the aerial phase of plunge-dives was lower (70%, ≤ 4 m, $n = 132$) than in absence of whales (98%, ≥ 5 m, $n = 82$, Mann-Whitney $U = 2250.00$, $Z = -8.320$, $p < 0.0001$).

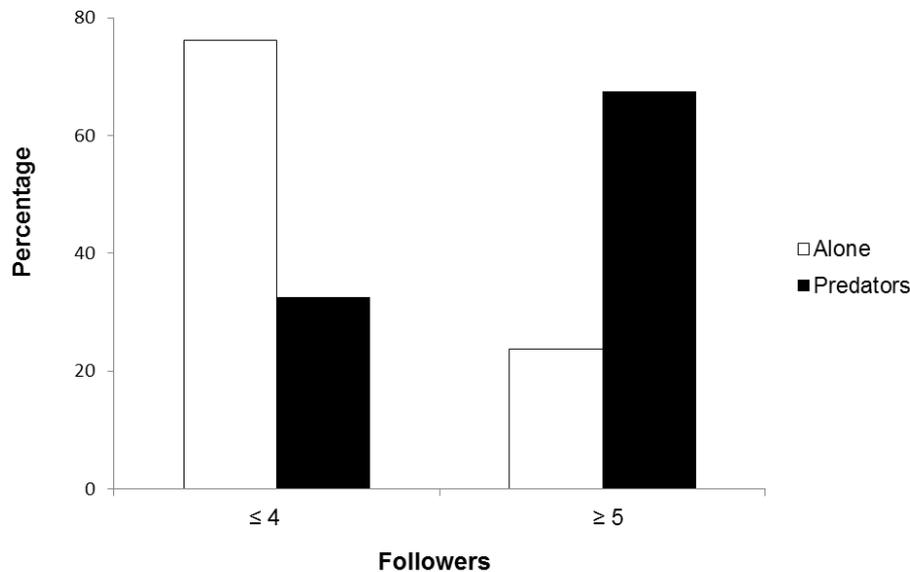


Figure 5. Percentage of plunge-diving followers in relation to the presence or absence of heterospecific predators.

4.5 Discussion

The present study has demonstrated synchrony in foraging by Australasian gannets, and compared key parameters of dive synchrony in the presence and absence of heterospecific marine predators. Synchronised foraging has previously been demonstrated in a wide range of species, and will likely be found in many others yet to be studied. The interesting questions, however, concern the mechanisms underlying synchronised foraging strategies in different species and circumstances, and the underlying functional drivers. Both mechanisms and functional correlates are difficult to measure directly in a field context, but measurements of the parameters using non-intrusive observations, as in the present study, can help to eliminate

hypotheses, formulate and test alternative hypothesis and provide data for broader comparative analyses.

For gannets two interrelated critical questions are what cues trigger plunge dives in a synchronous way, and what the functional implications of responding to these cues are? At a general level, synchronous diving could be due to local enhancement, where individuals respond to common cues, such as direct sightings of prey. Another possibility is that only a subset of birds respond directly to prey (most likely the initiators), and other birds follow without having observed the prey. Mimicking initiator birds in this way might be beneficial, because it enables birds to capitalise on the sensory information of others (Petit and Bon 2010). Specifically, because food of gannets is concentrated, the dive of the first bird will provide a reliable cue to the follower that diving will place it in a zone where it can use vision in underwater pursuit of prey (Machovsky-Capuska et al. 2012, Chapter 6). On functional grounds, it is therefore likely that gannets are triggered to dive by the sight of other diving birds.

Conversely, the fact that in the present study the latency to follow was shortened in the presence of other predators suggests that the mechanism of synchrony was local enhancement. This is because heterospecific predators such as whales and dolphins concentrate fish in the water column through herding (Vaughn et al. 2010; Machovsky-Capuska et al. 2011b, Chapter 5), thus increasing the probability that individual gannets will see target fish simultaneously triggering synchronous dives. Consistent with this is the observation that the sizes of bird groups were larger in the presence of predators (more groups consisted of > five individuals), suggesting a greater concentration of fish.

There is, however, no reason to assume that local enhancement and following diving conspecifics should be mutually exclusive. For example, local enhancement might be used in some circumstances (Chapter 2), and social cues in others. In this regard, an important question is whether initiators and followers are different categories of bird, or whether all individuals can be both initiators and followers. If the latter, this implies that both mechanisms apply to all individuals: when acting as initiators, they respond to direct sightings of prey, but in the role of followers they respond to social cues. Many vertebrate foraging groups, including primates, elephants, fish and birds, have the characteristic of being mixed in sex, age and experience and a minority of well-informed individuals, often elders, are seen to guide the entire group (King and Cowlishaw 2009). Foraging flocks of gannets are also comprised of mixed ages, sex, and levels of experience (Nelson 1978). Although an effect of age and experience on the fishing ability of plunge divers was observed in terns (Dunn 1972), boobies (Yoda et al. 2007) and pelicans (Carl 1987), little is known of the initiators' characteristics (e.g. sex, age, experience) in gannets' foraging flocks and whether their actions may be related to their nutritional state. This is challenging, but important information to collect.

A reason to expect that gannets would rely to a greater extent on social cues when foraging in the absence of large marine predators concerns the risks of plunge-diving in the presence of such predators. Machovsky-Capuska et al. (2011a, Chapter 7) showed that death due to accidental collisions presents a non-trivial risk to foraging gannets. The higher densities of gannets in multi-species feeding associations, combined with the possibility of colliding in the dive with a heterospecific predator, would increase the incentive to dive only when a clear path to a specific prey is visible, and not to blindly follow the dive of an initiator bird.

Consistent with this are the lower altitudes of plunge-dives that we observed in the presence of heterospecific predators possibly reflecting a slower descent speed that might minimise the risk of accidental injury. However, the greater altitudes observed in conspecific feeding assemblages may reflect the gannets' ability to predict their performance and establish the real location of the prey ball from the air using their multifocal lenses (Machovsky-Capuska et al. 2011b, 2012, Chapters 5 and 6) and may anticipate their 10 m diving depth threshold using the momentum phase of the dive, positioning themselves to immediately switch into pursuit using wing-flapping (Ropert-Coudert et al. 2009; Machovsky-Capuska et al. 2011b, Chapter 5).

Spatial and temporal fluctuations in prey concentrations make it difficult to discern with certainty, the real stimulus that motivates decision-making while plunge-diving. However, it is also possible that direct prey sightings and social cues interact in influencing the group dynamics of diving in gannets. For example, the sight of conspecifics diving might not elicit a gannet to dive, but lower the threshold for responding to direct indicators of prey (Van Gils et al. 2004; Piatt et al. 2007).

In demonstrating synchrony in the plunge diving of gannets, our study has raised several questions regarding the costs and benefits of synchronous foraging in these seabirds (Figure 6). It has also highlighted the influence of whales and dolphins on the plunge-diving synchronisation process. Although it was not possible to definitively establish whether these synchronised events are based on collective decisions, the use of mimetic rules similar to those observed in white-faced capuchin monkeys, remains a possibility as does local enhancement. Gaining a better understanding of the temporal dynamics and sensory-cognitive mechanisms governing cohesion during group movement is a central issue to understanding the evolution of social behaviour (Conradt and List 2009).

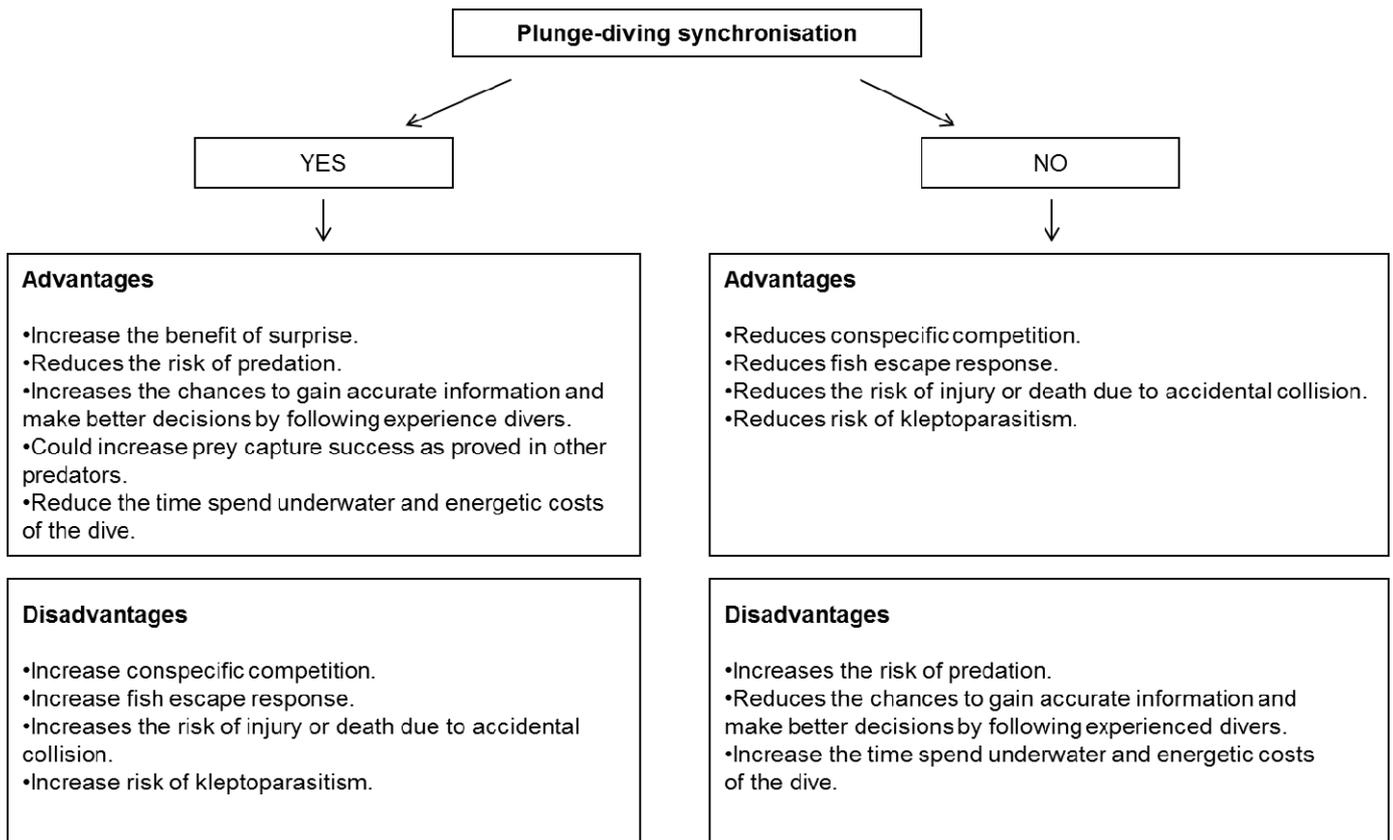


Figure 6. Schematic framework for understanding advantages and disadvantages of dive synchronisation in gannets.

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CHAPTER 5

Dive strategies and foraging effort in the Australasian gannet revealed by underwater videography

5.1 Abstract

Gannets (*Morus* spp.) are specialist plunge divers that perform short and shallow V-shaped dives and long and deep U-shaped dives in pursuit of pelagic fish and squid. We used underwater videography to examine the patterns of behaviour and relative success rates of V- and U-shaped dives in Australasian gannets (*M. serrator*). A significantly greater proportion of U-shaped dives were associated with successful prey capture than V-shaped dives (95% vs. 43%, respectively). The maximum number of prey captured per dive by the gannets was higher than previously reported, reaching up to five fish in a single U-shaped dive. However, V-shaped dives were more profitable in terms of grams of prey captured per time spent underwater in successful dives. In contrast, a population-level comparison of the mass of fish captured per total time spent underwater (i.e. including unsuccessful dives) suggested that the two dive profiles were equally profitable. Gannets also adjusted their dive shape in relation to the depth of their prey rather than prey type, as previously hypothesised.

5.2 Introduction

Plunge-diving has evolved as a highly specialised hunting technique among water bird families including gannets and boobies (Sulidae), tropicbirds (Phaethonidae), pelicans (Pelecanidae), gulls and terns (Laridae), and kingfishers (Cerylidae, Alcedinidae). To perform a plunge dive, an avian predator must first locate prey from the air and dive at high speeds into the water for pursuit and capture (Cunningham 1866, Machovsky-Capuska et al. 2012, Chapter 6). Gannets (*Morus* spp.) plunge dive for fish and squid (Nelson 1978), at times in feeding events called multi-species-feeding-associations (MSFA) that involve other birds (e.g. shearwaters, gulls, terns), predatory pelagic fish (e.g. tuna, sharks) and mammals (e.g. sea lions, whales, dolphins) (see also Chapters 4 and 7). Some marine mammals herd fish towards the surface, where the fish remain within diving depth for seabirds (Camphuysen and Webb 1999; Machovsky-Capuska et al. 2011b, present chapter). However, potential disadvantages to plunge divers of these high-density associations include competition (Clua and Grosvalet 2001), risk of predation (Heithaus and Frid 2003) and risk of accidental collision (Machovsky-Capuska et al. 2011a, Chapter 7).

Until recently it was generally believed that gannets hunt predominately by using 'steep relatively vertical plunge diving from a considerable height' (Nelson 1978; Garthe et al. 2000). However, by using motion data loggers it has been demonstrated that the Northern gannet (*M. bassanus*) and Cape gannet (*M. capensis*) use a variety of diving strategies including surface diving, plunge-diving, and pursuit plunging (Ropert-Coudert et al. 2004, 2009). Northern and Cape gannets display two dive types: (1) V-shaped dives, which

are shallow, of short duration, involve mostly the underwater momentum of the plunge, and may occasionally include a short phase of active propulsion by using wing flapping to pursue prey that had escaped the initial plunge, and (2) U-shaped dives, which are deeper and longer than the former dive type and always involve the bird shifting from the momentum phase to active propulsion by using wing flapping to pursue prey (Garthe et al. 2000; Ropert-Coudert et al. 2004, 2009).

In Northern gannets it has been suggested that the shape of the dive is related to type of prey, with V-shaped dives being used to capture larger pelagic fish such as mackerel (*Scomber scombrus*) and herring (*Clupea harengus*) with escape speeds of ca. 1.16 m s^{-1} , and extended U-shaped dives being used for smaller and slower pelagic fish such as capelin (*Mallotus villosus*), with escape speeds of ca. 1.03 m s^{-1} (Garthe et al. 2000). However, the use of remote telemetry data loggers did not allow direct observations of the association between prey type and hunting strategy (Garthe et al. 2000), and consequently the question of why gannets should employ V-shaped dives in some circumstances and U-shaped dives in others remained unresolved. In contrast, Elliott et al. (2008) suggested that the shape of a dive may instead be related to the pursuit of prey schools at a specific depth.

Australasian gannets (*M. serrator*) are the second rarest member of Sulidae (Nelson 2005), and they are closely related to the Northern and Cape gannets. They have been reported to dive up to 20.5 m and 23 m depth in New Zealand and Australian waters, respectively (Green et al. 2009; Ismar 2010), although they usually dive to about 2 m (Green et al. 2009). Green et al. (2009) reported that Australasian gannets remain submerged for a

maximum of 42 s, although they routinely dive for less than 6 s. These gannets feed mainly on pilchard (*Sardinops* spp.), anchovy (*Engraulis* spp.), saury (*Scomberesox* spp.), and jack mackerel (*Trachurus* spp.) (Robertson 1992; Bunce 2001). Plunge-diving in Northern gannets has been suggested to be a highly accurate foraging technique (Wanless et al. 2005), but no data on prey capture success are available for these species.

Herein the association between dive profiles and hunting strategy in the Australasian gannet, using underwater videography, is examined. This study enabled me to test success rate (prey captured per dive) and efficiency (grams of fish captured per unit time underwater) of V- and U-shaped dives, and discuss the influence of marine mammals on dive patterns. These analyses facilitated our understanding of the conditions under which Australasian gannets adopt V- and U-shaped profile dives.

5.3 Material and Methods

This study was carried out from 24 August to 31 October 2005 and 8 to 12 August 2006 in Admiralty Bay (40° 57' S, 173° 55' E) and Current Basin (40° 90' S, 173° 90' E), in the Marlborough Sounds, New Zealand. This region has been characterised by high primary productivity due to unique local oceanographic conditions (Heath 1985). These conditions underlie the presence of a large number of marine mammals and seabirds (Markowitz et al. 2004; Vaughn et al. 2008; Chapter 3; Schuckard et al. 2012, Appendix 1).

A total of 50 min of underwater video footage of Australasian gannet dive behaviour during 11 stationary dusky dolphin (*Lagenorhynchus obscurus*)

feeding bouts were recorded. Video recordings were made using a combination of surface-swimming and breath hold dives ranging in depths from 3 to 10 m (Vaughn et al. 2008), using a Sony DCR-HC 1000 video camera (focal length 3.6 mm, shutter speed 1/500 s, 30 frames s⁻¹) in an Amphibico Invader electronic underwater housing (Vaughn et al. 2007). Footage was analysed frame by frame using Adobe Premiere Pro CS4. Individual gannets were followed from the moment they penetrated the water to the moment they surfaced. The water surface and the water bubble trajectory were used as vertical and horizontal references. Dive depth was determined using Adobe Photoshop CS4 extended version 11.0.2. The mean length of an adult gannet was used as a size reference as it swam next to a prey ball and perpendicular to the video camera. Nelson (1978, Chapter 7) reported the mean of Australasian gannet body length as 89 cm, but did not give the error around this mean. Since the error is important for assessing the accuracy of our method, we measured the length of 20 Australasian gannet carcasses at autopsy, and obtained a mean \pm standard deviation of 88.9 ± 5.0 cm. Given the close concordance of our measurement and that of Nelson (1978), we used 89 cm as our reference value.

Dives were categorised as V- or U-shaped (Figure 1) in accordance with Garthe et al. (2000). For each dive, the duration of the underwater momentum phase, in which gannets descend through the water column without wing propulsion, was compared with prey pursuit, in which gannets are propelled through the water by actively moving their wings. Dives were coded as successful if a fish was observed in the gannet's beak. For both dive patterns, foraging efficiency (in g s⁻¹ underwater) was calculated, assuming a

single prey item weighing 32.5 g (Bunce 2001; Schuckard et al. 2012, Appendix 1). We also calculated overall efficiency, for each dive profile, both in successful and unsuccessful dives. The angle of penetration of the water surface water was measured only for dives in the plane perpendicular to the camera optical axis, using the water surface as the horizontal plane.

For statistical comparisons, data were tested using χ^2 , t -tests and 1-way analysis of variance (ANOVA), using PAWS Statistics version 18. We report data as means \pm standard deviation. Statistical significance was defined as $p < 0.05$.

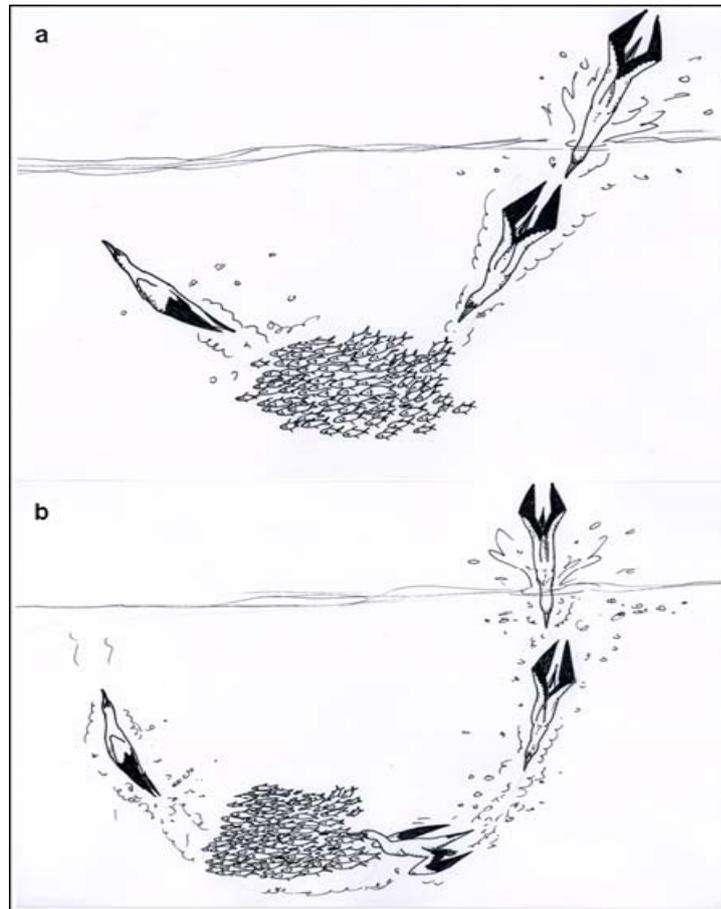


Figure 1. The air bubble trajectories produced underwater by a diving Australasian gannet characteristic of: (a) V-shaped dive and (b) U-shaped dive. Drawing not to scale. Illustration by Laura van Zonneveld.

5.4 Results

From a total of 85 dives, mean dive duration was 7.9 ± 5.4 s, and mean dive depth was 2.5 ± 2.0 m. More than 80% of dives ($n = 71$) were less than 4 m deep, and 80% of the dives ($n = 68$) lasted less than 13 s (Figure 2). U-shaped dives were longer (t -test, $t = 13.758$; $df = 45$; $p < 0.0001$) and deeper (t -test, $t = 17.722$; $df = 45$; $p < 0.0001$) than V-shaped dives (Figure 2). For V-shaped dives ($n = 39$), the mean duration was 3.4 ± 1.8 s (range = 1.1 ± 8.2 s) and mean depth was 2.9 ± 2.5 m (range = 1.1 ± 4.0 m), whereas for U-shaped dives ($n = 46$), the mean duration was 10.7 ± 5.3 s (range = 1.0 - 40.1 s), and mean depth was 4.0 ± 1.5 m (range = 1.0 - 9.1 m). While no significant differences were observed in the average duration of the underwater momentum phase of V- and U-shaped dives (t -test, $p = 0.07$), the wing flapping phase was longer in U-shape dives (t -test, $t = -9.742$; $df = 65$; $p < 0.001$) than in V-shaped dives.

We were unable to definitively identify the species of prey from the video footage, but the size and body shape was consistent with the small pelagic pilchard *Sardinops neopilchardus*. However, from a total of 11 feeding bouts studied, we identified 7 bouts (63%) in which the gannets continued to dive at fish schools as the schools changed depth within the water column. In these cases the gannets used V-shaped dives when fish were at shallow depth and U-shaped dives when the fish were deep. This observation reveals a link between depth of prey and dive profile, while controlling for prey type.

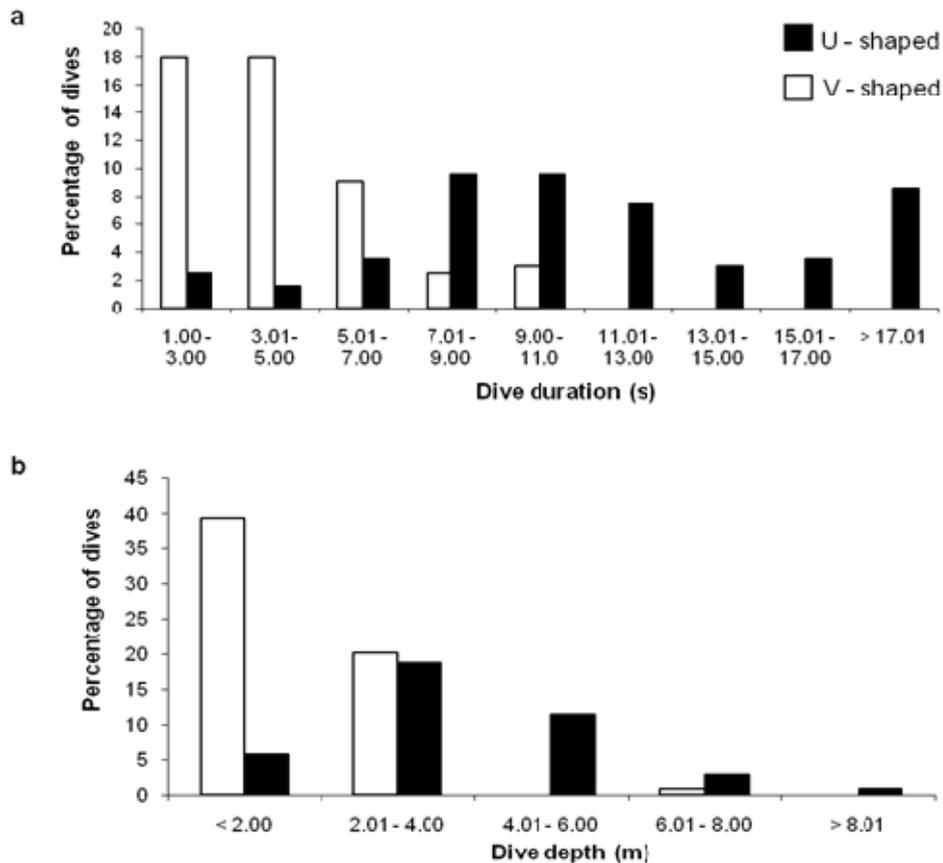


Figure 2. The frequency of U-shaped ($n = 46$) and V-shaped dives ($n = 39$) of Australasian gannets relative to (a) dive duration (seconds) and (b) depth (meters).

Prey capture success in U-shaped dives (95%) was higher than in V-shaped dives (43%) (χ^2 , $F = 28.232$; $df = 1$; $p < 0.0001$). Of the successful U- and V-shaped dives, respectively 7% and 5% included more than one fish captured, with maxima of five and two fish captured in a single dive.

A comparison of the efficiency of the two dive profiles revealed that the V-shaped profile was significantly more profitable than the U-shaped profile (ANOVA, $F = 16.628$; $df = 1$; $p < 0.0001$) (Figure 3). However, the overall efficiency was similar for the two dive profiles. Since it was not possible to

track an individual bird across successful and unsuccessful dives, we could only perform this calculation on a population-basis (i.e. for each dive profile, we calculated g of fish captured in all dives divided by time spent underwater during all dives). Thus, I was unable to calculate the error around this estimate.

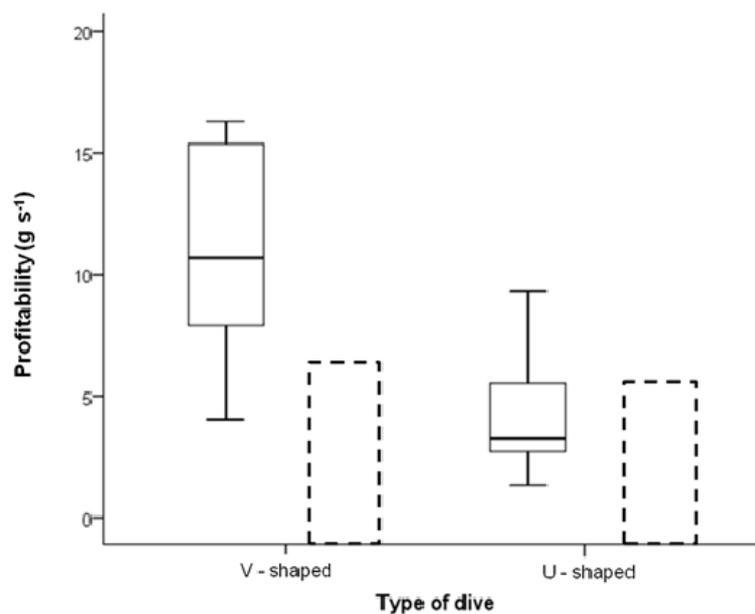


Figure 3. Foraging efficiency in V- and U-shaped dives in Australasian gannets. The box plots show efficiency calculated as g s^{-1} of fish captured underwater during successful dives (with the median, 25% and 75% quartiles, error bars representing standard deviation). Bars surrounded by dashed lines show the g s^{-1} of fish captured underwater in successful and unsuccessful dives.

I was interested in determining whether dive differences developed during the aerial phase before the bird had hit the water, or during the course of the aquatic phase of the dive. The analysis ($n = 25$) showed that during U-shaped dives, gannets entered the water at a significantly steeper angle than in V-shaped dives (T-test, $t = -3.837$; $df = 23$; $p < 0.001$, Figure 4), suggesting

that the dive profile is at least partially determined in Australasian gannets before entering the water.

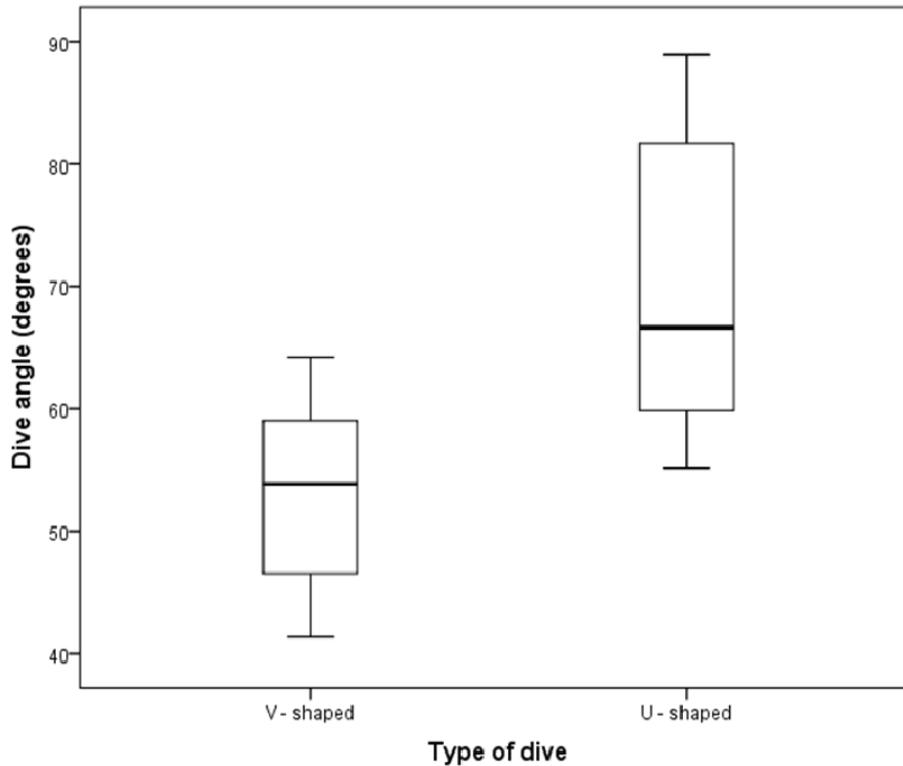


Figure 4. Dive angles in Australasian gannets relative to the horizon during V-shaped and U-shaped dives (n=25). Box plots (with the median, 25% and 75% quartiles, error bars representing standard deviation).

5.5 Discussion

Analyses presented herein provide the first report of prey capture success, as well as detailed evidence of dive strategies and foraging effort in Australasian gannets (see also Green et al. 2009). Data on gannet diving strategies have previously been obtained by a variety of techniques including devices attached to the birds, such as capillary tubes (Adams and Walter 1993), data loggers (Garthe et al. 2000; Hamer et al. 2000), and from autonomous underwater vehicles (Brierley and Fernandes 2001). While motion data

loggers provide a sampling frequency sufficient enough to represent an alternative to direct observations (Ropert-Coudert et al. 2004), an efficient way to determine prey consumption rates in seabirds is to fit them with stomach temperature loggers (Wilson et al. 1995). However, the deployment of several devices on the body of a flying seabird is likely to interfere with natural behaviour (Phillips et al. 2003). Although underwater videography does not allow multiple comparisons of diving strategies of single individuals, it provides a valuable high-resolution tool to explore at-sea behaviour in marine predators (Davis et al. 1999; Takahashi et al. 2004; Grémillet et al. 2010), including examination of patterns of diving in Australasian gannets highlighted in the present study.

5.5.1 Dive shape, foraging effort and prey capture success

Findings that V-shaped dives were shallower and shorter in duration than U-shaped dives are consistent with Garthe et al. (2000). Maximum diving depths and durations recorded in the present study (9.13 m and 40.07 s) were less than those reported by Green et al. (2009; 23 m and 42 s) and Ismar (2010; 20.5 m) for *M. serrator*. Dive depths recorded herein were also shallower than those found for *M. capensis* (12.5 m; Adams and Walter 1993) and *M. bassanus* (24 m; Ropert-Coudert et al. 2009). Results presented herein also revealed that the momentum phase of the two dive profiles was on average similar, and may be related to the biomechanics of gannets' body entering the water column (Ropert-Coudert et al. 2009; Machovsky-Capuska et al. 2012, Chapter 6). However, U-shaped dives were associated with long periods of active wing flapping pursuit and are thus likely energetically more expensive

than V-shaped dives (Ropert-Coudert et al. 2009). We acknowledge the possible limitation that our data were restricted by underwater visibility, whereas previous results were obtained using data loggers.

It has been suggested that dive profiles in seabirds and pinnipeds may be used as an indicator of the type of prey being pursued, but observational evidence for this is limited (Elliott et al. 2008). In the present study, the resolution of the video footage did not allow a definitive identification of the prey species in many instances, although the size and body shape were consistent with the small pelagic pilchard. However, results indicate that Australasian gannets alter their depth of foraging to track the depth of a specific school of fish, showing that in these circumstances dive profile is associated with foraging depth, as suggested by Elliott et al. (2008).

The relative efficiency of the two dive profiles revealed a greater percentage of successful prey captures and a greater maximum number of fish captured during single U-shaped dives than has been reported for any gannet species. Conversely, V-shaped dives were more profitable in terms of grams of prey captured per second underwater during successful dives. However, the index of overall efficiency per unit time underwater, including both successful and unsuccessful dives, was similar for the two dive profiles (Figure 3). These results are, however, subject to the caveat that it was not possible to follow individual birds on both successful and unsuccessful dives and consequently our estimates of overall efficiency are calculated from population values and do not have associated error estimates.

Furthermore, there are other aspects relevant to efficiency that remain to be quantified. First, in our comparisons we were unable to take into account

the time spent in the aerial phase of the dive. Second, diving at shallow depths for a short period of time may reduce the risk of gannets being captured by other predators (Crawford and Cooper 1996; Heithaus and Frid 2003) or the risk of injury or death due to accidental collisions (Machovsky Capuska et al. 2011a, Chapter 7).

5.5.2 Possible influence on dive profile by other marine predators

Analyses presented of Australasian gannet dive types in relation to depth suggests that V- and U-shaped dives could be indirectly related to the foraging behaviours of conspecifics and of other marine predators. Diving often takes place in multi-species feeding associations (MSFA) that involve a high density of marine predators with different foraging tactics (Clua and Grosvalet 2001), and the species composition of these MSFAs might influence whether gannets use V- or U-shaped dives. Thus, gannets might be more likely to use V-shaped dives when feeding with dolphins, which herd the prey to shallower depths. Further, dolphin herding behaviour at times appears to cause prey balls to become stationary, and it is likely easier for gannets to capture fish from stationary than from mobile prey balls (Vaughn et al. 2008). Gannets might be more likely to use V-shaped dives when feeding on stationary balls due to an improved ability to detect and focus on the fish during a prey capture attempt. In contrast, when gannets aggregate in large numbers during a feeding bout, fish sometimes attempt to escape predation by descending to greater depths (Vaughn et al. 2010). In these circumstances, gannets were observed in our study to shift from V- to U-shaped dives and continue their pursuit.

5.5.3 Can gannets predict their dive performance?

It has been suggested that air-breathing marine animals physiologically prepare for dives of a specific depth before the dive by loading oxygen prior to submergence (Thompson and Fedak 2001). Penguins also apparently assess the likelihood of prey capture by preparing for dives before entering the water (Wilson 2003). Experiments on gentoo penguins (*Pygoscelis papua*) indicated that U-shaped dives represent foraging in suitable habitats, whereas V-shaped dives represent the penguins assessing prey density (Wilson et al. 1996). I was therefore interested in whether the dive profile of Australasian gannets is similarly determined prior to submergence, or whether it evolves in response to events during the aquatic phase.

To address this question, I tested for possible differences developed during the course of the aerial phase of the dive and the results suggest that the two dive categories were different even before the birds entered the water. These results may indicate that gannets predict the depth of their prey. However, although gannets are visual predators (Lee and Reddish 1981) that are able to see in the violet-sensitive range of the spectrum (Machovsky Capuska et al. 2011b, Appendix 2), it is still unclear how their visual mechanisms cope with light reflection and refraction while detecting prey between the air and water interface. To date, studies on aerial and underwater visual acuity in pursuit diving birds involve several penguin species (Sivak and Millodot 1977; Howland and Sivak 1984; Sivak et al. 1987) and also great cormorants (*Phalacrocorax carbo*) (Katzir and Howland 2003; Strod et al. 2008). Although gannets and cormorants are phylogenetically related, their foraging strategies are rather different (Nelson 1978). Cormorants detect and

pursue prey only after having submerged their head and eyes (Katzir and Howland 2003), whereas gannets detect their submerged prey from the air, plunge dive and then may switch to active pursuit in the water column (Machovsky-Capuska et al. 2012, Chapter 6).

This study has provided several new insights to the diving strategies of a plunge-diving predator, the Australasian gannet (Figure 5).

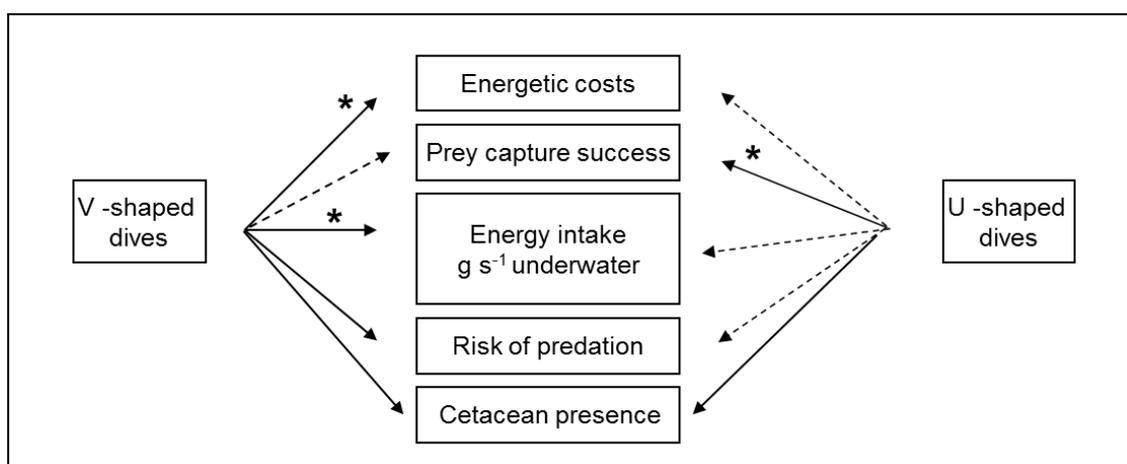


Figure 5. A model of the use of V- and U-shaped dives in Australasian gannets in relation with different ecological variables. Statistically significant results are denoted with asterisks. Potential advantages and disadvantages are denoted by solid lines and dashed lines, respectively.

The challenge ahead is to integrate these with additional information and provide a model for gaining a broader understanding of the functional considerations underlying this interesting foraging strategy (Figure 5). In particular, further studies are needed to understand the role of vision in the decisions made by gannets foraging in complex marine environments, energetic and nutritional considerations, and the relationships between the foraging strategies of gannets and other marine predators. Such questions

demand an inter-disciplinary approach that employs a variety of methodologies.

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CHAPTER 6

Visual accommodation and active pursuit of prey underwater in a plunge-diving bird: the Australasian gannet

6.1 Abstract

Australasian gannets (*Morus serrator*), like many other seabird species, locate pelagic prey from the air and perform rapid plunge dives for their capture. Prey are captured underwater either in the momentum phase (M) of the dive while descending through the water column, or in the wing flapping (WF) phase while moving, using the wings for propulsion. Detection of prey from the air is clearly visually guided, but it remains unknown whether plunge diving birds also use vision in the underwater phase of the dive. Here the question of whether gannets are capable of visually accommodating the transition from aerial to aquatic vision is addressed. Furthermore an analysis of underwater video footage is undertaken to assess if gannets use vision in the aquatic phases of hunting. Photokeratometry and infrared video photorefractometry revealed that, immediately upon submergence of the head, gannet eyes accommodate and overcome the loss of > 45 D (dioptres) of corneal refractive power which occurs in the transition between air and water. Analyses of underwater video showed the highest prey capture rates during WF phase when gannets actively pursue individual fish, a behaviour that very likely involves visual guidance, following the transition after the plunge dive's M phase. This appears to be the first demonstration of the capacity for visual accommodation underwater in a plunge diving bird while capturing submerged prey detected from the air.

6.2 Introduction

Many vertebrates regularly alternate their activities between air and water (Thewissen and Nemula 2008). The need to function in both media, at the sensory and motor levels, imposes major constraints, evolutionary pressures and physiological trade-offs on the individual's morphology, physiology and sensory systems (Kröger and Katzir 2008). In the face of these opportunities and constraints, many species, among them piscivorous birds, successfully perform fine-tuned sensory and motor tasks in both media.

Piscivorous birds may be grouped into two categories based on their foraging patterns. One group comprises birds that search for aquatic prey from the air, and capture it using rapid motions such as bill-strikes [e.g., herons (*Ardeidae*)], or plunge-dives [e.g. kingfishers (*Cerylidae*), terns (*Sternidae*), fish eagles (*Accipitridae*) and osprey (*Pandionidae*)]. The second group both detects and captures fish underwater, after submergence of their eyes [e.g., penguins (*Spheniscidae*), auks and guillemots (*Alcidae*) and cormorants and darters (*Phalacrocoridae* and *Anhingidae*, respectively)] (Cramp and Simmons 1977). Common to both groups, however, are certain aspects of their visual ecology, including prolonged exposure to reflected sunlight and skylight rich in short wavelengths and continuous changes of intensity (glitter/shimmer) due to water surface motion (Lythgoe 1979; Loew and McFarland 1990). The eyes of birds in both groups must therefore be shaped by similar and different environmental pressures.

Birds that plunge-dive or strike at fish, perform visual detection and location of submerged prey from the air under complex optical conditions including variation in the reflection and refraction of light (Labinger et al. 1991; Katzir and Camhi 1993; Katzir and Martin 1994; Katzir et al. 1999). Visual constraints in birds that pursue

their prey underwater extend to the dioptrics of the eye as well as to differences in photic environments. The avian eye has primarily evolved to perform in air, and the quality of the image formed on the retina is determined predominately by the cornea and to a lesser extent by the lens (Walls 1967). The cornea in air is bordered on its inner surface by the aqueous humor, with a refractive index of 1.33, and on its outer surface by air, with a refractive index of 1.0 (Katzir and Howland 2003). Under these conditions, the cornea is the principal refracting agent of light rays and is responsible for approximately two-thirds of the refractive power of the eye. Underwater, the media bathing the inner and outer surfaces of the cornea (the aqueous humor and water, respectively) are of similar refractive indices, and the refractive power of the cornea is thus lost, leaving the lens as the sole agent for visual accommodative adjustments (Sivak 1980).

For the image to remain sharp on the bird's retina upon submergence, the lens must be capable of providing the refractive power lost by the cornea (Martin 1998; Sivak and Millodot 1977; Howland et al. 1997; Howland and Sivak 1984; Glasser and Howland 1996; Land 1990). Since the refractive power of the cornea and the lens are a function of the curvature of its surfaces, lenses of fish (Land 1990), amphibians (Mathis et al. 1988), penguins (Sivak et al. 1987), cetaceans (Mass and Supin 2009) and seals (Sivak et al. 1989) have evolved to be spherical and, thus, provide maximal refractive power.

It has been found that mergansers (Anatidae), cormorants (Phalacrocoracidae) and other underwater pursuit-diver birds also have strongly curved corneas and experiments indicate a pronounced capacity for lenticular accommodation (Hess 1909, 1913, cited in Glasser and Howland 1996; Sivak et al. 1977; Levy and Sivak 1980), although there is still no agreement on the muscular

mechanisms involved. The refractive power of the cornea of great cormorants, *Phalacrocorax carbo sinensis*, in air is ca. 50 D and when they voluntarily submerge their eyes they maintain emmetropia (in less than 20 - 40 ms), e.g. they fully compensate for the loss of this amount of corneal refractive power (Katzir and Howland 2003).

Gannets (*Morus* spp., Sulidae) capture pelagic prey (fish and squid) by plunge diving into the sea from heights often exceeding 5 m (M'Clymont 1903; Oliver 1955; Wodzicki and Robertson 1955). Once submerged, they either adopt a V-shaped dive profile, in which the bird surfaces immediately after a downward momentum phase of the plunge that occasionally includes a short phase of wing flapping, or a U-shaped profile in which the momentum phase is followed by a longer phase of active propulsion using wing beats (Garthe et al. 2000; Machovsky-Capuska et al. 2011a). This provides for flexible underwater hunting tactics (Garthe et al. 2000), where gannets are able to use the speed of momentum or switch their feeding style to active pursuit using wing flapping (McGillivray 1853; Garthe et al. 2000; Ropert-Coudert et al. 2004, 2009).

The detection of prey from the air (McGillivray 1842; Cunningham 1866; Lee and Reddish 1981; Eriksson 1985) is regarded as visually guided. However, evidence that vision is the sensory modality used during active pursuit of prey underwater has been provided only for the detection and pursuit of prey in great cormorants, a species that does not plunge dive (Strod et al. 2004, 2008; White et al. 2007; Martin et al. 2008). At the optical, visual and photic levels the search and detection, plummeting and underwater momentum phases of the dives of gannets are similar to patterns observed in other plunge divers or strikers, such as kingfishers (Alcedinidae) or herons, whereas wing flapping is similar to that observed in pursuit

divers, such as cormorants (Figure 1). Gannets thus, face two major visual obstacles, related to the air/water interface and to amphibious accommodation, distinguishing gannets' foraging tactics from other seabirds.

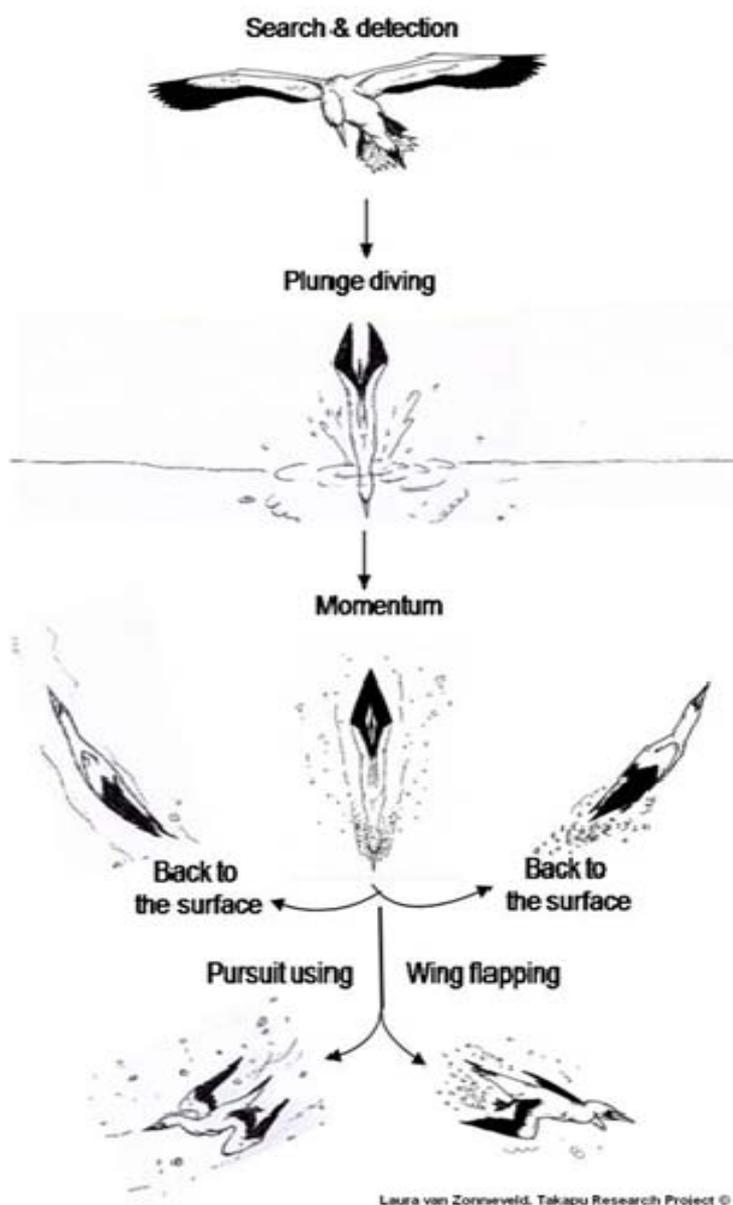


Figure 1. Dive patterns of Australasian gannets: Prey capture in the Momentum (M) and in the Wing Flapping (WF) phases. Illustration by Laura van Zonneveld.

Herein I examine the potential role of underwater vision in Australasian gannets while plunge diving, using infrared photorefractometry, photokeratometry and underwater videography. The aims were to: i) establish if Australasian gannets are capable of visual accommodation underwater, and if so, measure the amount of corneal refractive power that is overcome and ii) search for behavioural evidence that gannets use aquatic vision in hunting by analysing underwater video footage of foraging gannets.

6.3 Materials and Methods

6.3.1 Analysis of underwater video footage

A total of 55 minutes of underwater video footage (at 30 frames per second) of Australasian gannet foraging associated with stationary prey balls that were formed by the presence of dusky dolphins (*Lagenorhynchus obscurus*) was analysed frame by frame using Adobe Premiere Pro CS4. The footage was collected between 24th August and 31st October 2005, 8th - 12th August 2006 and 17th September 2009 in Admiralty Bay and Current Basin in the Marlborough Sounds, New Zealand. For the analysis, a dive was considered to be the period from the time that the gannet penetrated the water to its return to the surface. In the 95 dives analysed, prey capture was observed both in the underwater momentum phase of the dive (M), in which the gannets descend through the water column without wing propulsion, and in the wing flapping phase (WF), in which gannets are propelled through the water by active wings movement (Figure 1). To evaluate the role of each phase in hunting, I quantified the number of successful prey captures and the rate of prey capture (prey captured per time in the dive) during the M and WF phases. Data were statistically

tested using χ^2 and t-test (*PASW Statistics* version 18). Diving data reported as mean \pm standard deviation. Statistical significance was defined as $p < 0.05$.

6.3.2 Visual accommodation in air and underwater

The states of underwater accommodation were determined based on photokeratometry and on Infra-Red (IR) photorefractometry. *Photokeratometry* is a photographic method of determining the curvature of the cornea and hence its refractive power. The photokeratometer used was essentially that described previously (Howland and Sayles 1985; Howland et al. 1997). It consisted of a Canon EOS-10D SLR camera with a Canon EF 35 mm 1:2 lens operated at full aperture for minimum depth of field. A light ring (Zeiss), was mounted on the camera's objective lens with ca. 20 apertures, each < 0.5 mm in diameter, forming a circle of a radius of 35 mm around the lens optic axis. The camera flash (Wocron-250PC-Auto) was projected via an optic fibre to the light ring. For calibration, we used a set of 5 steel ball bearings, 8, 10, 15, 20 and 25 mm in diameter. Each ball was measured to the nearest 0.1 mm using Vernier calipers and was photographed with the photokeratometer mounted on a tripod. The focus of the camera lens was set at infinity and in taking the photographs, the camera-to-ball distance was adjusted for the sharpest image. For each ball, the distances between opposite reflections of the keratometric reflection circle were determined from three readings, approximately along the 0° , 45° , 90° and 135° meridians. The mean of the measurements was calculated, and I regressed the ball bearing diameters against the mean reflection distances measured on the film plane. The resultant regression equation was used to estimate the corneal radii (e.g., half of the diameters of the calibration ball bearings) of gannets' eyes in the field.

The dioptric power of a cornea (F , in dioptres, D) was determined by the equation: $F = 337.5/R$, where R is the corneal radius (measured in mm). This equation expresses the power of the human cornea as a function of the radius of its first surface (Borish 1955). The diameters of the light rings reflected off the examined corneas were measured from photographs (un-edited) of eyes taken in the field. All photographs with a sharp image of the reflected ring of light were used in the analyses. The diameter of each reflected ring was measured and the respective corneal diameter calculated from the regression equation above.

Eye photography was performed at the Cape Kidnappers colony (39° 38' S, 177° 05' E) during 2011, under permission of the New Zealand Dept. of Conservation (ECHB-23237-RES) and of the Massey University Ethics committee (09/76). A bird to be measured was captured at the periphery of the colony, using a shepherd's hook, and then restrained by hand (as in Chapters 2 and 3). Using the photokeratometer, the second experimenter took ca. five photographs of one eye, followed by ca. five photographs of the contra-lateral eye (Figure 2). In taking the photographs, the camera-to-bird distance was adjusted for the sharpest image. Pronounced eye movements and rapid flicking of the nictitating membrane resulted in a proportion of the digital images being unsuitable for analysis. For each eye of each bird, the two photographs that provided the sharpest and best-centered images of the photokeratometric light reflections were used for extracting the values of the distances between opposite reflections along the four meridians.

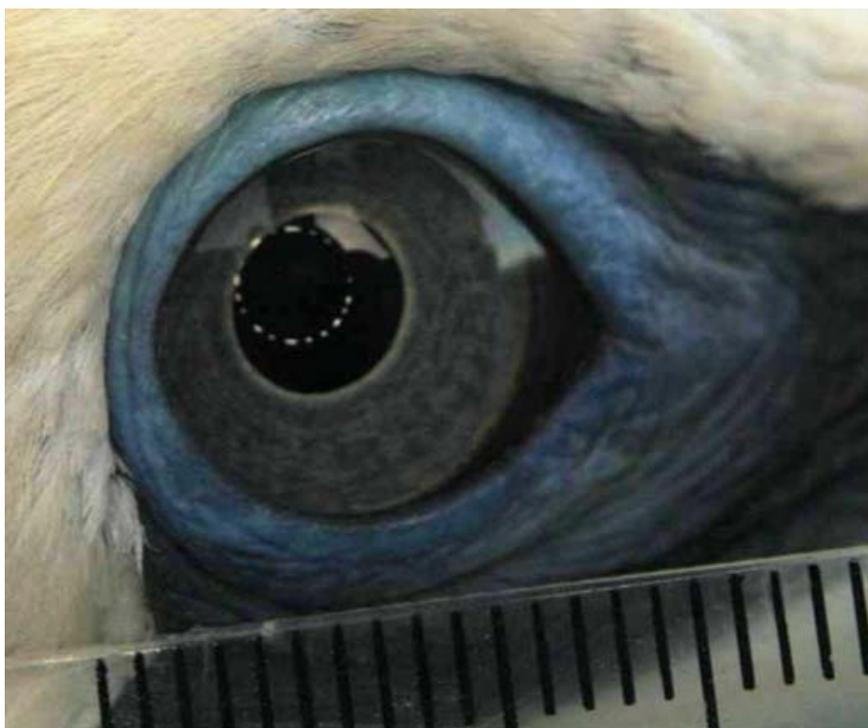


Figure 2. The eyes of a gannet, photographed with a photokeratoscope and showing the light ring reflected off the cornea. Scale – 1 mm. Photo by Gadi Katzir.

Photorefraction was performed using an infra-red (IR) video retinoscope to measure their natural accommodation. The underlying principles of the system are provided in detail in Schaeffel et al. (1987). In brief, the IR retinoscope is based on a light source adjacent, and eccentric, to a video-camera lens' axis that projects light rays parallel to the camera's axis and records the reflection from the *fundus*. The use of IR minimises disturbance to the animals. The light reflected off the *fundus* appears as a crescent in the pupil, and the position of the reflex indicates the sign of the defocus relative to the camera. In hyperopia, the reflex appears at the top of the pupil, while in myopia the reflex appears at the bottom of the pupil. The amount of defocus (D) is obtained from the size of the reflex: $D = E/(2ADFR)$, where E is the eccentricity of the light source, A is the distance of the camera to the eye, DF is the dark fraction in the pupil and R is the pupil radius (all units in meters or diopters, i.e.

reciprocal meters). To improve the precision of the measurements, the light sources (LEDs) are set in five rows, providing five different eccentricities (2, 6, 10, 14 and 18 mm). LED illumination was either in a temporal sequence, providing consecutively five different crescents, or set to a given eccentricity only. During the field tests both methods were used. Due to a certain ambiguity of the precise eccentricity of the light at specific instances, the calculations of defocus here were for the eccentricity of 10mm.

The IR retinoscope comprised a CCD camera (Watec LCL902K; 30Hz), with a Nikon lens (55mm / 1:1.2) fitted with a supplementary lens. The video camera was connected to a Toshiba laptop and the images captured using Movie-Maker™. Due to the mobility of the birds' head and eyes, no attempt was made to verify the amount of defocus by the use of correction lenses.

Tests were conducted over two consecutive days in March 2011. The IR retinoscope, on a tripod, was positioned ca. 1.0 - 1.2 m from the front wall of an experimental Perspex aquarium, with the camera's optical axis perpendicular to the wall. The aquarium (80 x 40 x 50 cm; length x width x height) was kept three-quarters full of water. The setup was placed ca. 20 m from the edge of the gannet colony and measurements were performed under natural low light levels (ca. 0.01 Lux), to minimise stress to the birds and to achieve maximal pupil opening and thus enhance the IR effect.

Test birds were captured and transferred by hand to the setup. The gannet's head was aligned so that its bill pointed ca. 45° downwards. Then, in a single smooth motion, the gannet's head was submerged in the water for 2 - 5 s, to a depth of water ca. 10 cm above the eye and ca. 5 - 10 cm from the aquarium's wall. The second investigator, positioned so as to view the aquarium's long axis and level with

the water surface, filmed the bird from when it was ca. 50 cm above the water level to the end of its submergence. I moved the bird towards the aquarium and submerged its head in the plane parallel to the aquarium wall. For all birds, only the left eye was filmed and filming was conducted when the bird was $\approx 1.0 - 1.2$ m from the camera lens providing an optical distance, i.e., (distance in air + distance in water/1.33) of ca. 1.0 m. Selected video sequences were captured using Adobe Premier 6.0 to determine states of accommodation. Once tested, the bird was immediately released at the colony edge nearest its capture site.

6.3.3 Evaluation of the individual video frames in optical analysis

Images of individual frames from the video recordings were transferred to Photoshop for measurement using pixel counting. Pixel dimensions and pupil size in underwater frames were calibrated by measuring the width of the base of the bill from the frames taken in air, where a ruler was included in the picture for scale, as well as the corresponding bill width in underwater pictures. The underwater pupil sizes were then scaled accordingly. Measurements were made to the nearest pixel (representing approx. 0.11 mm in air and 0.29 mm in water). The darkened portion of the pupil was also measured, the dark fraction of the pupil was calculated, and the data entered into the equation already mentioned ($F = 337.5/R$), using the relevant values of eccentricity. Because, in photorefractive, myopic illuminated crescents appear in the pupil on the same side as the light source, while hyperopic crescents appear on the opposite side, it was easy to distinguish hyperopic and myopic reflexes.

6.4 Results

6.4.1 Diving behaviour

Ninety five dives were analysed from the behavioural video footage. Results showed that the duration of the momentum (M) phase ($n = 95$, 0.85 ± 0.035 s) was significantly shorter than the wing flapping (WF) phase ($n = 81$, 5.94 ± 0.44 s) ($t = 11.398$; $df = 80$; $p < 0.0001$; two-tailed paired t-test). Additionally, significantly more successful prey captures were observed in the WF ($n = 47$) than the M phase ($n = 25$; $\chi^2 = 24.785$; $df = 1$; $p < 0.001$; two-tailed test), and the proportion of successful dives was significantly higher in the WF (91.1%) than the M phase (45.5%) ($\chi^2 = -6.936$; $df = 1$; $p < 0.001$; two-tailed test). Further, more capture attempts were observed in WF ($n = 67$) than the M phase ($n = 58$; $\chi^2 = 8.24$; $df = 1$; $p < 0.01$; two-tailed test). Of the successful dives, in 5% of the events a gannet captured fish during the momentum phase, and immediately thereafter switched to wing flapping pursuit and captured another fish.

6.4.2 Corneal power

The eyes of 14 gannets (10 adults of unknown sex and 4 juveniles) were photographed using a photokeratometer. For all birds, at least one sharp image was obtained for each eye. The diameter of the light circle, reflected off the cornea, was 3.34 ± 0.17 mm (mean \pm standard error) in adult gannets and 2.99 ± 0.26 mm in the juveniles. These yielded calculated mean globe diameters of 15.39 mm in the adults and 13.89 mm in the juveniles and a calculated mean corneal refractive power 43.93 ± 2.15 D (dioptries) for adults and 48.93 ± 4.21 D for juveniles.

6.4.3 Pupil size

The size of the gannets' pupils in air, immediately prior to submergence and underwater was measured. Under the low light levels (starlight), the pupils were wide open (Figures 3, 4). Overall, pupil diameter underwater (vertical 8.98 ± 0.81 mm, horizontal 6.51 ± 0.72 mm; mean \pm standard error, $n = 5$) was similar to that in air (vertical: 9.48 ± 0.69 , horizontal: 6.75 ± 0.72 ; $n = 5$). Furthermore, no apparent differences were observed in pupil diameter between states of hyperopia, emmetropia and myopia (Figure 4). In comparison, in air, under direct sunlight, pupil diameter was 4.44 ± 0.38 mm ($n = 5$).

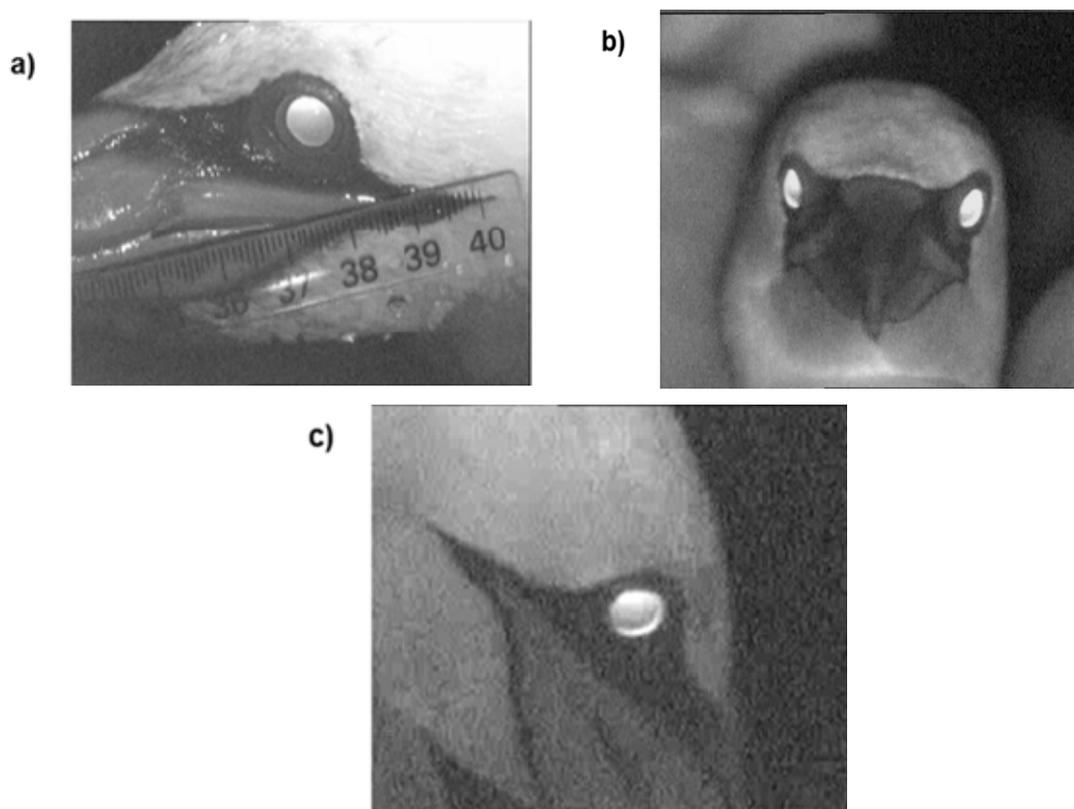


Figure 3. Infra-Red (IR) light reflected from the eyes' *fundus* showing (a) a fully open pupil eye in air, in darkness, of a hand restrained gannet, with the higher intensity crescent at the dorsal part of the pupil, indicating a refractive state of hyperopia (Scale – 1 cm), (b) an unrestricted gannet in the colony, in air, showing a binocular viewing of the camera, (c) A concentric ring at the periphery of the pupil, that may be indicative of lens multi-focality. Photos by Gadi Katzir.

6.4.4 Underwater accommodation

In most filmed sequences, the eyes in air and underwater were in a refractive state of hyperopia (Figure 4) while images of underwater states of myopia were rare. For five gannets, sharp images were obtained for the determination of pupil size, and two birds were analysed for underwater accommodation. Underwater myopic defocus values (mean, dioptres \pm standard deviation) calculated for an eccentricity of 10 mm, were respectively 9.04 ± 3 D for bird1 and 9.72 ± 3 D for bird 2.

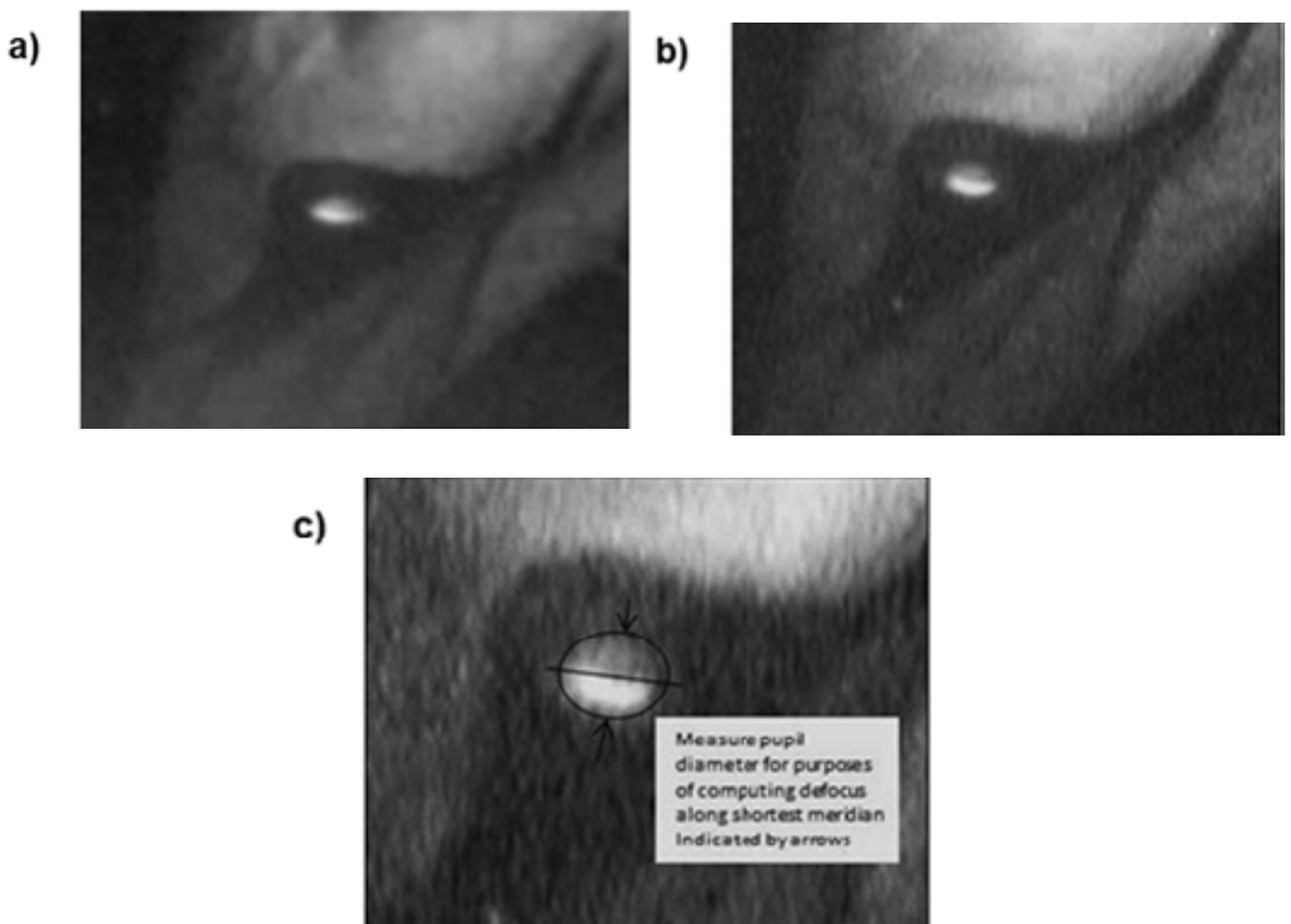


Figure 4. (a, b) The light pattern reflected off the *fundus*, through the pupil of a gannet's eye underwater. The light crescent of higher intensity at the lower part of the pupil indicates a state of myopia, (c) The procedure employed for determining the Dark Fraction of the pupil. Photos by Gadi Katzir.

The results clearly show that, underwater, the gannets are capable of reaching a state of myopia. In so doing they overcome the loss of corneal refractive power and the focusing demand. The transition from aerial to underwater accommodation is rapid: not infrequently the eye was in a state of hyperopia while the bill was touching the water surface and in a state of myopia at the instant of the subsequent clear underwater image (ca. 2 - 3 frames, 80 - 120 ms later) with the entrance of the eye into the water blurred by water sprayed.

6.5 Discussion

Kröger (2008, p. 115) noted that “It has been a particular challenge to natural evolution to find eye designs that are equally useful in both air and water”. In plunge divers such as gannets, it is highly likely that plunges are guided using visual detection of prey from the air (McGillivray 1842; Cunningham 1866; Lee and Reddish 1981; Eriksson 1985). The current study of their underwater hunting behaviour suggests that gannets use vision also in the aquatic phase of the hunt, and the optical analysis has demonstrated some of the mechanisms that have evolved to enable these birds to meet the challenge of rapidly transitioning from aerial to aquatic vision.

As has been shown previously (Garthe et al. 2000; Ropert-Coudert et al. 2004, 2009; Machovsky-Capuska et al. 2011a), the video footage used in this study clearly distinguished a Momentum phase (M) and Wing Flapping phase (WF) in gannet dives. It has been suggested that capturing prey during the M phase provides gannets the benefit of surprise (Johnston 1989). However, the current results showed that Australasian gannets are more successful in prey capture in the active pursuit (WF) phase than in the M phase of the dives.

What might account for the greater capture success in the WF phase, where the advantage of surprise does not apply? Current analysis suggests that aquatic vision plays a role. In the M phase, the acceleration of flow around a gannet's body associated with the high entrance velocity in the plunge results in pressure dropping locally below the vapour pressure, causing bubbles (cavitation; Batchelor 1990) markedly affect underwater image quality (Cummings and Johnsen 2007). Also, body manoeuvrability may be constrained by its high entry speed and cavitation (Losilevskii and Weihs 2008). In contrast, the slower movement in the WF phase enables the use of vision unobstructed by cavitation. That gannets in fact do capitalise on the greater opportunity to use vision in the WF phase is suggested by the rapid directional adjustments the birds make to compensate for evasive movements of prey during the pursuit. The large number of fish, and the extensive mixing of water associated with multi-species feeding events, makes it highly unlikely that olfaction could provide a sufficiently directional cue for such pursuits. The high turbulence would, likewise, greatly limit the use of mechanosensory cues in the pursuit of individual fish. Further, mechanosensory cues could not have been used in the case of underwater kleptoparasitism where gannets specifically targeted fish that had already been immobilised in the beaks of other conspecifics (Machovsky-Capuska et al. 2011b). Overall, this analysis suggests that the WF phase is the main stage in the foraging strategy of gannets.

However, if the image is to remain sharp on the retina (i.e. be emmetropic) upon the gannet's submergence, to allow capturing the fish with the bill, the optics of the eyes should undergo pronounced changes so as to accommodate underwater. Cormorants are capable of large magnitude, rapid accommodation upon head submergence, overcoming loss of corneal power greater than 50 D in ca. 40 ms

(Katzir & Howland 2003). This is achieved, most probably, through a rapid change in the shape of the lens. Underwater visual acuity of great cormorants, determined behaviourally (ca. 9 arcmin) is lower than in air (ca. 3 arcmin) and yet remains similar to that of their potential prey fish (Strod et al. 2004, 2008; White et al. 2007). Results presented herein suggest that Australasian gannets are, similarly, capable of compensating for the loss of refraction at the cornea in water by lenticular accommodation. Gannets' eyes are larger than cormorants', providing a lower corneal curvature and hence a lower refractive power (ca. 44 D in gannets compared with ca. 50 - 60 D in cormorants). Corneal refractive power of juvenile gannets was higher than that of adults as their eye sizes have probably not reached their full size and the lower radius of curvature provided for a higher refractive power (Katzir & Howland 2003).

Earlier studies have suggested that the capacity for underwater accommodation in pursuit diving birds such as mergansers and cormorants is brought about by the joint performance of the enlarged iris muscles acting on the highly pliable lens (reviewed in Glasser and Howland 1996). However, observations on the hand-held gannets in the present study, and of voluntary dives of great cormorants (Katzir and Howland 2003) do not support a pupil constriction upon submergence and accommodation. In structure and function, the iris acts as two separate muscles – a peripheral one that constricts the lens and a central one that controls the aperture. Pupil size plays an important role in image formation by governing retinal illumination and depth of field (Martin 1994). The wide open pupil aperture underwater, in both gannets and great cormorants, must result in a trade-off between lower resolution and higher image illumination, which is especially important in considering the sharp decline in ambient illumination with dive depth. Underwater accommodation in the

gannets was attained within 2 - 3 frames (80 - 120 ms) of submergence, also similar to the velocities observed in cormorants. It may thus be concluded that at the instant of entering the water from heights often exceeding 5 m (M'Clymont 1903; Wodzicki and Robertson 1955), the gannets' optics shifts from aerial to aquatic vision, allowing them to better detect their prey.

This study has provided the first demonstration of the capacity for visual accommodation underwater in a plunge diving bird, suggesting that Australasian gannets are capable of coping with the optical demands of rapidly transitioning from aerial to aquatic vision. Further research is required to determine how gannets meet the visual challenges associated with the aerial phase of the hunt. In particular, how do they detect fish against a background that undergoes sharp spatio-temporal changes in the intensity of reflected light (glare)? And how do they compensate for refraction induced image displacement, and also cope with the apparent motion of the prey induced by refraction on a moving surface? Answers to such questions will further highlight the reasons why the eye has long been upheld as an exemplar in amphibious predators' optimization through evolution (Goldsmith 1990).

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CHAPTER 7

Evidence for fatal collisions and kleptoparasitism while plunge-diving in Gannets

7.1 Abstract

Plunge-diving is a highly successful strategy for dealing with the challenges confronted by birds feeding on pelagic prey. I examined for evidence of fatal injuries due to collision between conspecifics in plunge-diving Australasian and Cape gannets (*Morus serrator* and *M. capensis* respectively), by performing post-mortem examinations of carcasses recovered from New Zealand waters and analyzing video footage of gannet foraging events from South Africa. The presented analysis provides further evidence of accidental collisions between gannets and also revealed a case of attempted underwater kleptoparasitism, in which a diving bird targeted a previously captured fish in the beak of a conspecific.

7.2 Introduction

Pelagic prey are able to evade predation by descending to depths beyond the reach of diving birds. Among the adaptations that have evolved for dealing with these challenges is plunge-diving. This is a highly specialised foraging technique, which often takes place in high density assemblages of conspecific and heterospecific predators, in which the bird locates prey from the air and then plunges at high speed into the water for pursuit and capture (Cunningham 1866; Machovsky-Capuska et al. 2011, 2012, Chapter 5 and 6, respectively). Plunge-diving provides the advantage of surprise (Johnston 1989), so helping to avoid the problem of prey descending beyond reach, and is considered one of the most accurate foraging methods (Wanless et al. 2005; Machovsky-Capuska et al. 2011, Chapter 5). However, some authors have also noted likely disadvantages associated with plunge-diving. Feeding in high density assemblages can involve fierce competition (Camphuysen and Webb 1999), and contact with the water at high dive speeds can be hazardous (Zillmer 2003), particularly for younger, less experienced birds (Tator et al. 1981).

An additional hazard associated with this foraging mode is that diving at high speeds into dense assemblages of conspecific and heterospecific predators, sometimes in poor visibility, presents the risk of collision and associated injury or death. There is, furthermore, a two fold risk of collision, because a given bird is at risk of both colliding and being collided with. Surprisingly, however, there exists no record of which we are aware of injuries or death arising in this way in plummeting seabirds. Unintentional collision in the water column has been reported from high density feeding assemblages

of waterfowl (Bailey and Batt 1974), but as far as is known there is no record of this leading to injury or death.

Herein is a study in which evidence of injuries due to collision in plunge-diving seabirds, the Australasian and Cape gannets was provided. These birds feed in large groups (Nelson 1978; Chapter 4; Machovsky-Capuska et al. 2011, Chapter 5), usually in multi-species-feeding-associations (MSFA) involving common dolphins (*Delphinus* spp.) and Bryde's whales (*Balaenoptera edeni*, Burgess 2006; Chapter 4), and are therefore at risk from this cause of injury. Owing to the difficulties involved in detecting collisions by direct observation, an indirect approach was taken by analyzing video footage of gannet foraging events from South African waters and performing post-mortem examinations of carcasses recovered from New Zealand waters.

7.3 Material and Methods

7.3.1 Gannet carcasses

During 2009 and 2010, 50 Australasian gannet carcasses were opportunistically collected from the waters of the Hauraki Gulf, New Zealand. Two of them were found floating dead in the water, on 2 May and 17 May 2010 (36°35.41' S, 175°01.37' E and 36°34.03' S, 175°20.40' E, respectively). Each carcass was inspected for signs of injury due to collision while plunge-diving, including physical injuries to the beak, head, or neck. Photographs were taken of any such injuries, and the birds subjected to post-mortem examination following avian necropsy protocols (Work 2000). Stomach

contents were analysed and fish were removed from the oral cavity, oesophagus and stomach for species identification. Otoliths were isolated and diagnostic features subsequently used to enable identification to the lowest possible taxonomic level using published guides (Smale et al. 1995) and the reference collection held at Massey University, Albany. Digestion codes described in Meynier et al. (2008) were assigned to retrieved fish.

7.3.2 Video footage analysis

Only aerial footage of Australasian gannets plunge-diving in the Hauraki Gulf was included in this behavioural analysis. A total of 40 minutes of high resolution video footage was collected in October 2009 using a Canon XH A1S handycam with 20 mm zoom on board *Dolphin Explorer*, a 20 m dolphin tour catamaran at 5 m observer eye-height. Additionally, 10 minutes of aerial and 15 minutes of underwater video footage (25 frames per second) of Cape gannet foraging, collected on the 4 June 2008, 24 and 30 June 2009 and 8 July 2009 and loaned from Earth-touch© (<http://www.earth-touch.com>), was analyzed frame by frame using Adobe Premiere Pro CS4. The following categories of accidental collisions were recorded: 1) Gannets colliding with gannets (G-G), 2) Gannets colliding with sharks, whales and/or humans (G-SWH). Further to this, the G-G category was classified into two sub-categories: a) collision while powered by underwater momentum alone (e.g. no wing flapping), b) collision during underwater wing flapping. Thus, numbers of gannets diving were recorded to estimate the frequency of accidental collisions.

7.4 Results

7.4.1 Gannet carcasses

Two of the 50 gannet carcasses examined had injuries consistent with death due to accidental collision. Both carcasses (G2M and G17M) were recovered while floating dead in the water. The birds were considered to be fresh due to the presence of eye moisture and absence of *rigor mortis* (Stockin et al. 2007). The necropsy of G2M revealed a circular wound 3-4 mm in diameter penetrating approximately 3.5 mm into the left dorsal side of the cranium (Figure 1a). This injury extended through the cranium into the meninges of the right cerebral cortex and cerebellum, producing peripheral hemorrhaging and a severely reddened left frontal lobe (Figure 1b). The peripheral diameter of the wound closely fitted the circumference of the bill at 3.5 mm caudal to the tip of an adult Australasian gannet (Figure 1c), suggesting penetration by a gannet bill to be a likely cause of the injury. A large jack mackerel (*Trachurus novaezelandiae*) measuring 25 cm occupied almost the entire esophagus from immediately below the pharynx caudally, while a second smaller (15 cm) fish of the same species was present in the proventriculus. The prey were intact with no flesh digested, suggesting that the fish were eaten shortly prior to the gannet's death.

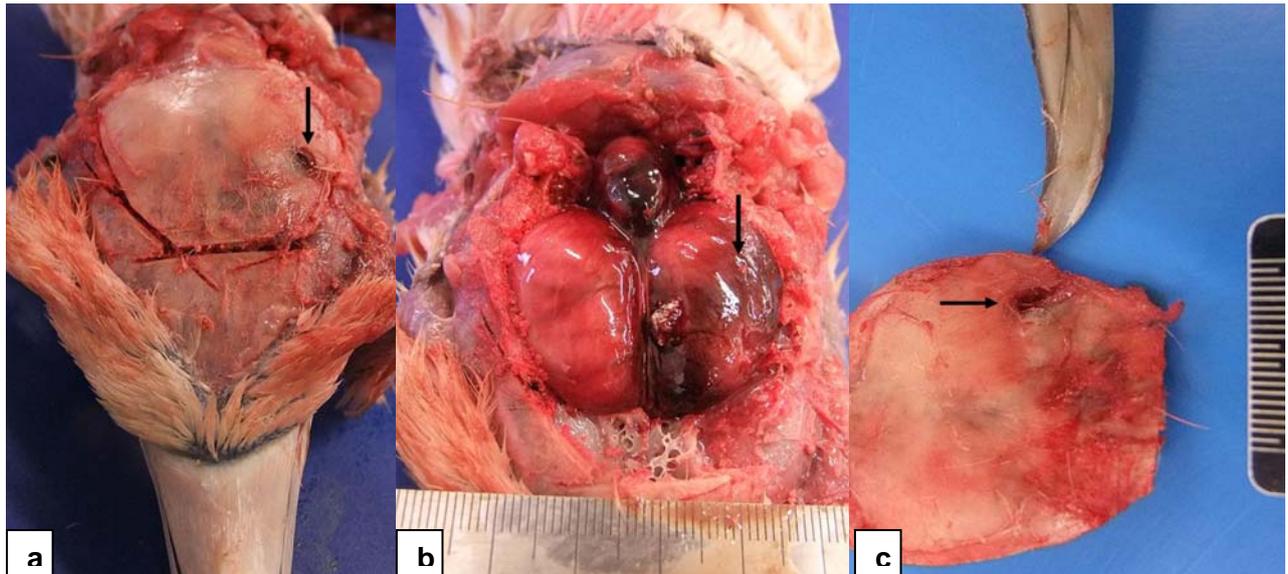


Figure 1. (a) 3-4 mm in diameter circular penetrating wound in the left dorsal surface of the cranium of a male Australasian gannet. (b) Peripheral hemorrhage and a severely reddened left frontal lobe of the brain. (c) The head wound diameter exactly fitted the dimensions of the bill tip of an adult Australasian gannet at the inferred depth of penetration. Photos by M. Alley.

The post-mortem examination of G17M revealed a 3 - 4 mm diameter x 4 mm deep circular penetrating wound in the left side of the neck (Figure 2a, b). The region of the first cervical vertebra connected to the occipital side of the skull was severely reddened, containing a 6 x 10 mm wide area of peripheral hemorrhaging. Two fresh and undigested pilchards (*Sardinops neopilchardus*), measuring 17.3 and 18.4 cm, occupied almost the entire oral cavity and the oesophagus from immediately below the pharynx caudally. A third large fresh jack mackerel was present in the proventriculus and four additional pilchards, which could not be classified as fresh due to the partial absence of flesh, were located in the stomach.

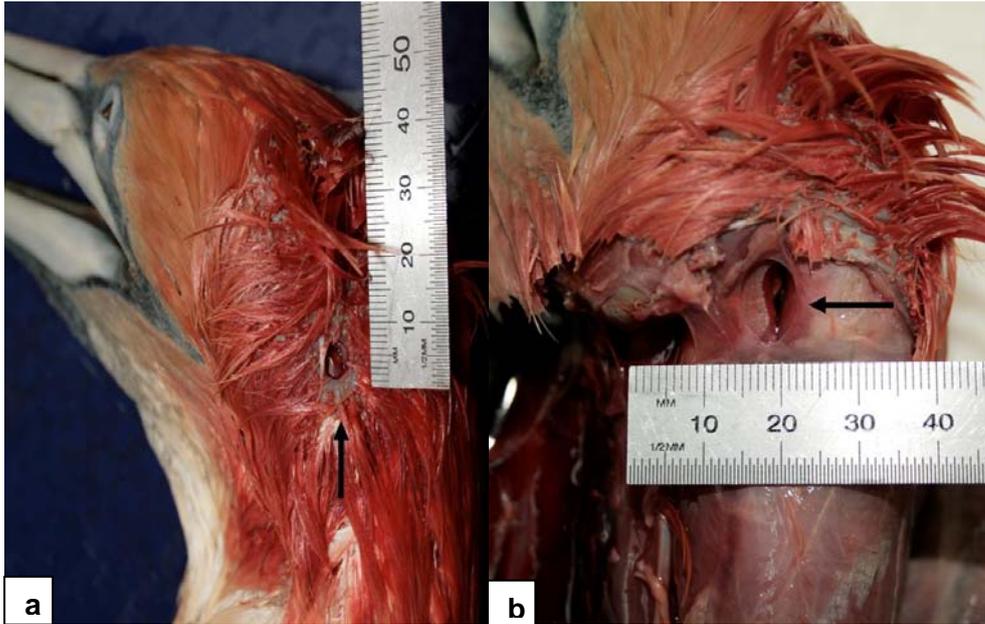


Figure 2. (a) A 3-4 mm diameter circular penetrating wound in the left side of the neck of a male Australasian gannet. (b) The injury was extended 4 mm deep into the neck. Photos by S. L. Dwyer.

7.4.2 Video footage analysis

No accidental collisions were recorded in detailed analysis of aerial video footage of Australasian or Cape gannets foraging. However, a large number of gannets were seen manoeuvring and repositioning during the momentum of plummeting into the water, although it was not possible to distinguish repositioning associated with prey capture and collision avoidance.

In contrast, analysis of 15 minutes of underwater footage revealed 3375 gannets diving and 25 cases of collisions. Of these, 20 were from G-G events and 5 from G-SWH. The estimated frequency of collisions per dive was 0.007 while the frequency of collisions between gannets was 0.006. Of

the impacts between Cape gannets, 18 occurred during the wing flapping stage, with 2 clear cases of collision during the underwater momentum phase.

A descending bird orientating towards a second bird holding a captured fish in its beak provided fascinating evidence of kleptoparasitism by foraging Cape gannets. The birds made contact, competing for the previously captured fish. The interaction lasted for 6 seconds, whereafter both gannets, still joined at the beak, disappeared from the frame. Such events might heighten the risk of accidental collision, through stimulating plunging gannets to orient towards other birds in the water column.

7.5 Discussion

The advantages of plunge-diving as a foraging strategy include the benefit of surprise (Johnston 1989) and the accuracy of approach to prey (Wanless et al. 2005; Machovsky-Capuska et al. 2011, Chapter 5). Plummeting into the water is a highly effective strategy as evidenced by the success of four families of seabirds (Sulidae, Phaethonidae, Laridae and Pelecanidae) that feed in this way (Nelson 1978). Our analysis of video footage demonstrated that collisions between diving gannets do occur in a minor frequency in MSFA (0.007 collisions per dive) and necropsy results of gannet carcasses suggest that collisions between foraging gannets can potentially result in severe head and neck trauma.

Post-mortem analysis of gannets G2M and G17M revealed penetrating wounds as would result from the high speed impact of an adult Australasian gannet beak. The momentum gained during a plunge dive allows gannets to

reach a depth of 10 m without wing flapping, at which point they achieve neutral buoyancy (Wilson et al. 1992). Velocities generated by this momentum are higher than in the wing flapping phase (Ropert-Coudert et al. 2009; Machovsky- Capuska et al. 2011, 2012, Chapter 5 and 6, respectively) and are likely sufficient to cause significant damage to an object upon impact. Furthermore, our observations indicate that these gannets were involved in foraging during or shortly prior to death, as would be expected if accidental collision in MSFA was the causes of the injuries. Complete digestion of fish takes a gannet between 2 and 6 h (Davies 1956), suggesting that the undamaged fish, still with intact skin, found in the beak and oesophagus of these birds were ingested comfortably within this period.

While the forces and high velocity impact required to penetrate the 2.5 mm thick skull of gannet G2M, the penetration to soft tissue observed in the neck of bird G17M could plausibly have resulted from a cause involving less force. One possibility is that the bird was injured during aggressive interactions with other Gannets while foraging below or under the water. We did, indeed, observe in the analysis of underwater video an aggressive interaction associated with attempted kleptoparasitism. Whether sufficient force to create such a wound could be generated by the neck muscles of a swimming bird is uncertain. Alternatively, this injury might have resulted from the interactive effects of plunge-diving and kleptoparasitism, whether deliberate or accidental.

As far as we are aware, this study is the first to report attempted underwater kleptoparasitism in gannets. Kleptoparasitism is likely a profitable way of obtaining food that could involve fierce interaction and fighting over

prey (Nilsson and Brönmark 1999), with associated risks including cost to the foragers in terms of fitness and even fatal injuries (Broom and Ruxton 2003).

Aerial video footage analysis indicated no accidental collisions between gannets, possibly due to adept maneuvering by the gannets in flight. A small number of underwater collisions were found among Cape gannets with a total frequency of 0.006 accidental collisions per dive. The majority of underwater collisions (23 out of 25) were observed during the slower wing flapping phase of the dive, with only two observed in the fast momentum phase of the plunge. Like the lack of observed aerial collisions, this might reflect the evolution of motion-sensitive mechanisms for collision avoidance. Although these mechanisms in animals have evolved to prevent collisions (Horridge 1987), every fast-moving animal is at risk of injury by impacts with objects (Ashby 1960). In gannets, the risk of accidental collisions is clearly density-dependent (Masotomi et al. 2007) and could be related to the very small degree of binocular parallax and the absence of invariance features in their field of view, in which case birds may not be able to detect their height and velocity with sufficient accuracy (Lee and Reddish 1981).

Finally, our analysis did, indeed, reveal several collisions of diving birds with marine mammals and predatory fishes, but post mortem analysis revealed no cases of damaged beaks, broken skulls or broken necks that might be expected from such collisions. Even the ratio of fatal injuries due to collisions was 2 in 50 carcasses, our video footage analysis provided evidence that accidental collisions between gannets are not reasonably common. Our priorities for the future are to use the ongoing survey of gannet carcasses to obtain a more accurate quantitative estimate of the risk of injury

resulting from collisions, and to better understand the relationship between gannet vision and the need to avoid dangerous collisions with other foragers.

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CHAPTER 8

General discussion

Australasian gannets (*Morus serrator*) are considered to be highly successful marine predators, experiencing an annual increase in population size in New Zealand of ca. 2.3 % (Nelson 2005). However, there is a severe lack of information on the foraging behaviour that contributes to this success in this region. In the present study GPS data loggers, field observations, Infra-red cameras, aerial and underwater high-resolution videography and post-mortem examinations were used to assess several aspects of the foraging behaviour of Australasian gannets, including: acquisition of foraging information (Chapter 2); long-range foraging strategies (Chapter 2); diet (Chapters 5, 7 and Appendix 1); decision-making process (Chapter 4); diving strategies (Chapters 4, 5 and 6); prey capture success (Chapter 5); visual sensitivity (Appendix 2); the role of underwater vision in prey pursuit (Chapter 6) and the risk of injury or death due to accidental collision (Chapter 7). Gaining a better understanding of the foraging decision-making dynamics in these animals is a central issue to comprehend how amphibious predators have evolved within the air/water interface.

Optimal foraging theory proposes that animals should maximise their energy gains while hunting in complex environments (Schoener 1971; Perry and Pianka 1997). Australasian gannets have a flexible diet (Schuckard et al. 2012, Appendix 1) and forage for patchily distributed marine pelagic prey using a complex decision-

making process (Machovsky-Capuska et al. 2011 a, b; 2012), as has been shown in other, closely related, members of the Sulidae family - Northern (*M. bassanus*) (Hamer et al. 2000, 2001; Montevecchi et al. 2009) and Cape gannets (*M. capensis*) (Lewis et al. 2002; Grémillet et al. 2004), Brown (*Sula leucogaster*) (Nelson 1978; Weimerskirch et al. 2009) and Red-footed boobies (*S. sula*) (Nelson 1978; Weimerskirch et al. 2005 a, b) -. Their foraging success relies on long-range foraging strategies to locate the food sources, short-range strategies to detect from the air and then capture prey underwater, and an accurate time-budget to balance their self-feeding with offspring feeding.

8.1 Long-range foraging strategy

Long-range foraging strategies involve decisions about when to depart, whether to forage solitarily or in groups, and how to acquire information about the locality and quality of unpredictable resources.

Among seabirds, several hypotheses of information acquisition about food sources have been suggested (Richner and Heeb 1995). First, information transfer between conspecifics, whether through deliberate or incidental signals, may increase the chances of finding food (Bradbury and Vehrencamp 1998). Although originally I hypothesized that bill fencing between partners may involve the exchange of foraging information regarding the location of foods analogous to the waggle dance in honeybees, no evidence was found to support this (Chapter 2). However, the possible role of bill fencing in assessing the nutritional states between partners requires further investigation.

Second, memory and local enhancement could serve as an orientation factor for patch detection, and this has been proposed to be important to Northern (Drury 1959; Garthe et al. 2007; Hamer et al. 2007; Pettex et al. 2010) and Cape gannets (Grémillet et al. 2004; Lewis et al. 2006). In the present study Australasian gannets were found to use a combination of foraging strategies, including possibly memory, to return to feeding habitats where prey was previously captured (Chapter 3) and then using local enhancement to locate the specific patches (Chapter 2). Third, foraging investment (trip duration and distance) in Australasian gannets (Chapter 3) could be shaped by food availability, oceanographic conditions and intraspecific competition as suggested in Northern (Hamer et al. 2001; Lewis et al. 2001; Garthe et al. 2007) and Cape gannets (Grémillet et al. 2004; Lewis et al. 2006; Mullers and Navarro 2010).

Finally, in most birds vision is fundamental for foraging, navigation, communication and reproduction. In seabirds, however, the distribution of UVS, and its functional role(s) are less clear (Bennett and Cuthill 1994). Seabirds, including Australasian gannets, are continually exposed to variable levels of ultraviolet radiation from the environment in which they breed and forage (Lythgoe 1979). The results presented herein (Appendix 2), revealed that Australasian gannets are able to see in the violet-sensitive range of the spectrum (Machovsky-Capuska et al. 2011c) as shown in Northern gannets by Håstad et al. 2005. As radiation in the UV range of the spectrum is documented to cause photo oxidation of the retinal tissues in the absence of adequate optical filters (Bennett and Cuthill 1994), it is possible that selection has favoured filtration devices such as oil droplets which remove UV light for protective purposes (Machovsky-Capuska et al. 2011c, Appendix 2). Although this finding shows that gannets do not use UV during navigation and

foraging, further studies are required to clarify the role of vision in long-range foraging strategies including homing to their colonies.

8.2 Short-range foraging strategy

Once the food patch has been discovered, a short-range decision-making process involves the search and detection of prey, targeting an individual or group, deciding which strategy to use, whether to attack independently or in synchrony with other predators, when to attack, for how long the pursuit should be maintained and how many prey should be captured at a time.

Social foraging is a highly effective strategy that increases the discovery rate of widespread and patchily distributed foods (Hamer et al. 2001). Its success, however, depends on many factors including social interactions among group members (Couzin et al. 2005), the coordination of foraging movements (Pinaud and Weimerskirch 2005), and the sharing of food discoveries (Waite 2001). Results presented in Chapter 4 offer evidence of plunge-diving synchronisation in Australasian gannets, highlight the impact of context (presence vs. absence of heterospecific predators) on the patterns of synchronised diving, and raised the possibility that mimetic behaviour is the mechanism underlying plunge-diving synchronisation. It has been suggested that diving in synchrony in Northern rockhopper penguins (*Eudyptes chrysocome*) and Adélie penguins (*Pygoscelis adeliae*) enhance prey capture success (Tremblay and Cherel 1999 and Takahashi et al. 2004, respectively). However, Saino et al. (1995) showed that White pelicans (*Pelecanus onocrotalus*) had a better prey capture success foraging alone than while

synchronizing their dives. In the particular case of the Australasian gannet, it is unclear whether plunge-diving in synchronization enhance prey capture success.

In Chapter 5 it was shown that gannets adjusted their dive shape in relation to the depth of their prey rather than prey type as previously suggested by Garthe et al. (2000) in gannets and by Zavalaga et al. (2007) in boobies. The results also revealed that a significantly greater proportion of U-shaped dives were associated with successful prey capture than V-shaped dives (95% vs. 43%, respectively), including an overall success rate of prey capture per plunge-dive of 72%. These findings are consistent with a successful range of 50 - 75 % of prey capture per dive suggested in Northern gannets by Wanless et al. (2005). The maximum number of prey captured per dive by Australasian gannets was higher than previously reported, reaching up to 5 fish in a single U-shaped dive. Although the importance of heterospecific predators such as whales and dolphins in the development of stationary prey balls has been suggested to increase gannet prey capture success (Vaughn et al. 2010; Machovsky-Capuska et al. 2011b, Chapter 5), further studies are required to establish whether this high level of accuracy per plunge-dive also reflects the fishing ability of individual gannets and if this relates to age and experience as observed in terns (Dunn 1972), boobies (Yoda et al. 2007) and pelicans (Carl 1987).

The aerial detection of prey among the selected group of plunge-diving members (gannets and boobies, pelicans, terns, kingfishers, fish eagles and osprey) has been regarded as visually guided (McGillivray 1842; Cunningham 1866; Lee and Reddish 1981; Eriksson 1985). The findings presented herein on plunge dive synchronisation using mimetic behaviour, the existence of aborted dives during the aerial phase and the height variation of the plunge-dives in relation to the presence or absence of heterospecific predators (Chapter 4) represents reliable evidence

corroborating the use of vision during the aerial phase of the plunge-dives in Australasian gannets. While chances of mortality seem low (less than 1%), the risk of injury or death as a consequence of accidental collision while plunge-diving in multi-species-feeding-associations (MSFA) events (Machovsky-Capuska et al. 2011a, Chapter 7) could be related to the challenges of prey detection against the aquatic background, the capacity to compensate for light refraction and reflection as well as their visual acuity. These issues remain unclear and require further exploration.

It has been suggested that plunge-diving predators' benefit from the effect of surprise when capturing fish and squid, however, the behavioural analysis presented in Chapter 6 indicates that Australasian gannets were more successful in prey capture during the visually guided underwater pursuit (Figure 1, Chapter 6). Although gannets are able to visually accommodate underwater upon head submergence in a range of 80 - 120 ms (Chapter 6), cavitation and body manoeuvrability while entering the water may reduce gannets' visual capabilities and subsequent prey capture success. During the visually guided aerial phase of the dive (Chapter 4) gannets may be able to predict their diving performance using the angle of entrance into the water and anticipate the depth of their prey (Chapter 5).

8.3 Future research directions

Overall, the research presented in this thesis advances the understanding of how Australasian gannets cope with the challenges of foraging at the air-water interface. The challenge ahead is to integrate these findings with additional research on the long- and short-range foraging strategies that would require in many cases a

multidisciplinary approach. In regards to the former, more studies are needed to test further the use of bill fencing as an integrator for coordinating the periods of absence from the nest with the foraging success and nutritional states of the partners. A systematic deployment of GPS data loggers could help to reveal patterns of information transfer regarding to foraging sites in relation to the foraging trip bearings as previously suggested (Pettex et al. 2010; Weimerskirch et al. 2010). In addition, long-term research programs should include the deployment of data loggers that enable researchers to collect foraging behaviour data in addition to environmental variables to develop a 3D scenario of the marine environment in which Australasian gannets are foraging and also gain a better understanding on the main foraging sites for this species and their site fidelity. Furthermore, in order to define the main factors that shapes the foraging behaviour on Australasian gannets, it's necessary to quantify and establish the spatio temporal rate of abundance and diversity of prey aggregations in parallel to the deployments of GPS data loggers from the colonies (Hamer et al. 2001; Garthe et al. 2007). The collection of regurgitations from foragers upon arrival at the colony would be also relevant to the study of prey fluctuations (Bunce 2001; Hamer et al. 2007) and foraging effort (Hamer et al. 2001). However, it would be wise to standardize the sampling protocols to enable researchers to used novel nutritional models (e.g. right-angled mixture triangle) to establish the nutritional composition of the prey species and how they contribute towards the diet of these predators (Raubenheimer et al. 2009).

From a short-range foraging angle, several questions remain to be answered. In this area, researchers have a real challenging system that involves dealing with spatio temporal foraging events that occur within the air/water interface. The use of synchronize high speed cameras in the air and underwater could bring a picture of

the variables that shape decision making process while plunge-diving. This video footage could help to unravel how the prey capture rate fluctuates in relation to the environmental variables (e.g. depth, visibility, sun position and wind), prey abundance, the presence and role of conspecifics and heterospecifics during these feeding events. Although we have made a significant progress on the role of underwater vision on prey capture in gannets, a significant investment should be dedicated on the anatomy and physiology of the gannet eye. Visual and behavioural experiments on how depth, visibility, sun position and reflection and refraction of light should be done to establish the visual acuity on these marine predators. These experiments would enable comparisons with well-studied aquatic birds such as herons (*Egretta* spp.) (Katzir and Martin 1994; Katzir et al. 1999), Pied kingfishers (*Ceryle rudis*) (Katzir et al. 1993), Great cormorants (*Phalacrocorax carbo*) (Strod et al. 2004, 2008; White et al. 2007).

Increasing multidisciplinary approaches on the study of the sensory ecology, behavioural ecology and nutritional ecology of these species would enable us to understand their evolutionary adaptations as predators that hunt between the air and the water.

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Appendix 3

Mutual Fencing in the Australasian gannet: partner asymmetries

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INTRODUCTION

In many monogamous birds one or both members of a pair frequently engage in repetitious displays clearly orientated towards the social mate. "Greeting" or "meeting" ceremonies are observed when the partners meet after a period of separation, and in many species occur throughout the duration of the pair bond (Wachtmeister, 2001). One such species is the Australasian gannet (*Morus serrator*), which invariably undergoes a "greeting ceremony" in the brief period separating the return of one bird from foraging and the departure of the other. Little is known about the structure or biological function of these displays. Here we report preliminary data on the first of these aspects, the sequential organization of the "greeting" ceremony of the Australasian gannet. We were, in particular, interested in:

- whether the display of the partners is symmetrical, or differed between the bird returning to the nest and that leaving to forage and
- whether it is systematically initiated by either the incubent or returning bird.



METHODS

Between November 2008 and February 2009, video footage (25 frames s⁻¹) from breeding gannet pairs was collected at Cape Kidnappers, New Zealand. Mutual fencing ceremonies (n=50) from the complete cycles of arrival at the nest by a returning forager and the subsequent departure from the nest of the incubent bird were recorded. The films were analysed frame-by-frame with Adobe Premiere Pro CS4 film editor to characterise the behavioural components and determine the timing and duration of each in the display. To describe the behavioural components, we adopted and updated some of the terminology of Warham (1958), Van Tets (1965) and Nelson (1978).

RESULTS

1. Behavioural components

In accordance with our interest in whether the display is symmetrical or asymmetrical, we distinguish those behavioural components that are collective (i.e. necessarily involve the participation of both partners) from those that are individual, and so can potentially be performed by one bird and not the other.

Collective



A sustained bout of bill clashing and facial contact in which bills could be inclined upwards. Previously described by Warham (1958), as "colliding beaks that make a crash sound" and Nelson (1978) as a rapid fencing or "scissoring" movement with their bills.

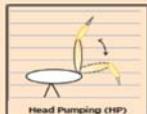


In this display, one bird reaches over the neck of the other in a sinuous movement. Also described by Nelson (1978) as a "neck-smoothing". Often occurs at the end of head pumping postures.

Individual



A characteristic head and beak waggle from side to side with the neck maintained outstretched (Warham, 1958; Van Tets, 1965). Also called head shaking (Nelson, 1978). A similar posture is described by Meseth (1974) in the dance of the Laysan albatross (*Diomedea immutabilis*).



Neck up-stretched, with the head erected or 90° to the neck. Often performed by the pair as a mirror image facing each other, either before and/or after bill touching.



A rapid and repeated movement of the whole neck up and down. It has also been observed in the triumph ceremony of the Canada goose (*Branta canadensis*) (Radesäter, 1974).

2. Symmetry of the display

Not all birds performed all of the above components in every mutual fencing display. We therefore tested whether the probability of occurrence of "individual" behaviours differed between the birds - i.e. was asymmetrical between the arriving and nesting partner.

There was no significant difference in the frequency of Head Pumping ($P = 0.05$), but the arriving birds showed a significantly higher frequency of Sky View, and the nesting birds a higher frequency of Head Wagging (Fig. 2).

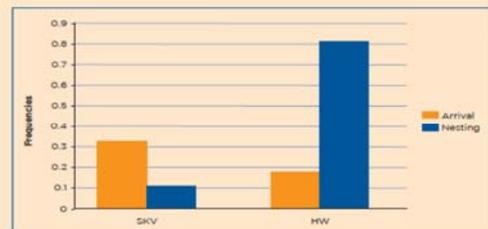


Fig. 2. Asymmetric display: Sky view vs. Head wagging in arrival and nesting gannets.

3. Display Initiation and predominant posture

We used a binomial test to examine whether there was a greater probability of the arriving or nesting bird initiating the mutual fencing display. Results showed that the display was initiated more frequently by the nesting bird ($P = 0.014$; Fig. 3). Further, the initiating component differed between the nesting and arriving bird (nesting: 71% Head Wagging, 29% other; arriving: 27% Head Wagging, 73% other; two-tailed $P = 0.001$ Chi Squared contingency test).

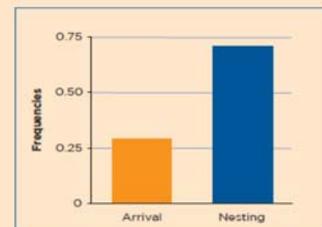


Fig. 3. Display initiation in arrival and nesting birds.

DISCUSSION

This preliminary analysis demonstrates that the nesting and arriving birds are distinguished by the roles that they play in the mutual fencing ceremony. The arriving bird is more likely to include in its repertoire Sky View, while the nesting bird is more frequently associated with Head Wagging. Further, our analysis demonstrates that displays initiated by the nesting bird start with Head Wagging more frequently than all other individual components combined. By contrast, on the relatively few occasions when the arriving bird initiated the ceremony it was unlikely to be through Head Wagging. The important question that our results raise is whether the partner asymmetries we have observed are associated with asymmetries in the function of mutual fencing. We are currently in the process of exploring this.

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Appendix 4: Publications

The following publications are the outcome of this PhD candidature and the result of the research presented in this dissertation:

Publications in peer-reviewed journals

Machovsky-Capuska, G. E., Howland, H. C., Vaughn, R. L., Würsig, B., Raubenheimer, D., Hauber, M. E., and Katzir, G. (2012). Visual accommodation and active pursuit of prey underwater in a plunge diving bird: the Australasian gannet. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 279, 4118-4125.

Schuckard, R., Melville, D., Cook, W., and Machovsky-Capuska, G. E. (2012). Diet of the Australasian gannet (*Morus serrator*) at Farewell Spit, New Zealand. *Notornis*, 59, 66-70.

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Publications in preparation

Machovsky-Capuska, G. E., Hauber, M. E., Libby, E., Couzin, I., Wikelski, M., and Raubenheimer, D. Bill fencing in Australasian gannets: is it a signal to enhance foraging efficiency?

Machovsky-Capuska, G. E., Hauber, M. E., Libby, E., Schuckard, R., Melville, D., Cook, W., Amiot, C., Houston, M., and Raubenheimer, D. Variable foraging patterns in chick-rearing Australasian gannets from New Zealand.

Machovsky-Capuska, G. E., Libby, E., Hauber, M. E., Amiot, C., and Raubenheimer, D. The temporal dynamics of collectivity: plunge-diving synchrony in conspecific and multi-species feeding assemblages in Australasian gannets (*Morus serrator*).

Conference proceedings

Machovsky-Capuska, G. E., Libby, E., Amiot, C., Hauber, M. E., and Raubenheimer, D. (2012). The use of personal and social information in foraging by the Australasian gannets (*Morus serrator*). *Proceedings of the Australasian Society for the study of Animal Behaviour Conference*. Geelong, Australia.

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Machovsky-Capuska, G. E., Hauber, M. E., and Raubenheimer, D. (2009). Mutual Fencing in the Australasian gannet (*Morus serrator*). *Proceedings of the Australasian Society for the study of Animal Behaviour Conference*, Albany, New Zealand.

Reports to the New Zealand Department of Conservation

Machovsky-Capuska, G. E., Schuckard, R., and Raubenheimer, D. (2012). Foraging strategies in Australasian gannets at Farewell Spit colony. *Department of Conservation, Nelson Conservancy*.