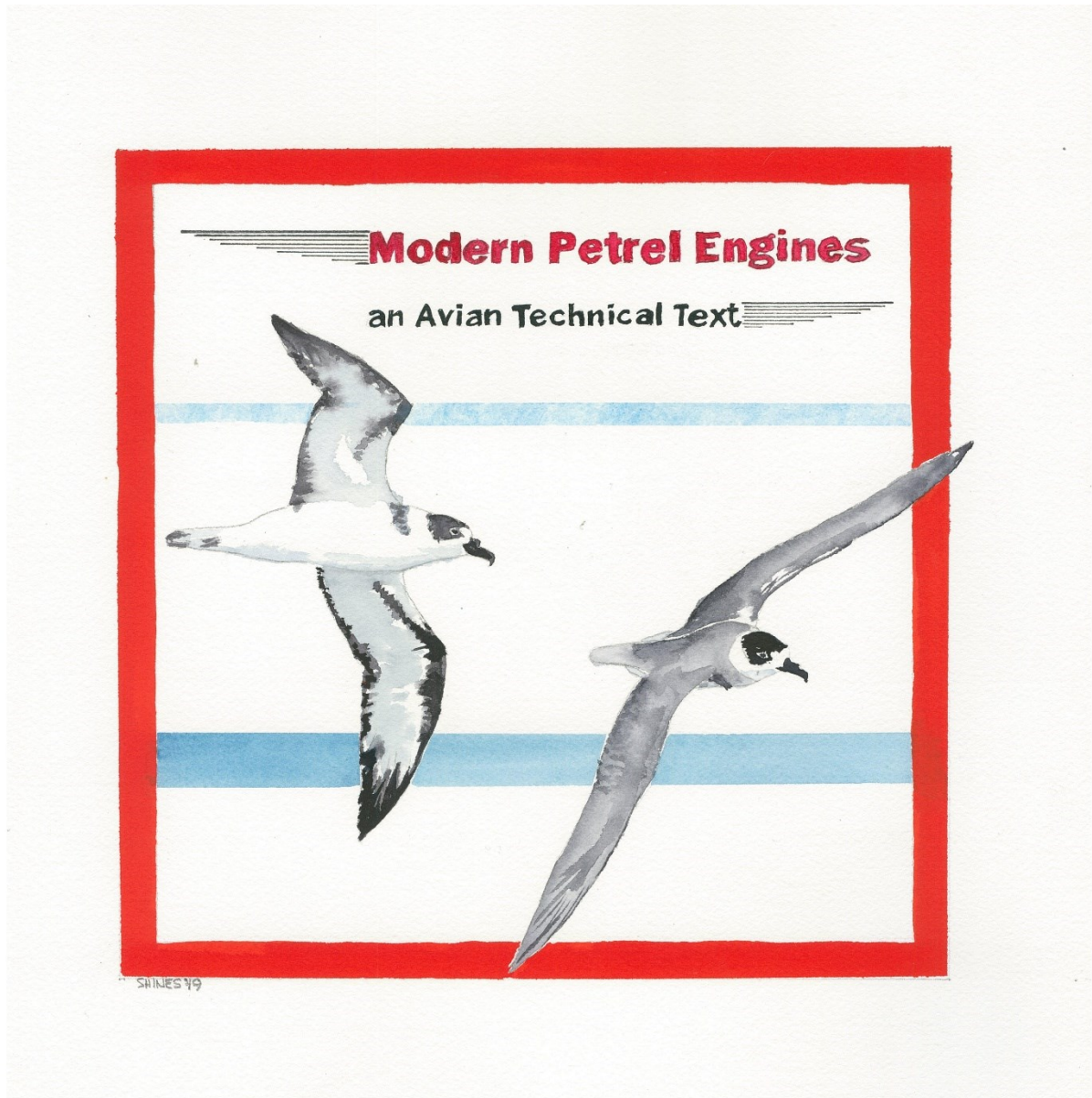# Movement ecology of sympatric gadfly petrels with implications for bio-logging, island trophic dynamics and conservation

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2022

Movement ecology of sympatric gadfly petrels with implications for bio-logging, island trophic dynamics and conservation

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A thesis submitted for the degree of *Doctor of Philosophy* at

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School of Biological Sciences

This thesis is dedicated to Harry R. Carter (1956 – 2017),

my friend and mentor who inspired me and helped me to become a better seabird ecologist.

Abstract

Movement ecology plays a central role in the study of ecology as the movement of organisms shapes the structure and function of ecosystems, communities, and populations. Our ability to conserve species and habitats depends upon a deep knowledge of animal movement and how these movements may regulate ecosystem functionality. Escalating anthropogenic activities have led to biodiversity decline at a record rate and the multifunctionality of ecosystems is degrading. Studying animal movements can help shape our knowledge of the threats faced by species and of how ecosystems function. In Chapter 1, I provide an overview of the key topics and structure of this thesis. In Chapter 2, I investigate the foraging distributions, behaviour and habitat preferences of three sympatrically breeding gadfly petrels that integrate resources over large spatial and temporal scales. I tested the ability of ensemble species distribution models (ESDM) to predict foraging habitat by using a spatially-independent cross-validation approach. My results demonstrated how these species adapt their foraging strategies to mitigate the resource-poor conditions of tropical areas. I found that the ability of ESDMs to predict foraging habitat on new spatial and temporal data was poor. This chapter builds upon knowledge of tropical seabird foraging behaviour and highlights conservation implications for tropical pelagic seabirds.

In Chapter 3, I investigate the implications of seabird movement on the accuracy of light-level geolocation: a widely employed tracking method that uses light curves to estimate positions of tracked animals. I investigated whether spatial accuracies typically expected of geolocator-tracked seabirds were applicable in the context of a multi-species study. I tested what factors influence accuracy, whether accuracy is improved given newly designed

geolocation algorithms; and how practitioners can improve assessment of accuracy. My results demonstrate that geolocator accuracy can be lower than what is typically expected by practitioners, and confirmed the hypothesis that accuracy is species dependent. I revealed that the idiosyncrasies of individual birds and spatial (i.e., being near to the Equator) and temporal (i.e., equinoxes) dynamics mean that practitioners should exercise greater caution in interpreting geolocator data and avoid universal uncertainty estimates. My results enabled the development of a simple function that practitioners can use to estimate relative accuracy of their data based on the geolocator-observed length of day or night.

In Chapter 4, I explore a novel role for seabirds as vectors of nutrient transfer as they move between marine foraging grounds and terrestrial breeding sites. I demonstrate that by preying on seabirds and other vertebrates, large arthropods can structure the trophic dynamics of isolated island food webs. In a novel way, this research builds on both our knowledge of the broad, ecosystem-wide implications of how seabirds contribute to terrestrial food webs and of the consequences of arthropod predation of vertebrates. In this chapter, I consider the role of this phenomenon on island trophic dynamics and its impact on the reproductive output of long-lived vertebrates. In Chapter 5, I discuss the implications of my thesis and provide future directions for research and management.

Overall, this thesis brings together various features of movement in tropical seabirds including foraging ecology and the implications of seabird movement for ecosystem function on isolated islands to address several issues related to research, conservation, and management.

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Thesis Declaration

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

This thesis includes two original research papers published in peer reviewed journals (*Methods in Ecology & Evolution* and *The American Naturalist*) and one original research paper that has been submitted for publication in *Frontiers in Marine Science*. The core theme of the thesis is on seabird foraging ecology, the consequences of seabird movement for their research and conservation, and of the implications of seabird movement for ecosystem function on isolated islands.

The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the candidate, working within the School of Biological Sciences under the supervision of Rohan H. Clarke and the co-supervision of Rowan Mott (University of Adelaide) and Nicholas Carlile (New South Wales Department of Planning Industry and Environment). The inclusion of co-authors reflects the fact that these works came from active collaborations between researchers and acknowledges input into team-based research. In the case of Chapters 2, 3 and 4 my contribution to the work involved the following:

Thesis Chapter	Publication Title	Publication Status	Nature and % of student contribution	Nature and % of co-authors' contributions	Co-author(s), Monash student Y/N
Chapter 2	Predicting the foraging habitats of sympatrically breeding gadfly petrels in the South Pacific Ocean	Submitted to *Frontiers in Marine Science*	Conceived and designed the study, conducted fieldwork expeditions, analysed the data, and wrote the manuscript (85%).	1) Rowan Mott, Thomas Clay, Grant Humphries, Nicholas Carlile, Rohan Clarke: helped with study design, data analysis and manuscript writing (12%) 2) Trudy Chatwin: assisted with field expeditions and approved manuscript (3%)	N
Chapter 3	Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles.	Published in *Methods in Ecology & Evolution*	Conceived and designed the study, conducted fieldwork, analysed the data and wrote the manuscript (85%).	1) Jeremy Ross: Helped conceive study idea, analyse data, and write manuscript (5%) 2) Rohan Clarke, Rowan Mott, Nick Golding, Nicholas Carlile: helped with study design, data analysis and manuscript writing (5%) 3) Raül Ramos, José Manuel Reyes-González, Teresa Militão, Fernanda De Felipe, Zuzana Zajková, Marta Cruz-Flores, Sarah Saldanha, Virginia Morera-Pujol, Leia Navarro-Herrero, Laura Zango, Jacob González-Solís: shared data and approved manuscript (5%)	N
Chapter 4	Arthropod Predation of Vertebrates Structures Trophic Dynamics in Island Ecosystems	Published in *The American Naturalist*	Conceived and designed the study, conducted fieldwork expeditions, lab analysis, analysed the data and wrote the manuscript (85%).	1) Daniel I. Terrington, David Dow, Wei Wen Wong: helped with field and laboratory work, proofread, and contributed to the manuscript (7.5%) 2) Rohan H. Clarke, Rowan Mott, Holly Jones, Nicholas Carlile: helped with study design, proofread, and contributed to the manuscript (7.5%)	Y (D. Terrington only)

I have renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Student name: Luke Robin Halpin

Student signature: Date: 30 January, 2022

I hereby certify that the above declaration correctly reflects the nature and extent of the student's and co-authors' contributions to this work. In instances where I am not the responsible author I have consulted with the responsible author to agree on the respective contributions of the authors.

Main Supervisor name: Rohan H. Clarke

Main Supervisor signature: Date: 30 January, 2022

Acknowledgements

I would like to express my deepest gratitude to my partner and best friend, Chris Lee, for dropping everything and moving across the world from Canada to Australia so that I could undertake this PhD project and pursue my research on seabird ecology.

I have dedicated this thesis to Harry R. Carter (1956–2017). Harry was a great friend and mentor who helped me to become a better seabird ecologist. Over the years, Harry and I shared many adventures as we worked together on various seabird projects including on the restoration of ashy storm-petrels in the California Channel Islands. Later we investigated the ecology and conservation of Leach's and fork-tailed storm-petrels on several islands off the west coast of Vancouver Island. It was Harry who encouraged me to pursue a PhD.

I am deeply grateful to my supervisors: Rohan Clarke, Rowan Mott and Nicholas Carlile for helping me grow my ideas and develop my skills as an ecologist, and for supporting me through my research. Thank you! I'd also like to thank the many people (there are too many to mention here) who have collaborated with me for sharing data, ideas and helping me to improve my research. I'd also like to thank Ken Morgan for endless helpful discussions about seabirds, for facilitating many opportunities for me to work with seabirds over the years, and for encouraging me to pursue a PhD.

This PhD has been a wild ride. I feel incredibly fortunate to have lived and conducted my research on Phillip Island over four years. Living and working on a remote and uninhabited island was a tremendous privilege and source of joy. I will always have a soft spot for white-necked petrels in particular – getting to know individuals, learning about their

personalities, and witnessing them return to their nests each year has been extraordinarily special.

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CHAPTER 1

General Introduction

1.1 Animal movement

Animal movement is a conspicuous and crucial feature of life on earth that occurs over multiple spatial and temporal scales (Swingland and Greenwood 1983; Nathan 2008). The continual movement of organisms on our planet plays a vital role in evolutionary processes and shapes the structure and function of ecosystems, communities, and populations (Stephens and Krebs 1986; Nathan 2008; Tucker et al. 2018). Movement of organisms is therefore essential for the persistence of species. Spatial and temporal scales of movement vary widely among organisms, but movement generally occurs in response to the dynamic nature of most environments: distribution of resources, environmental conditions, inter- and intra-specific competition, predation, parasites, and the need for gene flow (Fryxell and Sinclair 1988; Dingle and Drake 2007; Avgar et al. 2014).

Movements may be shaped by several life history factors (e.g., reproduction, body condition, age) that influence the needs of an individual. Nathan (2008) described four components to explain the underlying processes that trigger animal movement: 1) an animal's *internal state* represents its physiological condition that drives it to fulfil a goal (e.g. reproduction); 2) *Motion capacity* reflects the ability of an animal to perform self-propelled motion (e.g., walking, swimming, flying); 3) *navigation capacity* refers to an animal's ability to orient itself in space and time, and to select where and when to move; and 4) *external factors* relating to the biotic and abiotic characteristics of an animal's environment that exert further limitations and provide pathways to movement (e.g., ephemeral or seasonal resource availability, physical or geographic barriers and ocean currents). Foraging individuals typically navigate landscapes in which resources are patchily distributed and where high-density resource patches are scarce (Fauchald 1999). By

moving, many species not only satisfy their own needs, but perform important ecosystem functions such as seed dispersal, pollination, regulating the abundance of prey species or delivering nutrient inputs that would otherwise be unavailable (Jonsen and Fahrig 1997; Santos et al. 1999; Shuter et al. 2011).

Animal movements vary in scale from regular movements to and from patches of predictable resources to resource-driven meandering journeys over large areas in search of unpredictable resources (Runge et al. 2014). Some of the most well-known movements of animals include that of caribou (*Rangifer tarandus*) which make vast journeys between winter ranges to their calving grounds in the Arctic (Fancy et al. 1989), and that of gray wolves (*Canis lupus*), which make some of the largest cumulative annual movements among terrestrial mammals (Joly et al. 2019). In the animal kingdom, birds exceed all other classes in terms of their mobility and capacity to navigate over vast distances in a single year. An estimated 19% of extant bird species are migratory (Kirby et al. 2008). Arctic terns (*Sterna paradisaea*) navigate enormous distances of over 80,000 km annually between breeding locations in the Arctic region to overwintering sites in Southern Ocean (Egevang et al. 2010); bar-tailed godwits (*Limosa lapponica baueri*) make large trans-Pacific journeys of almost 12,000 km from central Alaska to New Zealand in little over a week (Gill et al. 2009); and in their sabbatical years between breeding, wandering albatrosses (*Diomeda exulans*) can circumnavigate Antarctica two or three times in a single year, covering distances of more than 120,000 km (Weimerskirch et al. 2015).

Movement of organisms is a critical natural process, but global anthropogenic activities have created external pressures that have affected animal movement and altered the natural processes that influence the availability of habitats and resources (Tucker et al., 2018). Thus, to effectively conserve species and ecosystem function, it is crucial that we: A) identify species' movement attributes and the biotic, and abiotic factors that compel them to move; B) identify the

spatial and temporal scales over which species move; and C) understand the impacts of species'

movements on ecosystem function; and D) identify and understand the external pressures created by

human activities that may constrain species' movement.

Conserving highly mobile species is especially challenging for those that occupy large

spatial areas or several spatially distinct regions in which threats may differ (Runge et al. 2014;

Harrison et al. 2018). Species that range across international boundaries present additional

challenges to achieving successful conservation (Harrison et al. 2018) and to establishing effective

protected area networks (Runge et al. 2014) because conservation mechanisms are often fractured

across international borders. Where regions share common threats, the magnitude of the threat in

each region may differ depending on the level of protection, leading to more severe impacts in one

region than the other (Suryan et al. 2007; Lascelles et al. 2014). Conserving highly mobile species

therefore presents an array of complex challenges for practitioners, and traditional spatially-explicit

approaches that do not factor movement into the decision making process are likely inadequate

(Runge et al. 2014; Allen and Singh 2016).

For many species, we still lack even basic information about movement ecology and

distribution, and this is especially so for species that range over large areas. Lack of information

about species' movement attributes means that they cannot be effectively protected. However,

advances in technology mean that these knowledge gaps are gradually being filled as evidenced by

the rise of new studies in the field of movement ecology (Ogburn et al. 2017; Fraser et al. 2018).

For example, the movements of an iconic and culturally important Australian species, the short-

finned eel (*Anguilla australis*) was only recently revealed thanks to new tracking technology

(Koster et al. 2021). As well, the previously unknown at-sea distribution of a small and critically

endangered seabird, the Whenua Hou diving petrel (*Pelecanoides whenuahouensis*) was only

revealed in 2021, allowing scientists to assess conservation threats to the species throughout its life cycle (Fischer et al. 2021).

Studies like these present new conservation opportunities, equipping conservation practitioners with the knowledge necessary to identify threats and more effectively conserve species and ecosystems. Animal tracking studies also present new opportunities to bolster public support for conservation initiatives. Public interest in ecology and conservation is arguably increasing, perhaps especially given the widespread participation in citizen science initiatives (Ellwood et al. 2017; Maund et al. 2020). As a result, the public's awareness of the crucial role of animal movement is perhaps also increasing given that data from animal-borne tracking devices now feature prominently in worldwide media (Ropert-Coudert et al. 2009). These factors can be taken as opportunities; especially considering that science communication is now widely accepted as an important tool to earn public support for the conservation of ecosystems and natural resources (Bickford et al. 2012).

1.2 Movement in tropical seabirds

Seabirds are particularly wide-ranging marine predators with extreme life histories (Ricklefs 1990; Weimerskirch 2002). They frequently undertake exceptionally long-distance journeys both during their reproductive and migratory life history stages (Shaffer et al. 2006; Magalhães et al. 2008; Egevang et al. 2010; Ramos et al. 2017; Ventura et al. 2020). Movements made by breeding tropical seabirds can occur over huge spatial scales that can rival in distance and duration even the largest annual migrations of some species. This is particularly true of seabirds in the order Procellariiformes (e.g., albatrosses, shearwaters, petrels and storm-petrels) that are well-known for their extreme long-distance journeys (Weimerskirch and Wilson 2000; Shaffer et al. 2006; González-Solís et al. 2007; Clay et al. 2017; Ramos et al. 2017; Halpin et al. 2018).

How seabirds move and how they are distributed in space and time are greatly influenced by complex and dynamic oceanographic processes (Ballance et al. 2006). Movements are often extreme because of several factors that influence the distribution and availability of resources. In tropical marine systems prey species are often ephemeral and patchily distributed across the environment (Grünbaum and Veit 2003; Weimerskirch et al. 2005) which forces seabirds to adopt strategies that help them to cope with the constant search for productive areas.

For the purpose of this thesis, I consider 'tropical' seabirds as those that reproduce within the tropics (i.e., areas between the Tropic of Cancer and Tropic of Capricorn located at 23°26′11.1″ north and south, respectively) as well as within the subtropical regions that extend from the boundaries of the Tropic of Cancer and the Tropic of Capricorn to approximately 35° north and south, respectively.

Most tropical seabirds are highly mobile (Ballance et al. 2006) and have evolved foraging strategies to cope with the oligotrophic conditions of tropical marine systems. In these regions, seabirds must invest more time and energy searching for prey resources relative to species at higher latitudes that exploit more predictable resources. In more productive waters at higher latitudes, alcids, diving petrels and penguins are more successful because they have adapted to forage deeper within the water column (Brown 1980), indeed penguins have lost their ability to fly and through evolution have traded flight for superior efficiency in swimming. However, tropical seabirds are generally restricted to foraging at the sea surface, or within just a few meters of it (Ashmole and Ashmole 1967; Ashmole 1968; Diamond 1978); and the evolutionary adaptations of some species (e.g., frigatebirds, genus *Fregata*) are so extreme that they do not enter the water at all (Ashmole 1963). Furthermore, many species that forage in tropical regions are thought to take advantage of mesopelagic fishes and squids which are often diel vertical migrants which make them nocturnally

available for shallow divers or surface feeding (Roper and Young 1975; Gjøsæter and Kawaguchi 1980; Harrison et al. 1983; Spear et al. 2007)

For these reasons, in the resource-poor waters of tropical regions, seabird assemblages tend to contain large numbers of species (e.g., boobies, terns, petrels and shearwaters) that demonstrate adaptations enabling them to exploit patchy and unpredictable resources across large to very large areas (Ainley 1977; Ballance et al. 1997). Seabird adaptations to dealing with resource-poor conditions are varied: some tropical seabirds associate with foraging aggregations of large marine predators such as tuna and cetaceans which drive prey to the surface (i.e., 'facilitated foraging') (Maxwell and Morgan 2013; Veit and Harrison 2017; Miller et al. 2018; Reynolds et al. 2019). Whereas others are morphologically adapted to forage over very large distances with reduced energetic costs of flight enabling them to reach distant resources and increase their chances of encountering prey patches (Pennycuick 1983; Ballance et al. 1997; Ventura et al. 2020).

Inter- and intra-specific competition for prey is high among seabirds in resource-poor tropical environments because concentrated foraging around seabird colonies causes depletion of local resources, which forces individuals to journey further in search of food: a phenomenon known as 'Ashmole's halo' (Ashmole 1963; Oppel et al. 2015; Weber et al. 2021). In response to this problem, many seabirds have adapted their behaviour by adopting bimodal foraging strategies whereby individuals undertake short, near-colony foraging trips to provision their dependent young, and long trips to reach distant resources to provision themselves (Weimerskirch et al. 1994; Oppel et al. 2015; Weber et al. 2021).

The reproductive strategies of seabirds also demonstrate adaptations to cope with resource poor conditions. For example, Procellariiform seabirds are long-lived, monogamous, strongly philopatric, exhibit low mortality and raise only one altricial offspring per breeding season over protracted

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nesting periods (Warham 1996; Brooke 2004). In long-lived seabirds – such as the

Procellariiformes – reproductive output is most likely limited by the availability of resources, which

influences the ability of parents to provision themselves as well as their offspring, which they

generally provision infrequently (Lack 1968; Ricklefs 1983). For these seabirds, resource allocation

is a trade-off between the needs of parents and the needs of their offspring (Weimerskirch et al.

1994; Mauck and Grubb 1995); and, in the face of increased energetic costs (or lack of resources)

parents can maintain their own nutritional condition and allocate fewer resources to their offspring

(Ricklefs 1983).

1.3 Seabirds as nutrient vectors

Animal movement plays a globally important role in the transport of nutrients (Doughty et al.

2016). When animals move across landscapes and between resource patches they influence

biomass, nutrient redistribution, and predators, which affect decomposers and primary producers

(McNaughton et al. 1988; Hobbs 1996; Joly et al. 2019; Hentati-Sundberg et al. 2020). For

example, free-ranging mammalian grazers in the Serengeti of Tanzania have been shown to

accelerate nutrient cycling in a way that is beneficial to their carrying capacity (McNaughton et al.

1997) and moose (*Alces americanus*) play an important role in transferring nitrogen from aquatic to

terrestrial systems (Bump et al. 2009). Terrestrial predators that feed on spawning salmon that

migrate from the ocean to freshwater transport marine-derived nutrients that enrich old-growth

forests and provide nutritional inputs at multiple trophic levels (Reimchen et al. 2003).

The importance of seabirds as nutrient vectors is unambiguous. Seabirds are globally important

for the transport of nutrients from the ocean to land (Polis and Hurd 1996; Sánchez-Piñero and Polis

2000; Harding et al. 2004; Ellis et al. 2006; Mulder et al. 2011; Smith et al. 2011; Otero et al.

2018). It is estimated that worldwide seabirds excrete 591 Gg of nitrogen and 99 Gg of phosphorous

annually (Otero et al. 2018). The convergence of large numbers of seabirds onto remote oceanic

islands therefore plays a key role in nutrient availability on islands due to their isolation and lack of other pathways for nutrient input. Typically, seabird transfer of these nutrients from sea to land occurs in the form of excreta, spilled food, feathers, dead chicks or adults, and abandoned eggs (Harding et al. 2004). On islands, nitrogen, which is essential for plant growth, is often inputted exclusively by seabirds. In these isolated systems, seabird nutrient input has important consequences across trophic levels with consumer populations heavily subsidized by seabird inputs (Sánchez-Piñero and Polis 2000; Croll et al. 2005).

It has been estimated that combined phosphorus transfer by seabirds and anadromous fish (fish that migrate between marine and freshwater) has declined globally to about 4% of what it was in the past as a direct result of declining populations of seabirds and fish (Doughty et al. 2016). On islands without introduced rats (*Rattus sp.*) plants and soil nutrient loads are higher than on islands with rats (Graham et al. 2018); and coral reefs adjacent to rat-free islands have faster growing herbivorous fish and higher biomass across trophic groups (Graham et al. 2018). However, many of the ecosystem services that seabirds provide have been lost or diminished because seabird populations have been decimated by introduced predators across 90% of the world's temperate and tropical islands (Jones. et al. 2008).

1.4 Seabird conservation

In addition to providing important ecosystem services, seabirds are regarded as ideal bio-indicators of the state of marine ecosystems because their behaviour, reproductive output, survival, and abundance can vary in response to oceanic conditions (Ainley et al. 1995; Hyrenbach and Veit 2003; Piatt et al. 2007; Wolf et al. 2010). The abundance and diversity of seabirds can also be used as indicators to infer regions with high marine biodiversity (Zacharias and Roff 2001; Karpouzi et al. 2007; Maxwell et al. 2013).

Despite their ecological importance, seabirds are among the most threatened groups of birds – many seabird populations have undergone rapid declines over recent decades (Croxall et al. 2012; Paleczny et al. 2015). Our ability to conserve seabirds is often confounded by a lack of fundamental information about their life histories and about their distributions at sea. This is especially true of some seabird genera (e.g., *Pterodroma*), and of many seabirds in tropical and subtropical regions (Bernard et al. 2021) which support particularly diverse communities, and which, in some regions, have received little research effort (Mott and Clarke 2018). There is a particular scarcity of information about the at-sea distributions and ecology of many South Pacific seabird taxa, despite this region representing the largest expanse of ocean on Earth (Croxall et al. 2012; Rodríguez et al. 2019).

Marine habitats used by seabirds often traverse ecological and geopolitical boundaries (Burger and Shaffer 2008; Jodice and Suryan 2010), meaning that birds may face population threats at multiple scales. Many wide-ranging seabird species spend much of their time searching for resources on the high seas – "global commons" that exist in international waters beyond the legal jurisdiction of a single nation. Generally, the high seas are regarded as important for non-breeding migratory seabirds (Harrison et al. 2018), but for many wide-ranging species, particularly those in the order Procellariiformes, the high seas also encompass regions that represent critical foraging habitat during breeding stages (Ramírez et al. 2013; Clay et al. 2017; Ramos et al. 2017). Although a lack of global coordination for managing the high seas makes conservation of these areas acutely challenging, growing awareness of the need for a high seas global governance framework presents opportunities to implement appropriately planned conservation measures (Davies et al. 2021).

One way that we can improve conservation outcomes for seabirds is by studying ecology and at-sea distribution and filling knowledge gaps for those species about which little information exists. This includes identifying seabird distributions, important foraging areas and revealing

species-habitat relationships (i.e., the environmental determinants that drive seabird foraging). It is now feasible to obtain these important data thanks to technological advances in data loggers, which have led to miniaturized devices and transformed what can be learned about the ecology and distributions of even the smallest of seabirds (Nathan et al. 2008; Block et al. 2011; Halpin et al. 2018; Fischer et al. 2021).

Tracking data obtained from breeding seabirds generally comes from devices that obtain positions from orbiting Global Positioning System (GPS) satellites which regularly provide location accuracies of less than 10 m (Hulbert and French 2001) to ~15 m (Forin-Wiart et al. 2015). However, GPS-logging devices small enough to deploy on seabirds can usually only function for short periods of days to weeks. This presents challenges for researchers that need to track seabirds throughout their migrations. One way that researchers solve this problem is by tracking seabirds with light-level 'geolocators' that can function for years on a single small battery. Geolocators are small (i.e. ~ 0.3–3.3 g) archival data loggers that measure and record solar intensity at regular intervals, some with the capability of measuring and archiving other information such as water temperature, wet/dry events and barometric pressure. When geolocators are retrieved, light-level data are downloaded and directed into astronomical equations that estimate spatial locations based on the timing of twilight events (i.e. sunrises and sunsets). Geolocator data can be interpolated into one or two positions per day with latitude estimated by day length, and longitude estimated by the timing of local midday or midnight relative to Greenwich Mean Time and Julian day (Hill 1994). Recently, geolocators – like GPS loggers – have become smaller and able to store more onboard data. These desirable features have led to an increase in their use on seabirds that were previously too small to be burdened with tracking devices (Bridge et al. 2011). Along with these sensor improvements, new and widely used methods have been developed to process and analyse light-level data (e.g. Merkel et al., 2016; Wotherspoon et al., 2016; Rakhimberdiev et al., 2017; Lisovski et al., 2019).

The popularity of geolocators as tools to study seabird movement is growing but the spatial accuracy of geolocators used on seabirds has to-date been tested under limited conditions using three species of albatrosses with narrow latitudinal breadth (Phillips et al. 2004; Shaffer et al. 2005). These studies estimated mean spatial accuracies ± Standard Deviation (SD) of 186 ± 114 km (Phillips et al. 2004) to 202 ± 171 km (Shaffer et al. 2005), which are coarse relative to the accuracy of GPS positions.

For several reasons, light-level geolocation is likely to produce location fixes with coarse spatial accuracy, particularly for estimates of latitude which are generally considered to become less accurate under increasingly "equatorial" solar profiles; that is, either nearer the Equator (spatial variation) or solar equinox (temporal variation) where and when day length changes more shallowly with latitude (Hill 1994; Ekstrom 2004; Lisovski et al. 2020). It has also previously been hypothesized that the performance of geolocators may be species-dependent (Shaffer et al. 2005). (Several other factors that influence geolocator performance are discussed in Chapter 3.) Of particular importance for tropical seabirds or those that overwinter near the equator, latitudinal effects may reduce spatial accuracy of geolocation in tropical seabirds relative to those at higher latitudes. These various factors may limit what inferences can be made about the space use of seabirds. Therefore, improving our knowledge of seabird distributions and ecology requires that we also improve and better assess the accuracy of the methods we use to study their movements.

1.5 Study species and location

1.5.1 Study location

My research was conducted on Phillip Island (29°07'S, 167°57'E), a small (207 ha) uninhabited subtropical island in the Norfolk Island Group, an Australian external territory in the South Pacific Ocean. Phillip Island is managed by Parks Australia and forms part of the Norfolk Island National Park (Director of National Parks 2018). It is a globally important colony for seabirds, supporting

considerable diversity with 13 species breeding there annually, including breeding populations of four gadfly petrel species (Priddel et al. 2010). The island is also important because it supports various endemic and range restricted plants and invertebrates (Coyne 2010).

1.5.2 Study species

In this thesis, I use three seabird species in the genus *Pterodroma* ("gadfly petrels") as exemplars of seabird movement in tropical systems. I investigate the movements and foraging ecology of sympatrically breeding black-winged petrels (*P. nigripennis*), white-necked petrels (*P. cervicalis*) and Kermadec petrels (*P. neglecta*). This is the first study to investigate and document the foraging behaviour and at-sea distributions of these three species. To investigate a novel role for seabirds as vectors of nutrient transfer, my research includes study of the predatory behaviour of a large endemic arthropod, the Phillip Island centipede (*Cormocephalus coynei*).

1.5.3   Gadfly petrels (genus *Pterodroma*)

Gadfly petrels (genus *Pterodroma*) are members of the order Procellariiformes (albatrosses, petrels, shearwaters, and storm-petrels). Gadfly petrels are among the most threatened of all seabirds (Croxall et al. 2012); and of the 35 species, 74% are classified from near threatened to critically endangered by the IUCN Red List (IUCN 2022). For many species in the genus little is known about their biology, foraging behaviour and at-sea distributions (Rodríguez et al. 2019). Gadfly petrels breed colonially and generally nest on isolated oceanic islands (Warham 1996; Brooke 2004). These long-lived, monogamous, and strongly philopatric seabirds exhibit low fecundity and low mortality, raising one altricial offspring per breeding season over an extended nesting period (Warham 1996; Brooke 2004). Gadfly petrels are highly pelagic, undertaking long foraging journeys over vast oceanic areas during both breeding and non-breeding life history stages (Rayner et al. 2012, 2016; Ramírez et al. 2013; Priddel et al. 2014; Ramos et al. 2016, 2017; Clay et al. 2017; Ventura et al. 2020).

The black-winged petrel is the most abundant seabird on Phillip Island (15,000 – 19,000 breeding pairs; Priddel et al., 2010; N. Carlile, unpublished data). The colony also supports the only Australian population of white-necked petrels (20 – 30 breeding pairs (Halpin et al. 2021)); and one of only two Australian populations of Kermadec petrel (56 breeding pairs (Carlile et al. 2021)). Elsewhere, established black-winged petrel breeding colonies occur in New Zealand on the Kermadec Is and Chatham Is; in Australia on Lord Howe I; in New Caledonia, Tonga and in French Polynesia on the Austral Is (Priddel et al. 2010; Miskelly et al. 2019). A white-necked petrel colony occurs on Macauley I (Kermadec Is) (Miskelly et al., 2019). Kermadec petrel colonies occur on the Kermadec Is, Lord Howe I as well as in French Polynesia on the Austral and Tuamotu Is; in Chile on Easter, Juan Fernandez, and San Ambrosio Is.; and in Mauritius on Round I (Priddel et al. 2010; Miskelly et al. 2019).

Phillip Island is also home to several native reptiles including the Lord Howe Island skink (*Oligosoma lichenigera*) and Günther's island gecko (*Christinus guentheri*). A large endemic chilopod, the Phillip Island centipede (*Cormocephalus coynei*) also occurs on the island, along with the endemic Phillip Island cricket (*Nesitathra phillipensis*), and native flightless crickets including *Dictyonemobius pacificus* and *D. lateralis* (Koch 1984; Otte and Rentz 1985; Rentz 1988).

An introduced population of European rabbit (*Oryctolagus cuniculus*) occurred on the island until the 1980s (domestic pigs (*Sus scrofa*) and goats (*Capra hircus*) were removed in the 1850s), destabilizing the ecosystem and causing widespread destruction of native flora and fauna. Since their successful eradication, the island has continued along a path of ecosystem recovery, but it still suffers from substantial topsoil erosion by wind and rain (Coyne 2010).

1.5.4   Phillip Island centipede (*Cormocephalus coynei*)

The Phillip Island centipede is a large endemic chilopod that reaches up to 23.5 cm in length and was only formally described in 1984 (Koch 1984). It is a member of a large genus of centipedes that is globally distributed across tropical and temperate areas (Koch 1984). This species is restricted to Phillip and possibly Nepean Is in the Norfolk Is Group – its presumed extinction on nearby Norfolk I was most likely caused by the introduction of the Polynesian rat (*Rattus exulans*) by Polynesian settlers between 800 and 600 years ago (Coyne et al. 2009). The species' small, area-restricted population likely warrants Vulnerable listing by the International Union for Conservation of Nature (IUCN). The Phillip Island Centipede speciated in the Norfolk Island Group (Koch 1984) and is likely to have historically depended on vertebrate resources in its diet. The centipede population on Phillip Island was heavily suppressed by a variety of introduced species and their associated impacts that led to habitat degradation from the early 1800s to the late 1980s (Coyne 2010).

1.6 Thesis aims

The principal theme of my research was to fill several critical knowledge gaps concerning the movement ecology of subtropical seabirds, and to consider the implications of their movement ecology for conservation, tracking methods and effects on island food webs. I use the three gadfly petrel species as exemplars for seabird movement in the relatively oligotrophic waters of subtropical South Pacific. My goal was to answer far-reaching questions about the distribution, foraging behaviour, and the movement ecology of the wider *Pterodroma* genus, which is globally distributed and contains 34 species.

1.6.1   Structure of thesis

This thesis is structured as a series of self-contained but interconnected papers. While some chapters may seem disparate in subject matter, each chapter is connected by the consequences of seabird movement and the associated implications for conserving seabirds and their habitats. Each

chapter has been written in the format of a scientific journal article and has been published or submitted for publication.

1.6.2 Chapter 2: Foraging habitat and conservation of gadfly petrels

In Chapter 2, my goal was to reveal the foraging behaviour and at-sea distributions of breeding gadfly petrels from Phillip Island using high precision GPS loggers. I used a variety of spatial methods including ensemble species distribution models (ESDMs) to reveal the foraging behaviour of gadfly petrels and determine how different species partition the environment during foraging. I tested whether gadfly petrel foraging habitat can be modelled and generalized to make predictions to new spatial and temporal environmental data using a spatially independent approach. I also discuss the implications of this research for the conservation of gadfly petrels and their foraging habitat.

1.6.3 Chapter 3: an investigation into the accuracy of light-level geolocation

In Chapter 3, my goal was to investigate the implications of tropical seabird movement on the accuracy of a light-level geolocation in seabirds. I used simultaneous deployments of GPS loggers and geolocators to investigate, A) whether the spatial accuracy typically reported in geolocation studies of seabirds is applicable in the context of a large-scale, multi-species study; B) if the accepted spatial accuracies in geolocation remain valid given the development of new and improved geolocation algorithms; C) what additional data (e.g., data logger derived sea-surface temperature) can improve the accuracy of geolocation in seabirds; D) what situational factors improve or worsen spatial accuracy in geolocation, and whether spatial accuracy differs depending on the species tracked; and E) how practitioners can improve their assessments of spatial accuracy in geolocation data.

1.6.4 Chapter 4: seabirds in the diet of an endemic arthropod

In Chapter 4, I explore how seabird movement and subsequent predation form a novel pathway for marine nutrient redistribution to islands through arthropod predation of seabirds; and consider the broad, ecosystem-wide implications of arthropod predation of vertebrates in an isolated system. In so doing, I test the hypotheses that A) vertebrates can form significant components of arthropod diet on islands depauperate of mammalian predators; and B) that large, predatory arthropods can reduce reproductive output in a seabird population. This chapter builds on the existing literature and knowledge of the importance of seabirds as ecosystem engineers and presents novel information about how seabirds contribute to terrestrial island food webs.

1.6.5 Chapter 5: General discussion

My work presented throughout the thesis is discussed in the broader context of seabird ecology and the consequences of seabird movement for conservation, tracking methods, and the preservation of island ecosystems. In this chapter, I also provide recommendations for future research and management based on the results of my research.

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CHAPTER 2

Predicting the foraging habitats of sympatrically breeding gadfly petrels in the South Pacific Ocean

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2.1 Abstract

Gadfly petrels (genus *Pterodroma*) are one of the most threatened groups of birds. They are exceptionally well adapted to forage over enormous areas to maximize chances of encountering prey. Their wide-ranging travel, extensive use of oceanic habitats beyond national jurisdictions (the high seas), and limited information on their at-sea distributions and foraging ecology pose several management challenges.

Here, we examined the foraging distributions and habitat preferences of three gadfly petrels that breed on Phillip Island (Norfolk Islands Group), in the southwest Pacific Ocean, and tested the ability of species distribution models (SDMs) to predict important marine habitats. GPS loggers were deployed in 2018 and 2019 on chick-provisioning black-winged petrels (*P. nigripennis*) and white-necked petrels (*P. cervicalis*) and in 2020 on Kermadec petrels (*P. neglecta*), and hidden Markov models (HMMs) were used to estimate behavioral states across 387 foraging trips. SDMs were built using six algorithms and the predictive performance of models constructed using conventional random cross-validation (CV) was compared to those constructed with spatially independent CV.

All three species demonstrated dual-foraging strategies with short trips closer to the colony and longer, presumably self-provisioning, trips with maximum distances from the colony of almost 3,000 km for black-winged petrels. Foraging areas of each species were distinctly partitioned across the Tasman Sea during long trips, but there was high overlap during short trips. Black-winged and white-necked petrels exhibited area-restricted search foraging behavior throughout their foraging ranges which spanned almost the entire Tasman Sea and into the western Pacific, whereas the foraging range of Kermadec petrels was restricted closer to the colony.

Approximately half of each species' foraging range extended into the high seas. Response curves and variable importance between the two SDM CV approaches were similar, suggesting that model fitting was robust to the CV approach. However, evaluation using spatially independent CV indicated that generalizability of ensemble SDMs to new data ranged from poor to fair for all three species. This suggests that the maximal-area foraging strategy of gadfly petrels (whereby they search opportunistically for resources across expansive oceanic habitats) results in lack of association with environmental features making predicting important habitats extremely challenging.

2.2 Introduction

Seabirds are top predators that play important functional roles in marine and terrestrial ecosystems (Stapp et al., 1999; Sánchez-Piñero and Polis, 2000; Smith et al., 2011; Graham et al., 2018) and are widely recognized as valuable bioindicators of changes in the state of ocean ecosystems (Diamond and Devlin, 2003; Boyd et al., 2006; Parsons et al., 2008). Despite their ecological importance, seabirds are among the most threatened groups of birds with many populations having undergone rapid declines over recent decades (Croxall et al., 2012; Paleczny et al., 2015). Seabird conservation is often confounded by a lack of basic information about life histories and distributions at sea. This is especially true of seabirds in the tropics and subtropics (Bernard et al., 2021), regions which support diverse seabird communities, and which have received little research effort (Mott and Clarke, 2018). There is a particular lack of information about at-sea distributions for many South Pacific seabird taxa, despite this region representing the largest expanse of ocean on Earth (Croxall et al., 2012; Rodríguez et al., 2019). Such fundamental ecological knowledge is key to achieving effective conservation and enables researchers and policy makers to more accurately identify current and future threats (Burger and Shaffer, 2008; Lescroël et al., 2016; Bernard et al., 2021).

While the lack of information on many seabirds persists, anthropogenic pressures continue to degrade marine habitats and transform the integrity and stability of marine ecosystems, including the extent, availability, and predictability of prey resources for marine predators (Halpern et al., 2008; Hoegh-Guldberg and Bruno, 2010; McCauley et al., 2015). Obtaining information about the foraging distributions of wide-ranging seabirds has historically been logistically and financially challenging and biased towards shipboard surveys in coastal or nearshore habitats. Furthermore, studies using tracking technologies have been restricted by device sizes that could be deployed only on larger-bodied species (Burger and Shaffer, 2008). However, recent advancement in electronic tracking technology has led to miniaturized devices and transformed what can be learned about the ecology and distributions of even the smallest of seabirds (Nathan et al., 2008; Block et al., 2011; Halpin et al., 2018; Fischer et al., 2021). Furthermore, the advancement of the biologging field presents new opportunities to investigate the importance of seabird habitat on the high seas (i.e., marine areas extending beyond the 200 nautical mile limit of countries' Exclusive Economic Zones) (Beal et al. 2021, Davies et al., 2021). Although the high seas are classically considered important for migratory seabirds (Harrison et al., 2018), for many wide-ranging species, particularly those in the order Procellariiformes, the high seas also represent critical foraging habitat during breeding stages (Ramírez et al., 2013; Clay et al., 2017; Ramos et al., 2017). Although a lack of global coordination for managing the high seas makes conservation challenging, growing awareness of the need for a global governance framework presents opportunities to implement appropriately planned conservation measures in the near future (Davies et al., 2021).

Procellariform seabirds in the genus *Pterodroma* ("gadfly petrels") are among the most threatened of all seabirds (Croxall et al., 2012). Yet, there is often a lack of basic information about their biology, foraging behavior and at sea distributions (Rodríguez et al., 2019). Gadfly petrels are colonial-breeding species that generally nest on isolated oceanic islands (Warham, 1996; Brooke, 2004). These long-lived, monogamous, and strongly philopatric seabirds exhibit low fecundity,

raising one altricial offspring per breeding season over an extended nesting period (Warham, 1996; Brooke, 2004). Gadfly petrels are highly pelagic, undertaking long foraging journeys over vast oceanic areas during both reproductive and migratory life stages (Rayner et al., 2012, 2016; Ramírez et al., 2013; Priddel et al., 2014; Ramos et al., 2016, 2017; Clay et al., 2017; Ventura et al., 2020). Among seabirds, gadfly petrels have especially high aspect ratio relative to wing loading, which makes them especially well-adapted for optimal use of wind conditions, enabling fast and efficient flight with low energetic costs (Spear and Ainley, 1997; Ventura et al., 2020). The few existing studies on gadfly petrels that use high resolution GPS tracking tend to demonstrate that these species often do not have distinct preferences for, or rely completely on, one or two static or dynamic oceanographic features when foraging (Clay et al., 2017) and make some of the longest foraging trips in the animal kingdom (Clay et al., 2019; Taylor et al., 2020; Ventura et al., 2020). While weaker foraging preferences for single or multiple oceanographic features may still be an important characteristic of gadfly petrel foraging, many gadfly petrel species still forage widely and far beyond oceanographic boundaries. Through optimal use of ocean basin-scale prevailing wind patterns, gadfly petrels appear to adopt a maximal-area foraging strategy to cover extremely large areas thereby increasing their chances of encountering food resources (Adams and Flora, 2010; Ventura et al., 2020). For example, Ventura et al. (2020) demonstrated that Desertas petrels (*P. deserta*) do not concentrate foraging in highly productive regions with predictable resources, and Clay et al. (2017) established that Murphy's petrels (*P. ultima*) do not have clear preferences for oceanographic or topographic features.

Here, we present the first Global Positioning System (GPS) tracking datasets for three species of gadfly petrel: black-winged petrel (*P. nigripennis;* IUCN status: Least Concern), white-necked petrel (*P. cervicalis*; IUCN status: Vulnerable) and Kermadec petrel (*P. neglecta*; IUCN status: Least Concern). We sought to first identify the hitherto unknown foraging behavior and at-sea distributions of these species using GPS loggers over multiple years at a single colony in the

South Pacific Ocean. Second, we constructed ensemble species distribution models (SDMs) with three main goals: 1) to determine how these three sympatric species partition the environment when foraging; 2) to test if foraging habitat of the gadfly petrels in the present study could be generalized to new data using a spatially independent model evaluation approach; and 3) to consider how important foraging areas can be identified in the event that SDMs poorly predict foraging habitat in chick-provisioning gadfly petrels.

2.3 Materials and Methods

2.3.1 Study site and species

Fieldwork was conducted on Phillip Island (29°07'S, 167°57'E, Figure 1). Phillip Island is a small (207 ha) and uninhabited subtropical island in the Norfolk Island Group, an Australian external territory in the South Pacific Ocean. Phillip Island is a globally important colony for seabirds and supports considerable diversity with 13 species breeding there annually. The island is particularly important because it supports breeding populations of four gadfly petrel species. The most abundant of the four species is the black-winged petrel (15,000 – 19,000 breeding pairs; Priddel et al., 2010; N. Carlile, unpublished data). The colony also supports the only Australian population of white-necked petrels (20 – 30 breeding pairs (Halpin et al., 2021)); one of only two Australian populations of Kermadec petrel (56 breeding pairs (Carlile et al., 2021ab)); and a remnant population of the formerly abundant providence petrel (*P. solandri;* 10 – 100 breeding pairs (Carlile et al., 2021ba)). Elsewhere, established black-winged petrel breeding colonies occur in New Zealand on the Kermadec Islands, Manawatäwhi/Three Kings (Great King, South West), Motuopao, Motupia, Simmonds, Motukokako (Piercy), East (Whangaokeno), Portland and Chatham Islands and on an islet off Cape Brett; in Australia on Lord Howe Island; in New Caledonia, Tonga and in French Polynesia on the Austral Islands (Gill et al., 2010; Priddel et al., 2010; Miskelly et al., 2019). White-necked petrel colonies occur on the Macauley Island (Kermadec Islands) (Miskelly et al.,

2019); and Kermadec petrel colonies occur on the Kermadec Islands, Lord Howe Island. as well as in French Polynesia on the Austral Islands and Tuamotu Islands; in Chile on Easter Island, Juan Fernandez Island and San Ambrosio Island.; and in Mauritius on Round Island (Priddel et al., 2010; Miskelly et al., 2019).
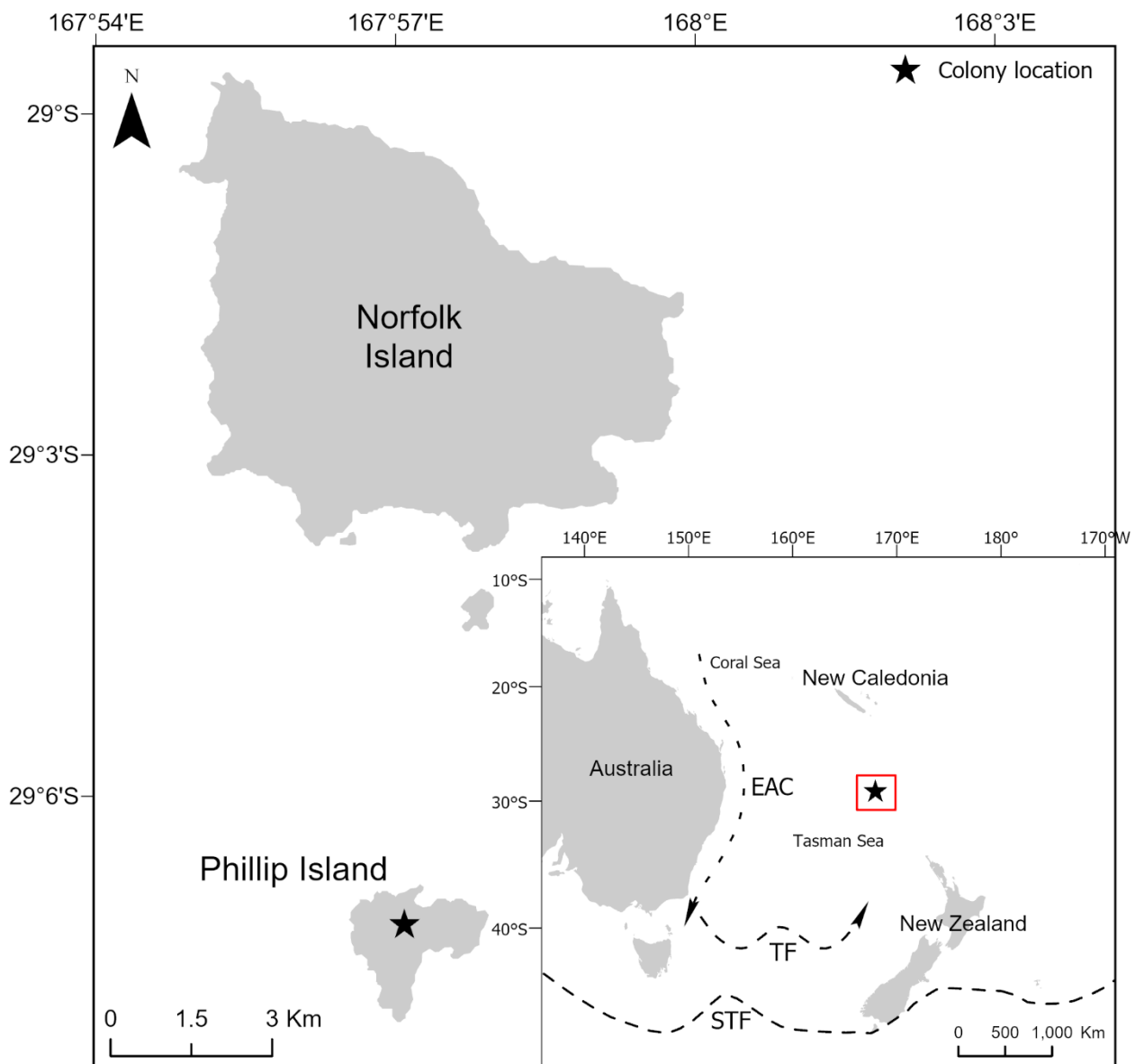
Figure 1. The location of the Norfolk Island Group in relation to Australia, New Zealand and New Caledonia. Included are the approximate locations and direction of flow of the East Australian Current (EAC) and the Tasman Front (TF) and Subtropical Front (STF).

All gadfly petrels produce a maximum of one offspring per year per pair. Adult black-winged petrels weigh on average 171 g ($n = 48$; this study) and nest predominantly in burrows, but occasionally deep crevices. Breeding occurs on Phillip Island from October to May with chicks hatching approximately in late January and fledging occurring in approximately May (Priddel et al. 2010). Little is known about white-necked petrel breeding biology, however, on Phillip Island adults weigh on average 464 g ($n = 27$; this study) and generally nest beneath stands of mature white oak (*Lagunaria patersonia*) among boulders, in rocky crevices, artificial cavities, and occasionally on the ground where dense vegetation cover is present. Breeding occurs on Phillip Island from approximately November to May or June (Priddel et al. 2010). White-necked petrel chicks generally hatch in January and February and fledge approximately in May and June. Adult Kermadec petrels weigh on average 444 g ($n = 52$; this study) and nest on the ground in sheltered areas between roots of mature white oak trees, or in dense thickets of introduced African olive (*Olea europea*). More protracted breeding occurs in Kermadec petrels with breeding occurring on Phillip Island from September to May. Eggs are laid from September with a peak in November. Egg laying then tapers off with fewer pairs producing eggs in January through to May. The population tracked in the present study is the summer-breeding group which breeds approximately from September with chick fledging occurring from March. Black-winged and white-necked petrels are strongly faithful to their nest sites, returning to the same nest site each year, but Kermadec petrels often use different nests within the same general area each year.

2.3.2 Seabird capture and sampling

Capture and tracking of gadfly petrels occurred exclusively during the chick-provisioning period for black-winged and white-necked petrels from February to April in 2018 and 2019 and in January 2020 for Kermadec petrels. All tracked birds were provisioning chicks at a similar stage of chick development. Adult birds were captured by hand in their nests during the early to middle chick-provisioning periods from February – April in 2018 and 2019 (black-winged and white-necked

petrels) and in January 2020 (summer-breeding Kermadec petrels). Black-winged petrels, were captured by hand at their nests both during the day and at night because they exhibit cathemeral nest site attendance. Due to the unpredictable timing of black-winged petrel nest attendance, we fitted one-way trapdoors to their nest entrances and checked for returning adults approximately every three to four hours while traps were installed. White-necked petrels, which display strictly nocturnal colony attendance, were captured by hand at their nest sites at night. Kermadec petrels, which display crepuscular colony attendance, were captured by hand at nests from early dusk to night.

All three study species are sexually monomorphic. To sex birds we collected $1 - 2$ µL of blood from the brachial vein using a sterile 26-gauge needle and whole blood was then placed onto FTA classic cards (Whatman International Ltd., Maidstone, UK). Sex of individuals was determined using PCR reactions following Griffiths et al. (1998) by DNA Solutions (Wantirna, Victoria, Australia). Prior to attachment of GPS loggers, birds were weighed using Pesola scales (± 0.3%, Pesola Präzisionswaagen AG, Switzerland) and fitted with a metal leg band supplied by the Australian Bird and Bat Banding Scheme.

We fitted petrels with custom Pathtrack Nanofix© archival GPS loggers (Pathtrack Ltd., Otley, United Kingdom) programmed to record position data every ten minutes and attached them to the two central rectrices using Tesa© tape (4651, Tesa Tape Inc., Charlotte, NC, USA). We fitted GPS loggers to 27 black-winged petrels in 2018 and 25 in 2019. In 2018, one GPS logger failed to record data, one was lost from the bird, and one was not retrieved before our departure from the colony. In 2019, one GPS logger was not retrieved before our departure from the colony. In 2018 we fitted 13 GPS loggers to white-necked petrels and 16 in 2019. One GPS logger in each year was not retrieved before our departure from the colony. In 2020 we deployed 9 GPS loggers on Kermadec petrels. All GPS loggers were retrieved. GPS loggers weighed an average of 3.23 ± 0.07 (g ± SD; range: 3.1–3.38 g; $n = 34$). Average percentages of body mass for GPS loggers were

1.88% for black-winged petrels (range: 1.22–2.32%; *n* = 48), 0.7% for white-necked petrels (range: 0.59–0.88%; n = 27), and 0.72% for Kermadec petrels (range: 0.64–0.88%; *n* = 9), lower than the 3% threshold that is thought to negatively affect procellariform seabirds (Phillips et al., 2003). The average duration (days ± sd) between GPS logger attachment and removal on individuals was 14.6 ± 9.2, 27.9 ± 11 and 12.1 ± 4.9, respectively, for black-winged, white-necked and Kermadec petrels.

2.4 Data processing and analysis

2.4.1 GPS Tracking data

All data were processed in the R programming language, version 4.1.2 (R Core Team, 2021), and spatial measurements were calculated on the World Geodetic System (WGS 1984) ellipsoid. Maps were produced in ArcGIS Pro (version 2.4.0; ESRI Inc., CA, United States) and data were projected in the Lambert Azimuthal Equal Area projection, centered on the breeding colony. GPS data were filtered to remove erroneous locations where successive relocations would require flight velocities exceeding 27.8 m.s^{-1} (100 km.h^{-1}) (Lascelles et al., 2016). GPS tracks were linearly interpolated using the package adehabitatLT (version 0.3.25; Calenge, 2006) by resampling all locations to an equal 10 min interval. We gap-filled GPS tracks except when periods of more than 1 hour occurred between location fixes.

2.4.2 At-sea distribution and behavior

To determine foraging characteristics, we split tracking data into individual foraging trips originating from and returning to the colony using the 'tripSplit' function in the package, track2KBA (version 1.0.1; Beal et al., 2021). For each complete foraging trip, we used the 'tripSummary' function in track2KBA to calculate the duration (days) from departure to return to the colony and the maximum distance from the colony (foraging range, km). We tested for differences in foraging trip duration and maximum distance from the colony between species in complete foraging trips using linear mixed effects models in the lme4 package (Bates et al. 2015)

and a post-hoc Tukey's HSD test for multiple comparisons. To account for repeated trips made by the same individual we included individual identity as a random effect. We considered that sex-related differences in foraging behaviors would be highly unlikely because birds were tracked exclusively during chick-provisioning. Gadfly petrels share parental duties equally, with sex-related differences in foraging absent in chick-provisioning gadfly petrels (Pinet et al., 2012; Clay et al., 2017). Nonetheless, we tested for intraspecific sex-related differences in maximum foraging range and trip duration using linear mixed effects models using the package lme4 with individual identities as random effects to account for repeated trips made by the same individual.

To identify important at-sea areas for each species, we first calculated the spatial scale of area-restricted search (ARS) using the function 'findScale' in the package track2KBA (Lascelles et al. 2016; Beal et al. 2021) for black-winged petrels (18 km), white-necked petrels (17 km) and Kermadec petrels (18 km). We then computed 50% kernel utilization distributions using the R package adehabitatHR (Calenge, 2006) and used the scale of each species' ARS as the kernel smoothing parameter (h). Following previous studies, we define the 50% utilization distribution as the 'core' foraging area where birds spent 50% of their time (Ford and Krumme, 1979; Soanes et al., 2013; Lascelles et al., 2016). We estimated the representativeness of each species' core foraging area as a function of sample size to ensure that data were sufficiently representative of the foraging distributions of the colony-level populations. To do this we used the bootstrapping approach described in Lascelles et al. (2016) using the function 'repAssess' in the track2KBA package (Beal et al., 2021). We classified foraging trips according to whether they were short or long. To do this, we first qualitatively determined the distance classifications for each species by examining histograms of the frequency distribution of maximum trip distances (see Results, Figure 2). We then classified short trips as those with a maximum distance from the colony of < 1000 km for black-winged; < 500 km for white-necked petrels and < 200 km for Kermadec petrels. We then produced

a map of the short and long trips to demonstrate bimodal foraging strategies exhibited by each species.

To distinguish the behavioral states of individuals during their foraging trips, we used hidden Markov models (HMMs). For each species, we fitted a three-state HMM to the interpolated GPS tracks using the momentuHMM package (version 1.5.4; McClintock and Michelot, 2018). Following Clay et al. (2020), to determine choice of initial values for step length and turning angle distributions, we selected these values randomly 100 times from within a range of biologically plausible values, then determined the most appropriate values as those that were closest to the most frequent estimation. We then estimated three behavioral states in the GPS tracks using two input variables: step lengths and turning angles. We considered directed flight (i.e., travel) to be associated with high flight speeds and shallow turning angles, area-restricted search (i.e., foraging) to be associated with moderate flight speeds and moderate to wide turning angles; and rest associated with low speeds and shallow to moderate turning angles. We used a gamma distribution for step lengths and a von Mises distribution for turning angles. We used the Viterbi algorithm in the package momentuHMM to estimate the most likely sequence of behavioral states from fitted models (Rabiner, 1989). Performance of the HMM behavioral state assignment was assessed by examining histograms of step lengths and turning angles for each species (Supplementary Figures 1 – 3), and each track was then visually assessed to ensure that state-space assignments were plausible. For each trip we calculated the percentage of time (% ± SD) that birds spent in each behavioral state and averaged the proportion across all trips to understand activity budgets. To test for differences between species in the proportion of time spent in ARS, we performed a one-way ANOVA test and a post-hoc Tukey's HSD test for multiple comparisons. For each trip we also calculated the average duration (hours ± SD) that birds spent in each behavioral state before switching to another state during a foraging trip. To determine whether nocturnal foraging might be

an important feature of the species we tracked, we tested for differences in the proportion of time that each species spent foraging in daylight versus darkness using Student's *t*-tests.

Lastly, to evaluate the extent of foraging across the species' ranges we mapped the occurrence of locations inferred to be foraging (i.e., area-restricted search) by the HMMs on a 50 x 50 km grid cell size for each year of tracking and, for black-winged and white-necked petrels, which were tracked in more than one year, we overlaid gridded rasters to produce maps showing repeated grid cell use between years.

2.4.3 Species distribution modelling

We used SDMs to both characterize important foraging habitats for gadfly petrels and to assess the generalizability of models between spatial regions. We modeled the foraging locations identified by the HMMs against a suite of environmental predictors (Table 1). Environmental predictors were selected based on ecological knowledge of the drivers of subtropical pelagic seabirds' foraging activity (Ballance et al., 2006; Hyrenbach et al., 2006; Ramos et al., 2015; Clay et al., 2017; Miller et al., 2018; Waugh et al., 2018). We used three static environmental predictors and seven dynamic environmental predictors in our models (Table 1). Static predictors were: 1) the bathymetric slope, represented in degrees, and 2) distance (km) to seamounts and knolls as indicative of shelf-breaks and bathymetric features that could represent productive areas of upwelling; and 3) transit distance (km) from the colony as a proxy for the importance of accessibility to foraging habitat given that all birds were centrally-placed (i.e., had an intrinsic requirement to regularly return to the colony to provision nestlings). The six dynamic oceanographic variables were: 1) sea surface temperature (°C), and 2) sea surface temperature fronts measured by calculating the standard deviation of the sea surface temperature (°C) within a 10 km buffer of the original 1 km resolution of the sea surface temperature grid as an indicator of frontal regions; 3) sea level anomaly (m) as an indicator of mesoscale eddies and ridges; 4) wind speed ($m.s^{-1}$) as an indicator of optimal transit conditions for

gadfly petrels (i.e., Ventura et al., 2020); 5) chlorophyll *a* concentration (mg.m^{-3}) as a proxy for ocean productivity; 6) the finite-size Lyapunov exponent (FSLE; days^{-1}) to test the preference of birds for foraging in sub-mesoscale transport fronts; and 7) the depth of the thermocline layer (m). FSLE is based on Lagrangian reanalysis of satellite altimetry-derived surface currents (d'Ovidio et al., 2004; Cotté et al., 2015). Further information on the original spatial resolution and sources of environmental variables is provided in Table 1. Predictor variable rasters were scaled to a 1 × 1 km grid cell resolution using bilinear interpolation and were projected in the Lambert Azimuthal Equal Area projection centered on the breeding colony. Predictor variables were standardized using the 'scale' function in the raster package (Hijmans and van Etten, 2021) to improve the spread of the data. We applied a variance inflation factor test to ensure that predictor variables were not collinear and found no collinearity problems among the ten predictor variables.

Variable	Unit	Native resolution	Description and data source
Chlorophyll *a* (chl-*a*)	mg/m^{-3}	4 × 4 km	Monthly mean chlorophyll *a* concentration. Chlorophyll-a, Aqua MODIS, NPP, L3SMI, Global, 2003-present. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chlamday.html)
Distance to colony	km	1 × 1 km	Static. Grid cell transit distance to the colony. Calculated in the present study. Accounts for transit distances around land.
Distance to seamount	km	NA	Static. Grid cell transit distance to the nearest seamount. Calculated in the present study. Accounts for transit distances around land. Global distribution of seamounts and knolls inferred, using a searching algorithm, from bathymetric data at 30 arc-sec resolution. (https://data.unep-wcmc.org/datasets/41)
Finite-sized Lyapunov exponent (FSLE)	day^{-1}	$^1/_{25}$ × $^1/_{25}$ °	Monthly mean backward-in-time FSLE and Orientations of associated eigenvectors. (https://www.aviso.altimetry.fr/en/data/products/value-added-products/fsle-finite-size-lyapunov-exponents.html)
Sea surface temperature front	°C	0.01 × 0.01 °	Monthly mean sea surface temperature front. Calculated in the present study as the standard deviation over a 3 x 3 grid of the 1 km resolution sea surface temperature data using the Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, Global, 2002-present. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41mday.html)
Sea surface temperature	°C	0.01 × 0.01 °	Monthly mean sea surface temperature. Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, Global, 2002-present. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41mday.html)
Sea level anomaly (SLA)	m	0.25 × 0.25 °	Monthly mean sea level anomaly. National Oceanic and Atmospheric Administration (NOAA) CoastWatch, Sea Surface Height Anomalies from Altimetry, Global, 2017-Present. (https://coastwatch.pfeg.noaa.gov/erddap/griddap/nesdisSSH1day.html)
Bathymetric slope	degrees	15 arc seconds	Static. Grid cell angle of depth slope. Calculated in the present study using the GEBCO Compilation Group 2021 gridded bathymetry data set (https://www.gebco.net/data_and_products/gridded_bathymetry_data/)
Wind speed	m/s^{-1}	0.25 × 0.25 °	Monthly mean horizontal speed of wind at 10 meters above sea level. ERA5 European Centre for Medium-Range Weather Forecasts (ECMWF) global reanalysis for the global climate and weather (https://cds.climate.copernicus.eu/cdsapp#!/dataset/10.24381/cds.f17050d7?tab=overview)
Thermocline depth	m	0.083° × 0.083°	Monthly mean ocean mixed layer thickness (GLOBAL_MULTIYEAR_PHY_001_030). Copernicus Marine Service (https://doi.org/10.48670/moi-00021)

Table 1. Static and dynamic oceanographic variables, resolutions, measurement units and sources used in models to predict the foraging habitat of gadfly petrels.

We used a multi-model ensemble approach to test whether the environmental features could predict gadfly petrel foraging habitat. Using the biomod2 package (version 3.5.1; Thuiller et al., 2009, 2021) we fitted six algorithm types: Artificial Neural Networks (ANN), Classification Tree Analysis (CTA), Generalized Additive Models (GAM), Generalized Boosted Models (GBM), Multiple Adaptive Regression Splines (MARS) and Random Forests (RF). We used the default model parameters in biomod2 for all models except GBM where the bag fraction was set to 0.75 and maximum number of trees was set to 3000 (e.g., Elith et al., 2008). GAMs were specified to use Restricted Maximum Likelihood (REML); and the number of learning trees in Random Forests was set to 1000. We modeled the GPS locations that were inferred by HMMs to be foraging behavior as the response variable. For each foraging location we randomly sampled a single matched pseudo-absence because a ratio of 1:1 presence:pseudo-absence is most suited to the learning algorithms that we used to model the characteristics of foraging habitat (Barbet-Massin et al., 2012). Pseudo-absences were generated within foraging extents, which we separately defined for each species, by computing a minimum convex polygon around all available tracking locations.

To evaluate the ability of the models to predict the probability of foraging on new data, we compared two approaches, 1) conventional random *K*-fold cross-validation (CV) with 80% of each species' data for model fitting and the remaining 20% for testing (Elith et al., 2008) and 2) spatially independent *K*-fold CV (Roberts et al., 2017) using the blockCV package (Valavi et al., 2019). The latter approach to assessing model predictive performance is more robust because it ensures spatial independence of testing and training data thereby accounting for spatial structure in cross-validation data. Conventional random selection of training and testing folds that are not spatially independent commonly leads to underestimated error in spatial predictions and overestimated model performance and predictive power (Telford and Birks, 2009; Roberts et al., 2017; Hao et al., 2019; Valavi et al., 2019). Five folds were specified for both approaches. Spatially-independent CV used a spatial blocking size of 800 km for black-winged and white-necked petrels but had to be reduced to

250 km for Kermadec petrels due to their much smaller range size. Spatial blocks were randomly assigned using 200 iterations to find evenly dispersed folds and were generated based on the extent of each species' foraging range. Block size was chosen as the approximate range over which observations become spatially independent and was determined by constructing empirical variograms using the function 'spatialAutoRange' in the package blockCV. Predictive performance of both approaches was then evaluated using the True Skill Statistic (TSS) and Area Under the Receiver Operating Characteristic curve (AUC_{ROC}). AUC_{ROC} is a widely used measure of a model's predictive performance and its ability to differentiate presence and absence locations (Lobo et al., 2008). AUC_{ROC} values and associated performance evaluations range from 0 to 1, with excellent $AUC_{ROC:} > 0.90$; good $AUC_{ROC}: > 0.80 \leq 0.90$; fair $AUC_{ROC}: > 0.70 \leq 0.80$; poor $AUC_{ROC}: > 0.60 \leq 0.70$; very poor $AUC_{ROC}: > 0.50 \leq 0.60$; and $AUC_{ROC}: \leq 0.50$ indicating predictive performance that is no better than random (Hosmer et al., 2013). We averaged the respective TSS and AUC_{ROC} values across model folds for each algorithm type and model. Due to the robust spatial independence of the blocked cross-validation approach we took the model evaluation metrics of this method as superior to those of conventional *K*-fold random CV models. We therefore interpreted the AUC_{ROC} values of the spatially blocked models as the more statistically credible approximation of model generalizability to new data for gadfly petrels.

Total consensus ensemble models were constructed based on all models for each CV method (so that fair comparisons between the performance of formal and ensemble models could be made). The conventional CV ensemble was built with an evaluation metric threshold applied such that models with $AUC_{ROC} < 0.8$ were excluded, but no evaluation metric threshold was applied to the spatial blocking ensemble due to the inherently low AUC_{ROC} values. Species-specific ensemble model response curves were constructed from the spatially blocked models and calculated as the median response across 10 replicate model runs within the biomod2 package using the algorithm-

independent evaluation strip method following Elith et al. (2005), which facilitates direct comparison of predicted responses from different statistical approaches on the same data.

We used multivariate environmental similarity surfaces (MESS; Elith et al., 2010) to check that differences in behavior of Kermadec petrels were not likely to have been caused by divergent environmental conditions in the year that they were tracked (January 2020) versus the years that black-winged and white-necked petrels were simultaneously tracked (February to April in 2018 and 2019). We computed MESS grids for each dynamic predictor for each month in which black-winged and white-necked petrels were tracked and used the overall MESS grid to assess the percentage of cells with negative values (cells with negative values represent those with conditions outside of the range present in the reference time period).

2.5 Results

Over three breeding seasons, we obtained 387 complete foraging trips from 80 individuals of three species of sympatrically breeding gadfly petrels (Table 2). Core foraging areas (i.e., 50% utilization distributions) used by the sampled individuals were estimated to be highly representative of the core foraging areas of the respective colony-level populations for black-winged petrels (87.5%) and white-necked petrels (93.5%), but representativeness was lower for Kermadec petrels (68.5%) due to the lower sample size.

2.5.1 Foraging characteristics

We found no sex-related differences in maximum foraging ranges and durations of trips made by black-winged petrels (foraging range: $F_{122} = 0.738$, $p = 0.541$; trip duration: $F_{122} = 0.613$, $p = 0.462$), white-necked petrels (foraging range: $F_{208} = 0.533$, $p = 0.595$; trip duration: $F_{208} = 0.198$, $p = 0.843$) and Kermadec petrels (foraging range: $F_{6.1} = -0.773$, $p = 0.469$; trip duration: $F_{5.8} = -0.59$, $p = 0.577$). Therefore, we pooled the data from both sexes within each species. When accounting

for random effects of individuals making repeated trips, maximum foraging ranges differed between black-winged and white-necked petrels and black-winged and Kermadec petrels (Tukey's post-hoc test: $p < 0.001$ for both relationships; Table 2), but not between white-necked and Kermadec petrels (Tukey's post-hoc test: $p = 0.098$). Similarly, after accounting for random effects of individuals, the duration of foraging trips was different between black-winged and white-necked petrels (Tukey's post-hoc test: $p = 0.0105$) and between black-winged and Kermadec petrels (Tukey's post-hoc test: $p < 0.001$), but not between white-necked and Kermadec petrels (Tukey's post-hoc test: $p = 0.0679$). Tracking data also indicated that all three species exhibited bimodal foraging strategies, alternating between short and long foraging trips (Figures 2, 3).

Behavioral state space modeling revealed that although all three species demonstrated area-restricted search foraging behavior throughout the entire range of their breeding distributions, they tended to concentrate foraging activity nearer (< 500 km) the colony (Figures 4-6). On average all species spent more than half of their time traveling, and a relatively small proportion of their time resting during foraging trips (Table 3). We found significant between-species differences in the proportion of time spent in ARS behavior ($F_2 = 10.98$, $p = < 0.001$). A Tukey post-hoc test revealed that black-winged petrels spent proportionally less time in ARS than white-necked ($p < 0.001$, 95% C.I. = [0.02 – 0.09]) and Kermadec petrels ($p < 0.001$, 95% C.I. = [0.04 – 0.14]), but there was no difference between white-necked and Kermadec petrels ($p = 0.2$, 95% C.I. = [-0.08 – 0.01]).

We found no significant difference in the proportion of time spent foraging during daylight and darkness in black-winged (daylight: 30.4 ± 14.2, darkness: 28.6 ± 17.1; t-test: $t_{(258)} = -0.986$, $p = 0.325$) and Kermadec petrels (daylight: 37.9 ± 17.7, darkness: 37.8 ± 20.8; t-test: $t_{(102)} = -0.013$, $p = 0.989$), but found that white-necked petrels spent proportionally more time foraging during daylight (daylight: 40.4 ± 15.4, darkness: 28.5 ± 21.2; t-test: $t_{(400)} = -6.72$, $p < 0.001$).
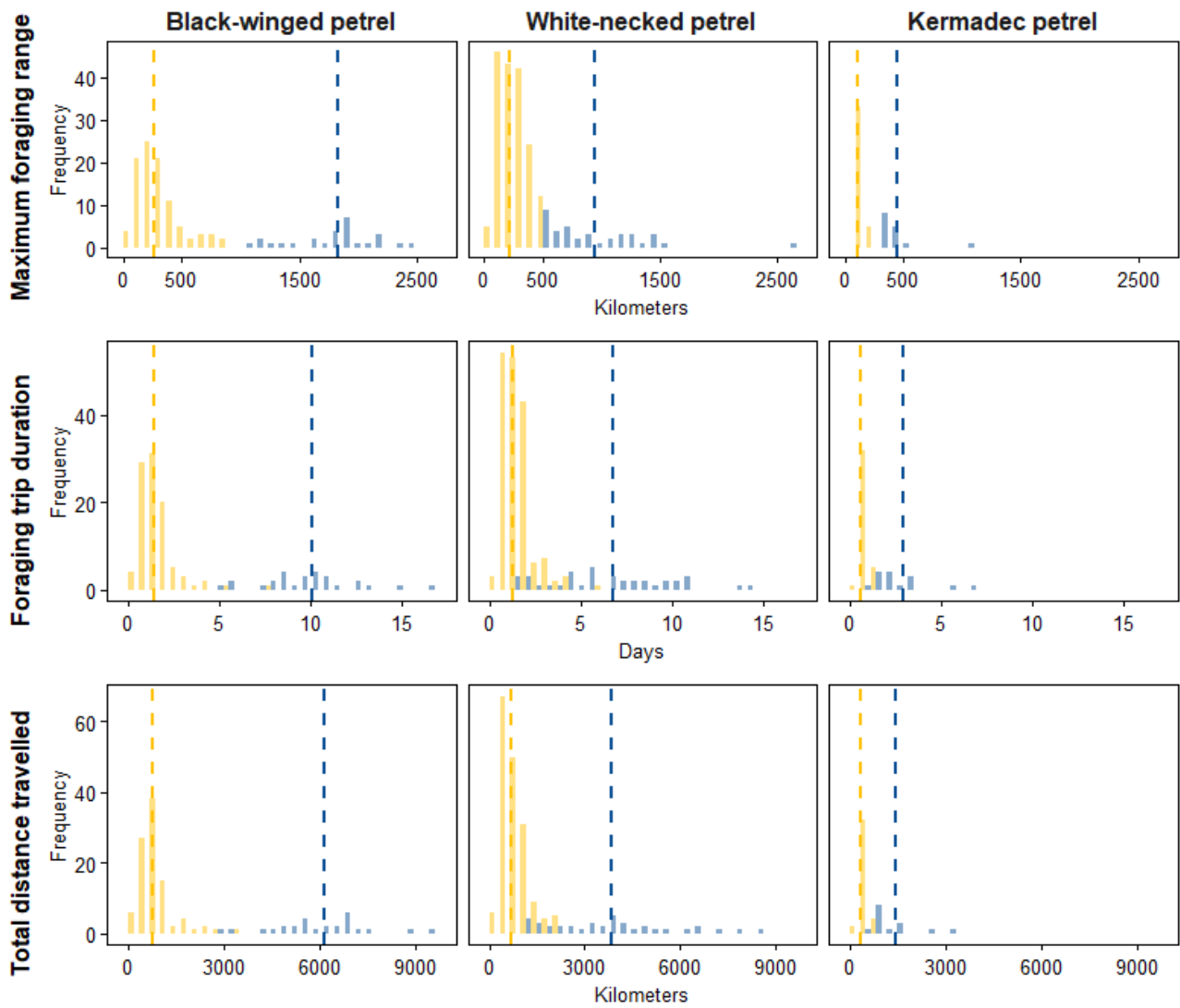
Figure 2. Frequency distributions of maximum foraging range (km; upper row), duration of foraging trips (days; center row) and total distance traveled (km; lower row) for short trips (yellow) and long trips (blue) for black-winged petrels (left column), white-necked petrels (center column) and Kermadec petrels (right column). The dashed lines represent the mean of the frequency for short trips (yellow) and long trips (blue).
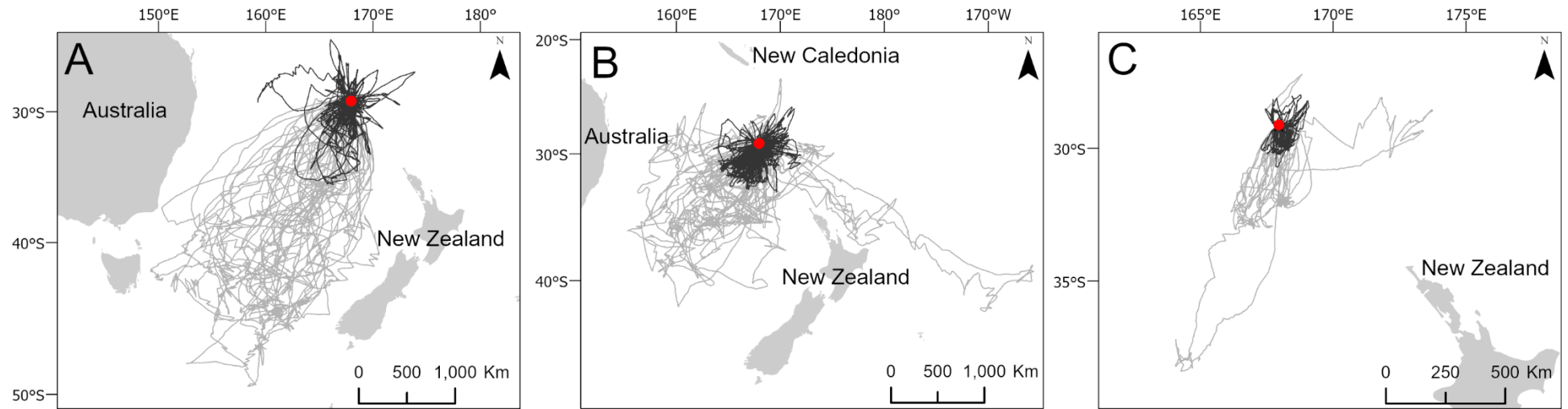
Figure 3. Maps demonstrating the short (black) and long (grey) foraging trips of black-winged petrel (A), white-necked petrel (B) and Kermadec petrel (C) bimodal foraging strategies. The colony location is indicated by a red circle. The number of trips in each category are detailed in Table 2.

Species	No. of individuals (males/females)	No. of complete trips (short/long)	Sample rep. (%)	Trip duration (days) Mean (range)		Foraging range (km) Mean (range)		Cumulative trip distance (km) Mean (range)	
				Short	Long	Short	Long	Short	Long
Black-winged petrel *Pterodroma nigripennis*	44 (27/17)	124 (87/37)	87.5	1.4 (0.1 – 7.6)	10.1 (5.2 – 16.9)	263 (19 – 846)	1,824 (1,131 – 2,487)	736 (29 – 3,160)	6,131 (3,004 – 9,642)
White-necked petrel *Pterodroma cervicalis*	27 (5/22)	210 (172/38)	93.5	1.3 (0.1 – 5.6)	6.8 (1.9 – 14.7)	222 (5 – 480)	943 (520 – 2,680)	681 (38 – 2,141)	3,850 (1,181 – 8,565)
Kermadec petrel *Pterodroma neglecta*	9 (5/4)	53 (37/16)	68.5	0.6 (0.2 – 1.2)	2.9 (1.2 – 6.9)	109 (57 – 229)	445 (331 – 1,086)	320 (125 – 583)	1,432 (812 – 3,298)

Table 2. Summary of the GPS tracking dataset for birds that returned data (i.e., tracking device was recovered and remained functional for at least one trip). Data indicate foraging trip characteristics for complete trips and sample representativeness of sympatrically breeding gadfly petrels from Phillip Island (Norfolk Islands Group) during chick-provisioning in 2018 & 2019 (black-winged and white-necked petrels) and 2020 (Kermadec petrels).

| Species | Behavioral bout duration (hours/trip) (Mean ± SD) | | | | | | Percentage of time per trip (Mean ± SD) | | | | | |
| | Travel | | ARS | | Rest | | Travel | | ARS | | Rest | |
	Short	Long	Short	Long	Short	Long	Short	Long	Short	Long	Short	Long
Black-winged petrel *Pterodroma nigripennis*	17.9 ± 9.3	20.0 ± 6.6	9.2 ± 4.5	9.6 ± 4.8	9.5 ± 5.6	9.1 ± 2.9	60.7 ± 18.8	69.7 ± 7.7	32.2 ± 14	25.3 ± 6.7	7.1 ± 8.3	5.0 ± 3.1
White-necked petrel *Pterodroma cervicalis*	17.9 ± 9.3	20.0 ± 6.6	9.2 ± 4.5	9.6 ± 4.8	9.5 ± 5.6	9.1 ± 2.9	52.7 ± 16.7	55.1 ± 13.1	35.4 ± 15.9	34 ± 9.1	11.9 ± 11.8	10.9 ± 10.1
Kermadec petrel *Pterodroma neglecta*	14.6 ± 5.5	21.3 ± 8.3	10.7 ± 5.3	11.7 ± 5.6	5.3 ± 2.8	7.5 ± 3.1	52.2 ± 17.1	54.0 ± 13.1	40.8 ± 12.2	36.3 ± 8.7	7.0 ± 11.3	9.7 ± 8

Table 3. Average percentage and durations that gadfly petrels spent in travel, area-restricted search (ARS) and rest during foraging trips. Behavioral states were inferred from hidden Markov models (HMMs).

2.5.2 At-sea foraging distribution

Foraging ranges extended over vast oceanic areas including, for black-winged (Figure 4) and white-necked petrels (Figure 5), almost throughout the entirety of the Tasman Sea and, to a lesser extent, at the southern limits of the Coral Sea at its 30° south limit. Approximately 55%, 35% and 42%, respectively, of black-winged, white-necked and Kermadec petrel area-restricted search foraging locations occurred in international waters (outside of EEZs). All three species foraged broadly within the warm waters of the wind-driven, southward flowing East Australian Current (EAC) and to the southern extent of the eastward-flowing Tasman Front (TF), which separates the Coral Sea to the north and the Tasman Sea to the south and flows from the east coast of Australia into the western Pacific Ocean.

Black-winged petrels made use of areas bordering the Subtropical Front in the south of the Tasman Sea and foraged over an area of almost 4 million km^2, white-necked petrels over approximately 5 million km^2 including to the east of New Zealand bording the Subtropical Front, but Kermadec petrels (Figure 6) remained relatively close to the colony with a foraging range that spanned almost 0.5 million km^2. Grid cell analysis of foraging behavior revealed that gadfly petrels engaged in area-restricted search behavior throughout their entire foraging ranges. However, most grid cells occupied by foraging black-winged petrels on long trips were concentrated in the south of the Tasman Sea (Figure 4). Foraging ranges of both black-winged and white-necked petrels were larger in 2018 than in 2019 (Figures 4 & 5). There was a high degree of overlap in foraging ranges of all three species, but black-winged petrels appeared to concentrate their long foraging trips considerably further south than the other species (Figures 4 – 6).
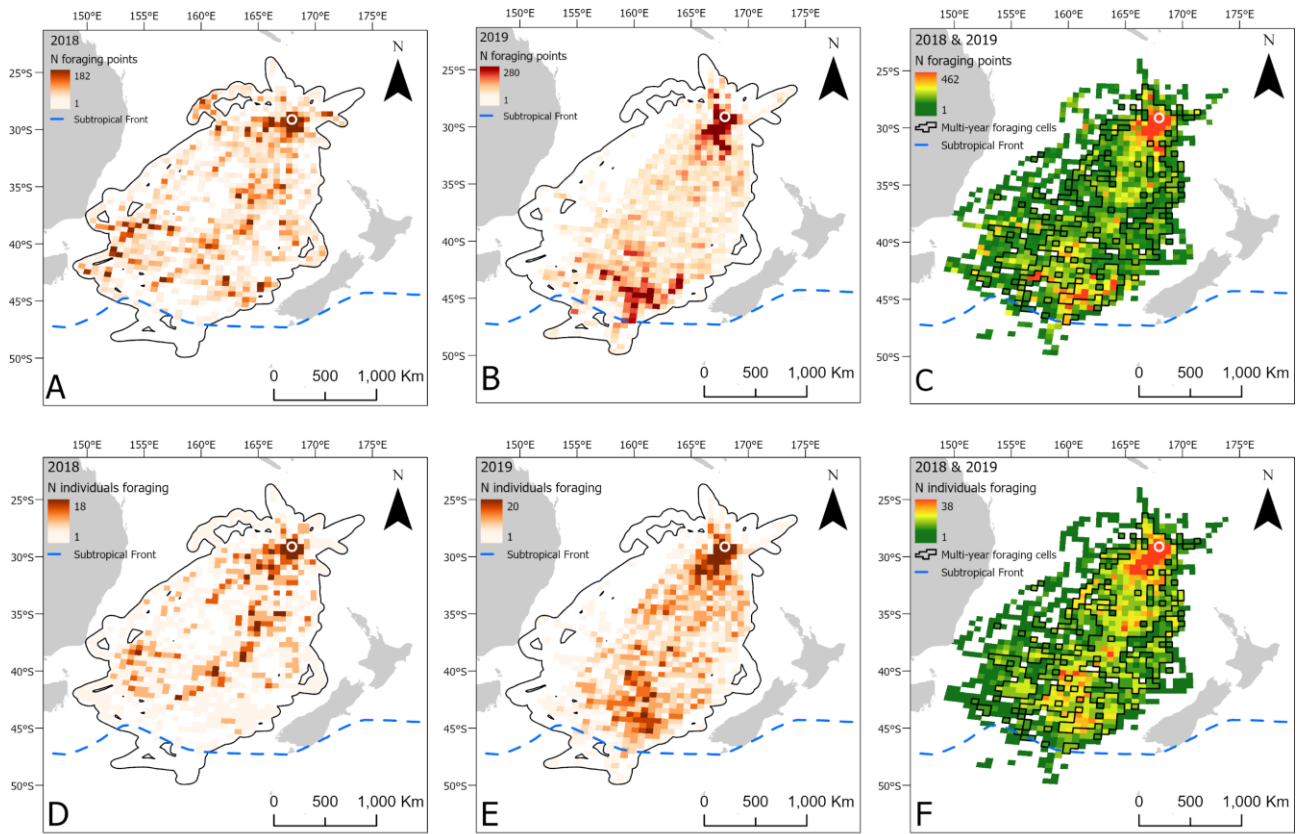
Figure 4. At-sea distribution and locations of foraging behavior in chick-provisioning black-winged petrels (Pterodroma nigripennis). Grid cells (50 x 50 km) depict the number of foraging locations in 2018 (A; n = 24 individuals) and 2019 (B; *n* = 24 individuals) and combined number of foraging locations in 2018 and 2019 (C). Number of individuals foraging in each grid cell in 2018 (D) and 2019 (E); and the combined number of individuals foraging in each grid cell in both 2018 and 2019 (F). Polygonised cells in C and F represent grid cells in which birds foraged in both years. The location of the breeding colony is represented by a white circle. Black polygons around the foraging areas (A – B, D – E) represent the home range (99% utilization distribution).
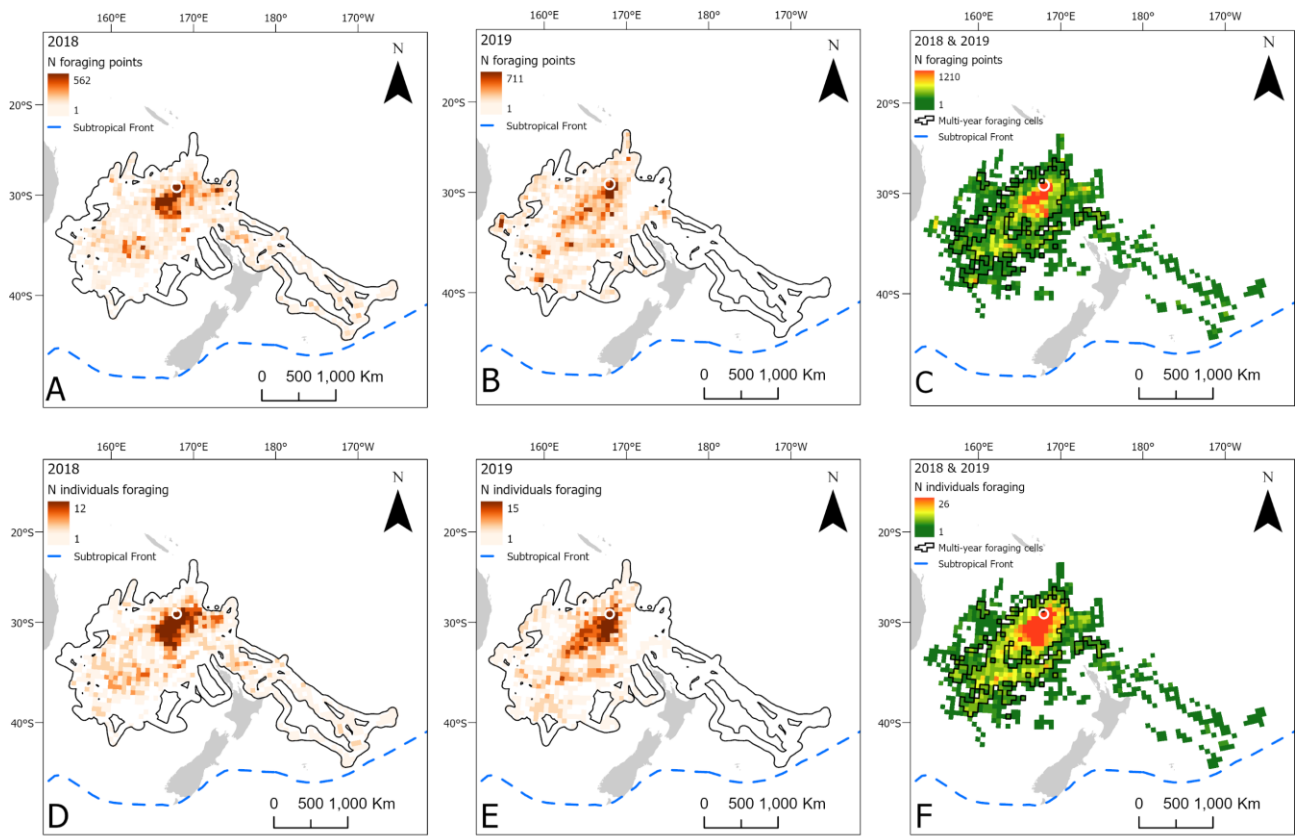
Figure 5. At-sea distribution and locations of foraging behavior in chick-provisioning white-necked petrels (Pterodroma cervicalis). Grid cells (50 x 50 km) represent the number of foraging locations in 2018 (A; *n* = 12 individuals) and 2019 (B; *n* = 15 individuals) and combined number of foraging locations in 2018 and 2019 (C). Number of individuals foraging in each grid cell in 2018 (D) and 2019 (E); and the combined number of individuals foraging in each grid cell in both 2018 and 2019 (F). Polygonised cells in C and F represent grid cells in which birds foraged in both years. The location of the breeding colony is represented by a white circle. Black polygons around the foraging areas (A – B, D – E) represent the home range (99% utilization distribution).
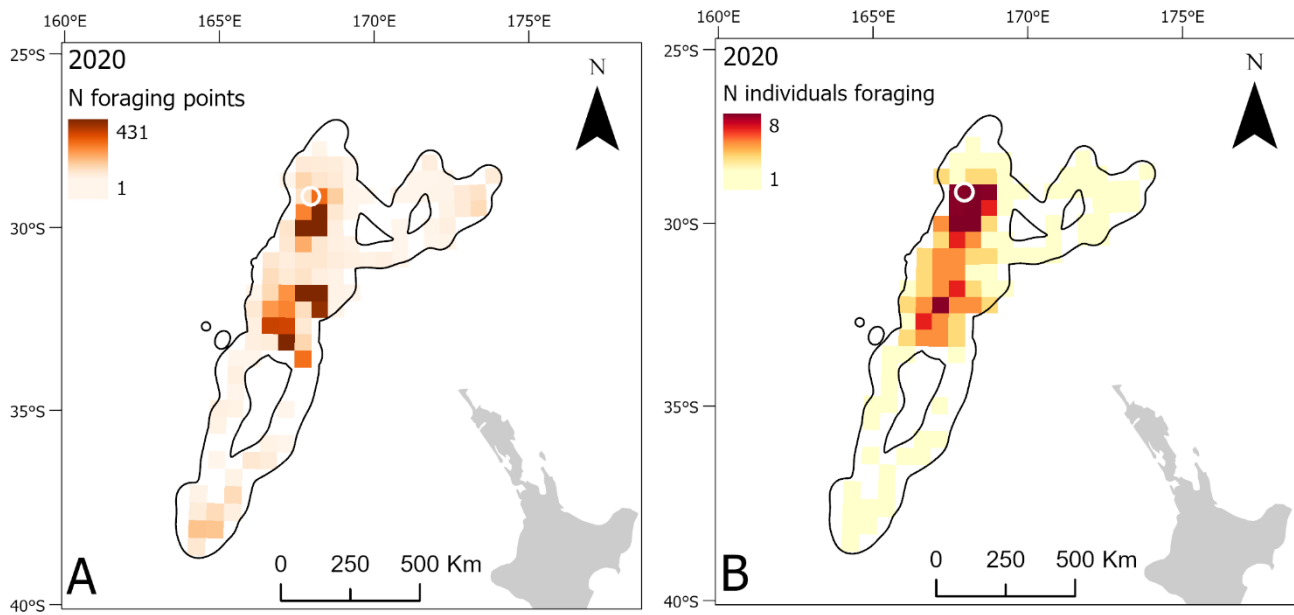
Figure 6. At-sea distribution and locations of foraging behavior in chick-provisioning Kermadec petrels (Pterodroma neglecta). Grid cells (50 x 50 km) represent the number of foraging locations in each cell in 2020 (A; *n* = 9 individuals) and the number of individuals foraging in each grid cell in 2020 (B). The location of the breeding colony is represented by a white circle. Black polygons around the foraging areas represent the home range (99% utilization distribution).
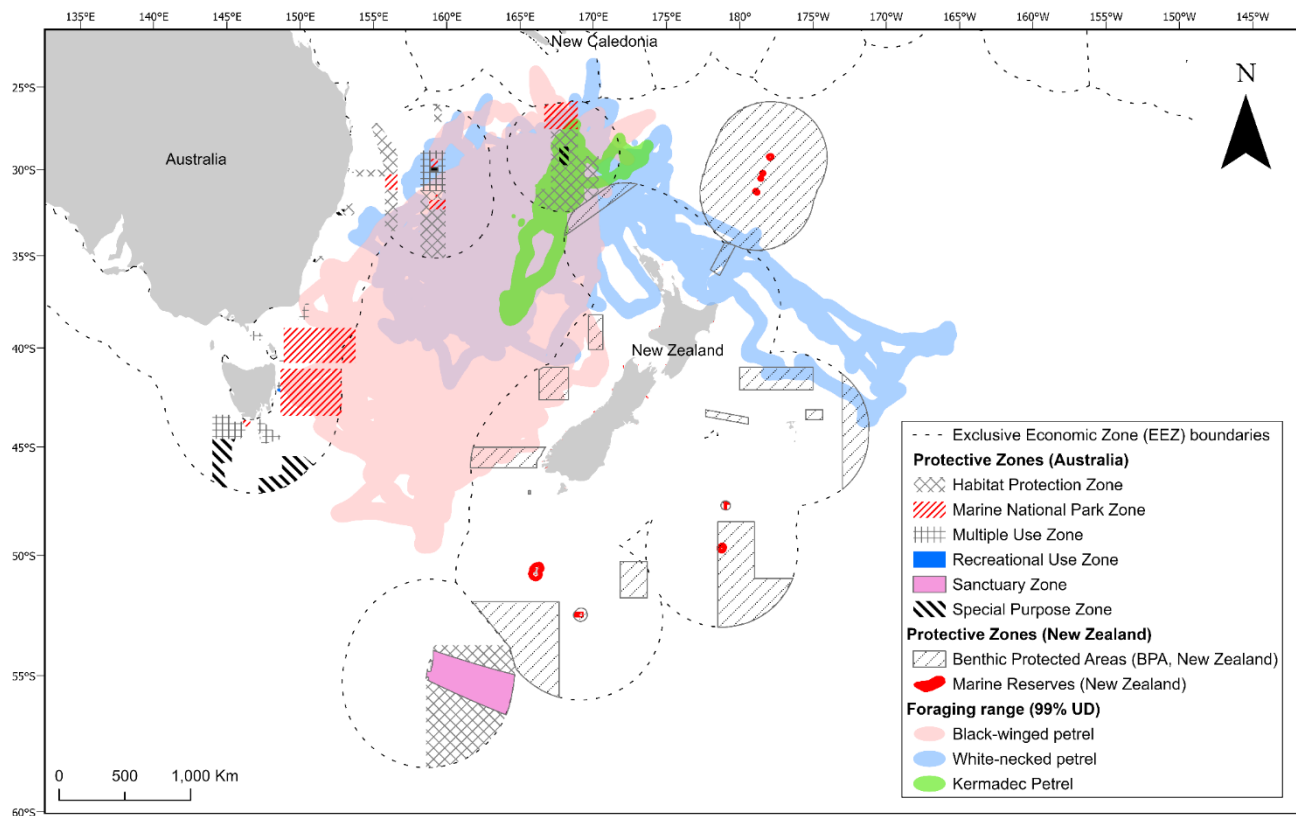
Figure 7. Foraging ranges of black-winged petrels (*Pterodroma nigripennis*), white-necked petrels (*P. cervicalis*) and Kermadec petrels (*P. neglecta*) in relation to existing protected areas and areas outside of national jurisdictions.

2.5.3 Species distribution modeling

Evaluation metrics for habitat models constructed with spatially independent CV were substantially poorer (AUC$_{ROC}$ of 0.55 – 0.77) than of models fit using conventional random CV (AUC$_{ROC}$ of 0.93 – 0.95). Despite these apparent differences in model performance, response curves and relative importance of predictor variable contributions of conventional CV and spatially independent CV ensemble models were similar (Supplementary Figures 4 and 5) indicating consistent environmental relationships, regardless of the CV methodology. Both methods are likely to have poor generalizability to new spatial and temporal environment data because the spatially independent CV method is specifically designed to evaluate how well model predictions transfer to new environmental contexts. Ensemble model predictive performance for black-winged petrels was

approximately equivalent to random classification ($AUC_{ROC} = 0.55$; TSS = 0.19), for white-necked petrels predictive performance was fair ($AUC_{ROC} = 0.71$; TSS = 0.39); and the performance of Kermadec petrel models was within the range of fair performance ($AUC_{ROC}: = 0.77$; TSS = 0.48) (Araujo et al., 2005; Hosmer et al., 2013). Distance from the colony (Figure 8) was the most important predictor, with all three species demonstrating a high probability of foraging closer to the colony. All species showed a preference for foraging in warmer sea-surface temperatures, and for black-winged and white-necked petrels SST was the second most important environment variable for predicting the location of foraging. Black-winged and white-necked petrels preferred to forage in areas with higher wind speeds (albeit wind speed had only low (3.1%) variable importance for white-necked petrels), but Kermadec petrels preferred lower wind speeds (Figure 7). Models presented some evidence that black-winged petrels expressed preference for foraging in areas with shallower thermocline depths (i.e., 9.9% variable importance; Figure 7), whereas white-necked petrel foraging was associated with deeper thermocline depths (i.e., 6% variable importance; Figure 7). Thermocline depth had weaker contribution to the Kermadec petrel models (i.e., 3.1% variable importance) with no obvious preference for foraging in waters with shallow or deep thermocline layers.

We found no evidence of any of the species showing preferences for foraging close to seamounts. Conversely, the probability of foraging was uniformly higher among all species at greater distances from seamounts; and birds did not appear to target bathymetric slopes. Kermadec petrels demonstrated some preference for foraging in areas with higher Chlorophyll *a* concentration compared to black-winged and white-necked petrels. Additionally, for all three of the petrels, species distribution models could not determine any clear preferences for foraging near sub-mesocale sea-surface temperature fronts, nor transport fronts (i.e., areas with lower FSLE values that represent the outer parts of transport fronts) or areas with higher sea level anomalies. However, black-winged petrels appeared to make some general use to the north of the Subtropical Frontal

Zone (Bostock et al., 2015; Figure 4) during long foraging trips. In 2019, only two white-necked petrels traveled to the east of New Zealand, possibly making use of productive waters to the north of the Subtropical Frontal Zone (Figure 5).

MESS grids indicated that only 0.04 ± 0.08 % (mean $\pm$ SD) of the foraging area during the time period when Kermadec petrels were tracked had environmental conditions outside the range of those during the time period when black-winged and white-necked petrels were tracked (Supplementary figure 6).
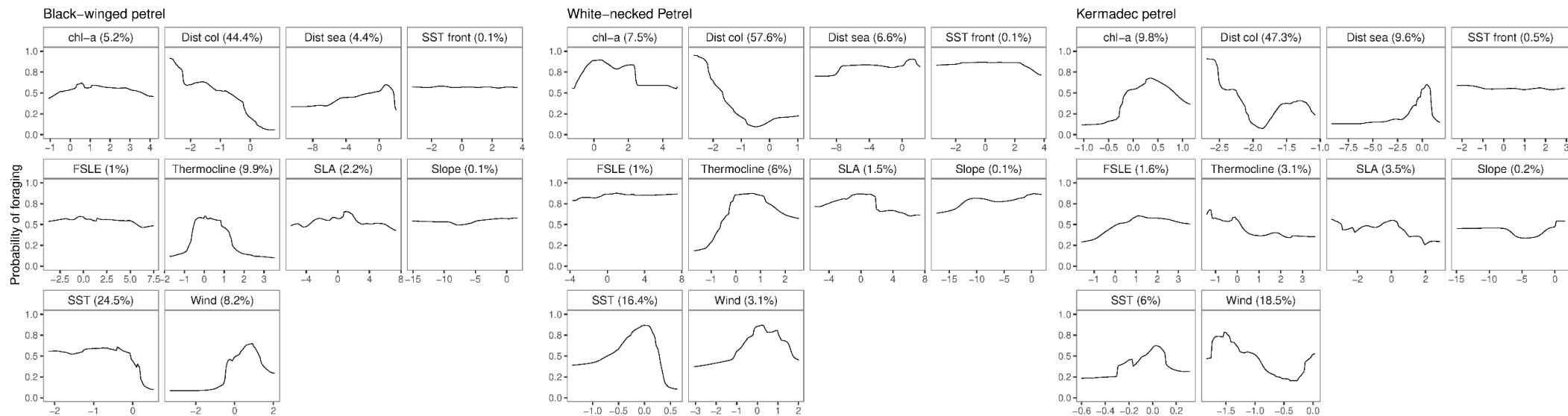
Figure 8. Response curves of scaled predictors and associated predictor importance in the spatially independent cross-validation ensemble models of black-winged (left), white-necked (center) and Kermadec (right) petrel foraging preferences. Predictor variables include chlorophyll *a* concentration (chl-*a*), distance from the colony (Dist col), distance from seamounts (Dist sea), sea-surface temperature fronts (SST front), Finite-sized Lyapunov Exponent (FSLE), thermocline depth (Thermocline), sea level anomaly (SLA), bathymetric slope (Slope), sea-surface temperature (SST) and wind speed (Wind).

2.6 Discussion

2.6.1 Foraging characteristics

Our tracking data and analyses demonstrate that summer-breeding gadfly petrels from the Norfolk Island Group use waters of the East Australian Current and the Subtropical Frontal Zone. Behavioral state-space modeling demonstrated that while they do use some oceanographic features, they also travel very widely, foraging throughout most of the Tasman Sea, apparently opportunistically exploiting resources as they travel (e.g., Ventura et al., 2020). These results support the hypothesis that, while gadfly petrels do make some broad use of oceanographic features, they also use a maximal-area foraging strategy, travelling over large areas to maximize chances of encountering unpredictable resources in relatively unproductive marine ecosystems (e.g., Clay et al., 2017; Ventura et al., 2020).

Among seabirds, gadfly petrels undertake some of the most extensive foraging movements during breeding when they must travel repeatedly to and from their nests to incubate eggs or provision themselves and their altricial offspring (Clay et al., 2019; Taylor et al., 2020). The three species we studied all demonstrated bimodal foraging strategies (e.g., Weimerskirch et al., 1994) whereby birds made both short and long foraging journeys. Concentrated foraging around seabird colonies depletes local resources, which forces individuals to journey further in search of food: a phenomenon known as 'Ashmole's halo' (Ashmole, 1963; Oppel et al., 2015; Weber et al., 2021). Seabirds exhibiting bimodal foraging strategies do so in response to near-colony resource depletion, whereby short foraging trips are used to provision their dependent young, whereas parents need to travel to more distant foraging grounds to meet their own energetic requirements (Weimerskirch et al., 1994; Oppel et al., 2015; Weber et al., 2021). Gadfly petrels appear exceptionally well suited to making long-distance self-provisioning journeys due to their unique morphological adaptations for fast, and energy efficient flight relative to other seabirds (Spear and Ainley, 1997; Ventura et al., 2020).

2.6.2 At-sea foraging distributions

Tracking data collected over multiple years highlighted that some areas experience more intensive foraging than others. This is true for both the number of individuals foraging in a given region as well as the intensity of foraging activity of individuals within that region. All three species had high foraging activity immediately surrounding the colony, with other hotspots of foraging activity relatively diffusely spread over the remaining large foraging extent, which is typical of other central place foraging seabirds that display dual foraging strategies (Magalhães et al., 2008; Raine et al., 2021). Hotspots of black-winged petrel foraging activity occurred between approximately 40°S – 47°S. The large spatial area over which gadfly petrels foraged encompasses areas of the Exclusive Economic Zones (EEZs) of Australia and New Zealand with a large proportion of foraging ranges encompassing the high seas, a "global commons" for which no country holds sovereign jurisdiction. In this study, approximately 55%, 35% and 42%, respectively, of black-winged, white-necked and Kermadec petrel foraging locations occurred outside of EEZs, which highlights the importance of internationally coordinated efforts to conserve gadfly petrel foraging habitat (e.g., Davies et al., 2021).

We demonstrated a large degree of spatial overlap in foraging areas among all three species, suggesting that competition for resources may be mediated over finer spatial scales through differences in prey acquisition methods, presumably as a result of morphological differences (e.g., body size), instead of large-scale spatial or habitat segregation (Spear et al., 2007). Diet diversity in pelagic tropical seabirds is generally low (Diamond, 1983) with most species restricted to foraging on squid and flying fish, which results in high diet overlap (Ashmole and Ashmole, 1967; Harrison et al., 1983; Ballance et al., 1997). Indeed, observations of stomach regurgitations and of parents feeding young during fieldwork of the present study suggest that the three species provisioned chicks with unidentified squid (Decapodiformes) and flying fish (Exocoetidae) and unidentified zooplankton (L. Halpin, personal observations, 2018-2021). Kermadec petrels are reported to be

partially kleptoparasitic (Spear and Ainley, 1993). That Kermadec petrels foraged closer to the colony and spent on average proportionally more time in area-restricted search behavior may be indicative of a kleptoparasitic foraging strategy, whereby birds do not need to travel far to find prey, but instead may harass other species close to the colony that have acquired food. This species also demonstrated preferences for foraging in areas with higher chlorophyll-a concentrations, suggesting that within their smaller foraging range, which encompasses more oligotrophic areas, they may need to seek patches with higher productivity to obtain sufficient prey resources. All three species intensively used the areas surrounding the colony in short foraging trips, but during long trips black-winged petrels tended to forage in cooler waters much further south than white-necked petrels. This may be indicative of black-winged petrels having increased flight proficiency relative to white-necked petrels thus enabling them to exploit resources further afield.

2.6.3 Foraging habitat

Model predictive performance was generally poor to fair as is often the case for habitat generalists that lack strong affinity to a particular habitat type or feature (Elith et al., 2006; Andrew and Fox, 2020). We believe that the poor predictive performance was due in part to the behavioral characteristics (i.e., more generalist habitat requirements) of gadfly petrels rather than factors such as the choice of environmental variables used to predict foraging habitat. Furthermore, the response curves and relative importance of the predictor variables to model predictions were very similar between conventional cross-validation and spatially independent cross-validation approaches, demonstrating that birds have weak or wide preferences for available habitat, regardless of the cross-validation methodology. While the predictive performance of the Kermadec petrel species distribution model was within range of what is generally considered acceptable, we suggest that the performance of this model should be taken with caution due to the lower representativeness of the sample size (68.5%) to foraging movements of the colony-level population. MESS grids indicated that environmental conditions were similar in the Kermadec petrel foraging area during the period

in which they were tracked compared to the other two species. We therefore do not believe that differences between the foraging characteristics of Kermadec petrels compared to the other two species were driven by differences in environmental conditions due to the different time periods in which the species were tracked.

Our results suggest that black-winged petrels target waters with shallower thermocline depths, which may indicate a more varied diet that includes zooplankton since planktivorous species tend to prefer waters with shallower thermocline depths (e.g., Spear et al. 2001; Ballance et al. 2006). Conversely, the preference for foraging in waters with deeper thermoclines expressed by white-necked petrels may indicate that the species is more piscivorous than black-winged and Kermadec petrels. That black-winged and Kermadec petrels spent almost equal proportions of their time foraging during darkness compared to daylight suggests that nocturnal foraging is likely to be an important feature of their behavior. These results are consistent with other studies indicating that tropical and subtropical seabirds often rely on deep water prey that perform diel vertical migrations to the sea surface at night (e.g., Hays, 2003). Such prey includes mesopelagic squid, fish and zooplankton (Ashmole, 1971; Imber et al., 1995; Dias et al., 2012). Similar to a closely related species, the Bonin petrel (*P. hypoleuca*; Harrison et al., 1983), black-winged petrels may be well-adapted for night time foraging and may rely substantially on diel migrant prey, possibly including bioluminescent squid (Ommastrephidae; Harrison et al., 1983) and zooplankton. Kermadec petrels are known to feed on diel migrant squids, particularly Onychoteuthidae (Imber et al., 1995).

Previous studies have suggested that, unlike many other pelagic seabirds, gadfly petrels have less clear habitat preferences, especially when engaged in long foraging trips during the breeding season (Clay et al., 2017, 2019; Ventura et al., 2020). Our study provides support for this hypothesis with evidence to suggest that the foraging strategy is likely based on opportunistic prey encounters rather than targeting of specific habitat features. For example, foraging occurred

throughout the species ranges, and travel accounted for a disproportionately large percentage of time allocation within foraging trips. Additional support for this hypothesis is that, across all three species, the most important model predictor of probability of foraging behavior was the distance from the colony. From a species distribution modeling perspective, this suggests that, like other centrally placed foragers, breeding gadfly petrels' foraging ranges are mainly constrained by their need to return to nests to provision chicks.

Possible evolutionary drivers of this lack of habitat specificity are that (sub)tropical waters and open ocean regions are less predictable than temperate and polar regions, and inshore waters. Indeed, it has been hypothesized that as ocean productivity decreases – which results in reduced prey abundance – seabird flight proficiency becomes more important because those with low flight costs will be able to reach more distant resources (Ballance et al., 1997). Furthermore, gadfly petrels' high mobility and large foraging ranges allows birds to be less reliant on specific oceanographic features associated with moderate to high productivity, such as fronts or eddies, which can be ephemeral and are highly dynamic in marine systems (Weimerskirch, 2007), and instead allows birds to opportunistically target prey items or patches they encounter while in flight.

Gadfly petrels tracked in the present study showed no affinity for foraging near seamounts. Several studies (e.g., Haney et al., 1995; Thompson, 2007; Morato et al., 2008) demonstrate that some seabirds – including gadfly petrels – occur in higher abundance near seamounts, particularly in the North Pacific and Atlantic. However, these studies have generally occurred during gadfly petrels' non-breeding stages (i.e., in the austral winter) when birds are not constrained to routinely return to the colony. Given the low energetic costs of long-distance travel, it could be that for chick-provisioning gadfly petrels, targeting foraging at seamount locations yields lower foraging success than ranging widely across the Tasman Sea. Furthermore, little is known about seabird prey distributions in the oceanic Pacific (Ballance et al., 1997). It is thus also possible that the squid and

flying fish prey targeted by gadfly petrels during chick-provisioning occur in no higher abundances at accessible seamounts within the species' foraging ranges than in pelagic waters.

2.6.4 Implications for conservation

The opportunistic foraging strategies of gadfly petrels and the enormous areas over which they forage mean that it may be challenging or impractical to use traditional approaches to identifying and protecting key foraging habitats, such as static marine protected areas (Oppel et al., 2018). Conservation of gadfly petrel foraging habitat may therefore require focus on maintaining functional and healthy marine ecosystems and reducing generalized threats (e.g., commercial fisheries that cause high seabird bycatch, marine pollution) to birds in these areas, which will ensure long term food supplies for these oceanic wanderers. Lack of generalizability of habitat suitability models poses a challenge for conservation planners. If it is not possible to predict where suitable habitat is under current environmental conditions, then spatially dynamic conservation measures, which have been proposed and enacted in other marine contexts, may be impossible to implement (Hobday et al., 2011; Maxwell et al., 2015). However, our analysis of at sea distribution presents some opportunities. Our tracking dataset identifies some areas of high foraging activity by multiple individuals between years. This approach to examining areas with repeated use between years is likely more useful for determining important foraging areas for gadfly petrels and other seabirds that may lack predictable foraging preferences for any static and dynamic oceanographic features. Moreover, the dual foraging strategy that we identified also creates potential for different conservation strategies to provide protection for the different trip types. The short foraging trips cover a much smaller area, meaning that methods such as marine protected areas could be effective at this spatial scale (Oppel et al., 2018). Some existing protections that prohibit commercial fishing occur in the Norfolk Island National Park Zone to the north of the Island (Figure 8), which encompasses a small portion of the areas used by gadfly petrels during short trips. Conversely, the vast extent covered during longer foraging trips by self-provisioning gadfly petrels means that

policy-based methods such as fisheries regulation (e.g., quotas and more comprehensive enforcement) or management of marine plastic pollution will likely represent the best tool in the conservation arsenal for conserving birds undertaking these long-distance trips (Oppel et al., 2018). While the risk of interactions with commercial fisheries is considered low for the small to medium sized gadfly petrels in our study (Waugh et al., 2012), their populations will benefit from increased efforts to prevent the degradation of marine ecosystems through pollution, over-fishing and climate change both within and outside of EEZs. Although the conservation of the high seas is much more challenging than within EEZs, several large high seas areas of the Tasman Sea – which are frequented by gadfly petrels in the present study – have been identified as ecological or biologically significant marine areas (EBSAs) by Parties to the Convention on Biological Diversity (CBD) (Bax et al., 2016). These areas have been the topic of discussions initiated by a United Nations (UN) call to establish marine protections beyond national jurisdictions.

That breeding gadfly petrels travel so far from their colony to obtain enough resources to meet their energetic requirements suggests that they may encounter different threats at varying scales. It also implies that reducing threats to their marine habitats and maintaining functional marine ecosystems across large scales is key to their survival. Provided that their nesting colony on Phillip Island remains free of introduced predators, conservation efforts for these gadfly petrels should focus on collaborative multinational cross-border efforts to conserve and restore marine ecosystem function in the Tasman Sea and the wider South Pacific.

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2.8 Ethics Statement

This research was reviewed and approved by Monash University School of Biological Sciences Animal Ethics Committee and New South Wales Department of Planning, Industry and Environment (DPIE) Animal Ethics Committee prior to commencement of the study. Field data were collected under Monash University animal ethics permit BSCI/2017/42, New South Wales DPIE Animal Ethics Committee Research Authority number: 021028 and Parks Australia wildlife research approvals. Petrels were captured and banded under Australian Bird and Bat Banding Scheme (ABBBS) project 8010 with authority numbers: 3385 (Luke Halpin) and 1373 (Nicholas Carlile).

2.9 Author Contributions

Luke Halpin conceived the project idea, acquired funding and scientific permits, conducted field expeditions, collected field data, analyzed the data, and led the writing of the manuscript. Rowan Mott assisted with formulation of ideas, data analysis and contributed to project development. Thomas Clay and Grant Humphries assisted with data analysis. Trudy Chatwin assisted with field expeditions and data collection. Nicholas Carlile and Rohan Clarke contributed to fieldwork, project development and ideas, acquisition of scientific permits and funding. All authors contributed critically to manuscript drafts and gave final approval for publication.

2.10 Funding

2.12 Data Availability Statement

The raster data containing the grid cell analysis of foraging gadfly petrels are provided in supplementary material. The tracking datasets used in this study are available on reasonable request from the Seabird Tracking Database (https://seabirdtracking.org; dataset IDs: 1499, 1453, 1422, 1452, 1423).

2.13 Supplementary Figures

2.13.1 Behavioral state-space (hidden Markov model) evaluation
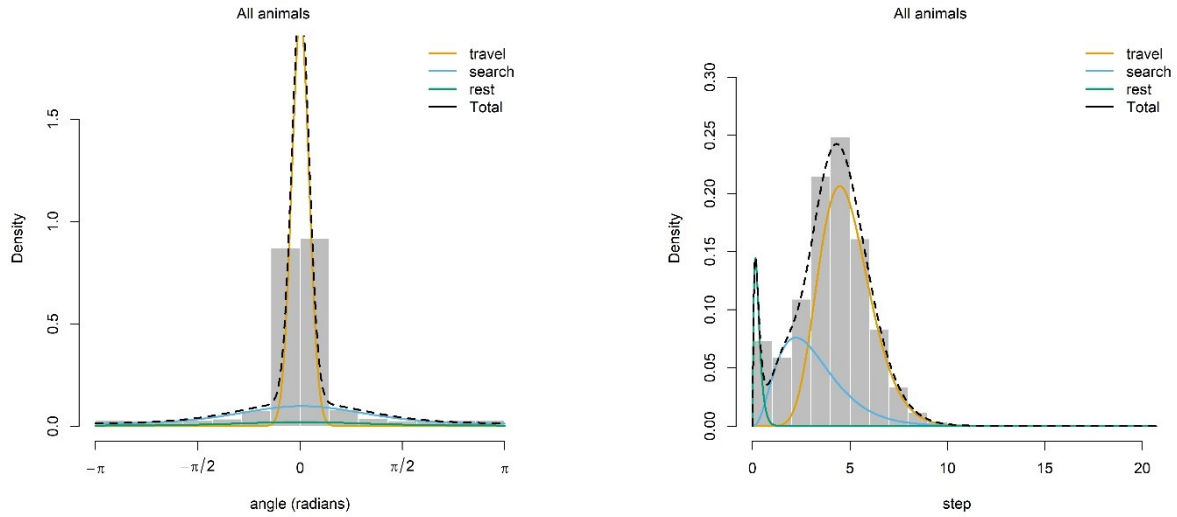
Supplementary Figure 1. Histograms and estimated probability distributions for turning angles (left) and step lengths (right) for black-winged petrels (Pterodroma nigripennis) of the three-state ("rest", "search", "transit") hidden Markov model (HMM).
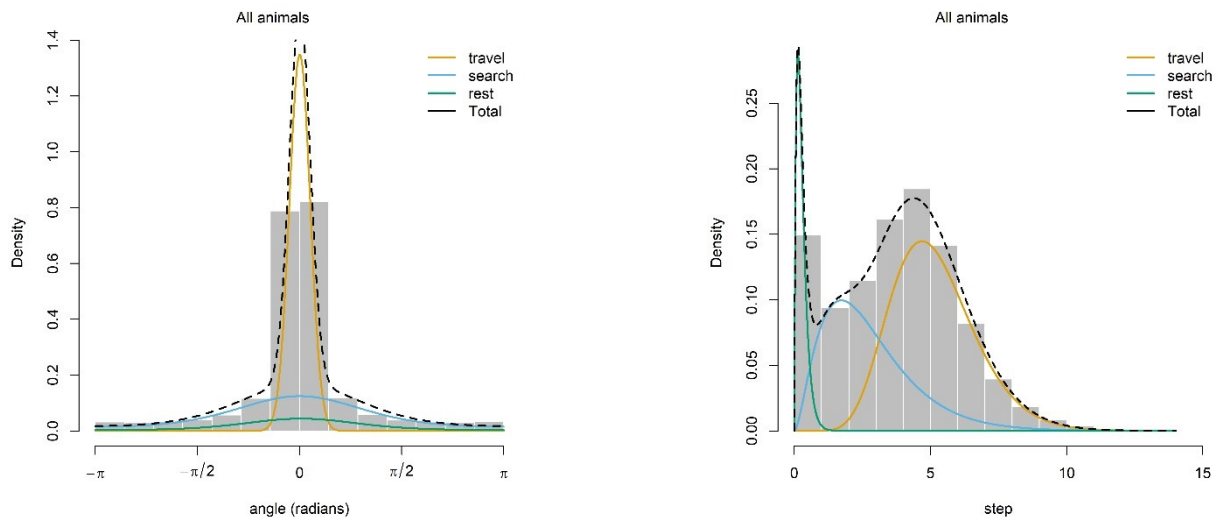
Supplementary Figure 2. Histograms and estimated probability distributions for turning angles (left) and step lengths (right) for white-necked petrels (Pterodroma cervicalis) of the three-state ("rest", "search", "transit") hidden Markov model (HMM).
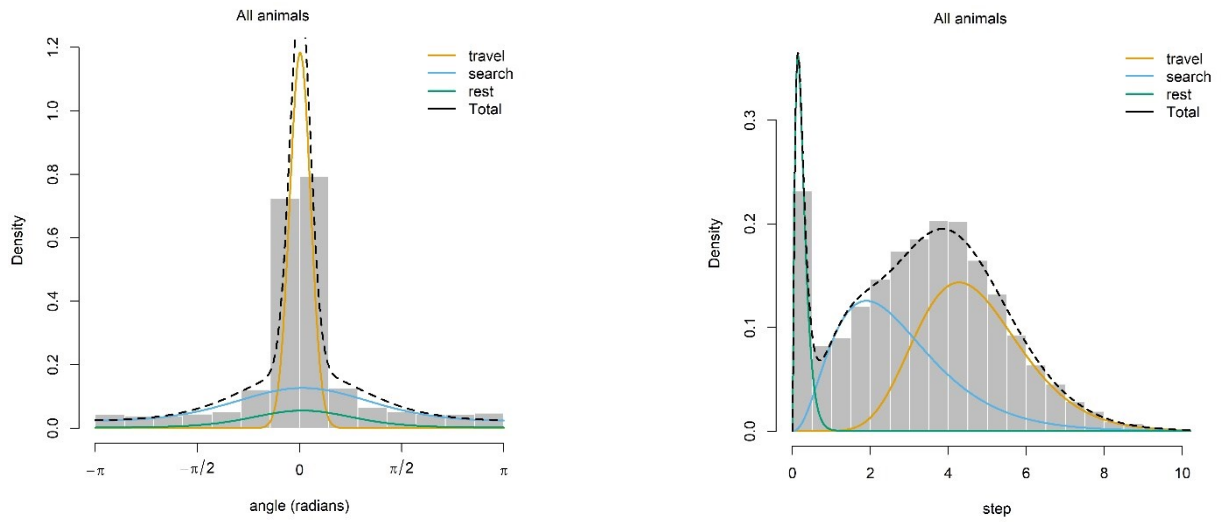
Supplementary Figure 3. Histograms and estimated probability distributions for turning angles (left) and step lengths (right) for Kermadec petrels (Pterodroma neglecta) of the three-state ("rest", "search", "transit") hidden Markov model (HMM).

2.13.2 Species Distribution Modeling (SDM) Evaluation

Spatially independent cross validation ensemble model response curves
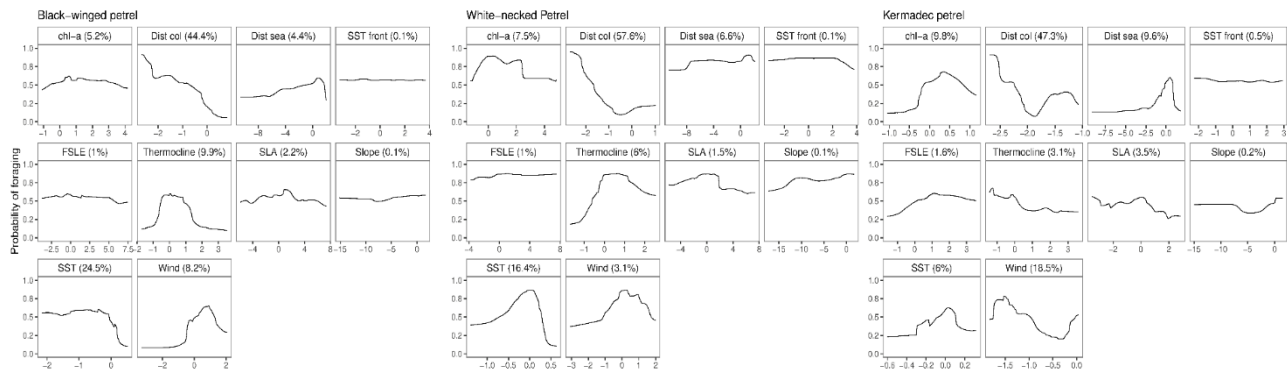
Supplementary Figure 4. Response curves of scaled predictors and associated predictor importance in the spatially independent cross-validation ensemble models of black-winged (left), white-necked (center) and Kermadec (right) petrel foraging preferences. Predictor variables include chlorophyll a concentration (chl-a), distance from the colony (Dist col), distance from seamounts (Dist sea), sea-surface temperature fronts (SST front), Finite-sized Lyapunov Exponent (FSLE), thermocline depth (Thermocline), sea level anomaly (SLA), bathymetric slope (Slope), sea-surface temperature (SST) and wind speed (Wind).

Conventional cross validation ensemble model response curves
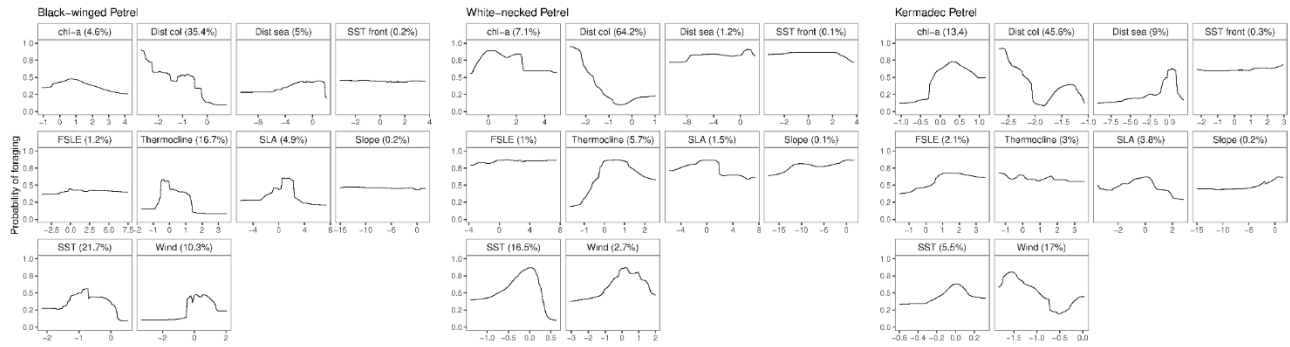
Supplementary Figure 5. Response curves of scaled predictors and associated predictor importance in the conventional cross-validation ensemble models of black-winged (left), white-necked (center) and Kermadec (right) petrel foraging preferences. Predictor variables include chlorophyll a concentration (chl-a), distance from the colony (Dist col), distance from seamounts (Dist sea), sea-surface temperature fronts (SST front), Finite-sized Lyapunov Exponent (FSLE), thermocline depth (Thermocline), sea level anomaly (SLA), bathymetric slope (Slope), sea-surface temperature (SST) and wind speed (Wind).

2.13.3 Multivariate Environmental Similarity Surface (MESS) analysis

Supplementary Figure 6 demonstrates the results of multivariate environmental similarity surfaces (MESS; Elith et al., 2010) used to check that differences in behavior of Kermadec petrels were not caused by substantially dissimilar environmental conditions in the year that they were tracked (January 2020) versus the years that black-winged and white-necked petrels were simultaneously tracked (February to April in 2018 and 2019). We computed MESS grids for each dynamic predictor for each month in which black-winged and white-necked petrels were tracked referenced against the year that Kermadec petrels were tracked. Overall, the conditions in January 2020 were not outside of the range of conditions experienced by birds in other years (see Supplementary Table 1).
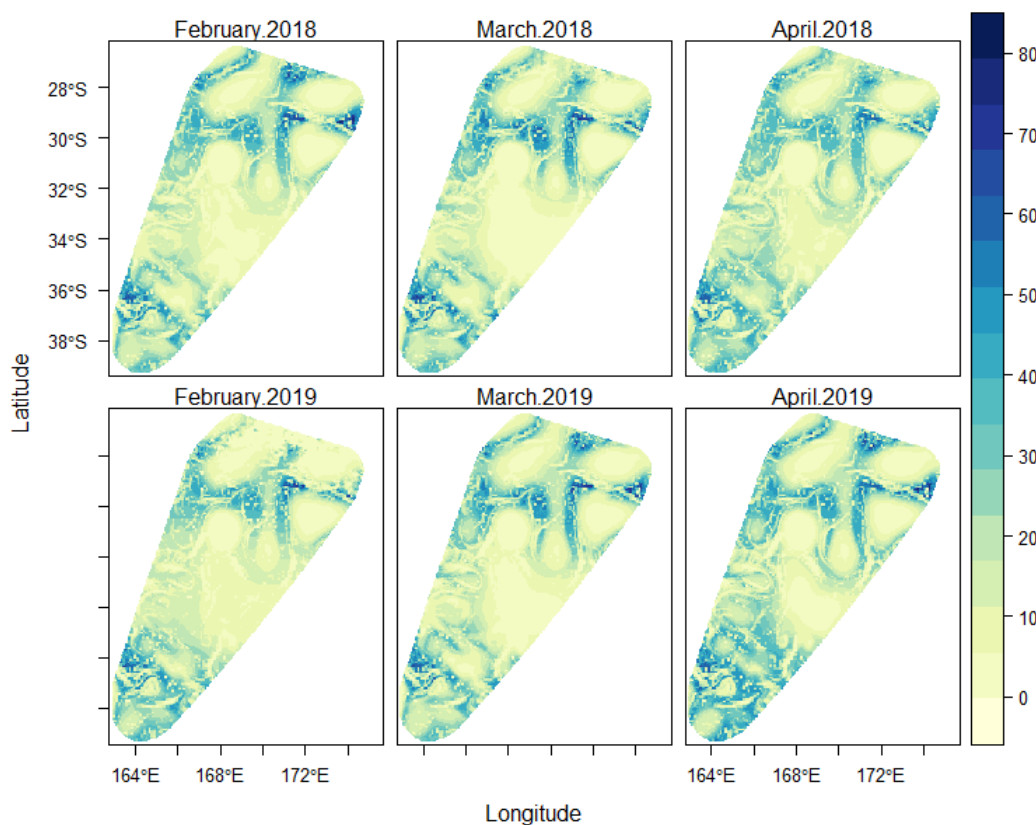
Supplementary Figure 6. MESS grids representing percentage similarity of environmental conditions in each month that black-winged and white-necked petrels were tracked compared to January 2020 when Kermadec petrels were tracked. Negative values represent dissimilar conditions.

Month Comparison	Percentage of cells with negative values
February 2018	0.00012
March 2018	0.00061
April 2018	0.0016
February 2019	0.21934
March 2019	0.00148
April 2019	0.00123

Supplementary Table 1. Percentage of raster cells with negative values resulting from the MESS grid analysis comparing the similarity of environmental conditions in the year when Kermadec petrels were tracked compared to other species. Negative cells represent those that are dissimilar to the cells of the reference raster.

CHAPTER 3

Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles.

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3.1 Abstract

Light-level geolocators are popular bio-logging tools, with advantageous sizes, longevity, and affordability. Biologists tracking seabirds often presume geolocator spatial accuracies between 186-202 km from previously-innovative, yet taxonomically, spatially, and computationally limited, studies. Using recently developed methods, we investigated whether assumed uncertainty norms held across a larger-scale, multispecies study.

We field-tested geolocator spatial accuracy by synchronously deploying these with GPS loggers on scores of seabirds across five species and 11 Mediterranean Sea, east Atlantic and south Pacific breeding colonies. We first interpolated geolocations using the geolocation package FLightR without prior knowledge of GPS tracked routes. We likewise applied another package, probGLS, additionally testing whether sea-surface temperatures could improve route accuracy.

Geolocator spatial accuracy was lower than the ~200km often assumed. probGLS produced the best accuracy (mean ± SD = 304 ± 413 km, n = 185 deployments) with 84.5% of GPS-derived latitudes and 88.8% of longitudes falling within resulting uncertainty estimates. FLightR produced lower spatial accuracy (408 ± 473 km, n = 171 deployments) with 38.6% of GPS-derived latitudes and 23.7% of longitudes within package-specific uncertainty estimates. Expected inter-twilight period (from GPS position and date) was the strongest predictor of accuracy, with increasingly equatorial solar profiles (i.e., closer temporally to equinoxes and/or spatially to the Equator) inducing more error. Individuals, species and geolocator model also significantly affected accuracy, while the impact of distance travelled between successive twilights depended on the geolocation package.

Geolocation accuracy is not uniform among seabird species and can be considerably lower than assumed. Individual idiosyncrasies and spatiotemporal dynamics (i.e., shallower inter-twilight shifts by date and latitude) mean that practitioners should exercise greater caution in interpreting geolocator data and avoid universal uncertainty estimates. We provide a function capable of estimating relative accuracy of positions based on geolocator-observed inter-twilight period.

3.2 Introduction

Light-level geolocators ("geolocators") are one of the most popular and practical tools available to study animal movement, with well-established, open access standards and techniques available to guide analyses of geolocation data (see Lisovski et al. 2020). However, there can be considerable uncertainty associated with the accuracy of location estimates derived from light-level data. Geolocators are small (i.e. ~ 0.3–3.3 g) archival data loggers that measure and record solar intensity at regular intervals, some with the capability of measuring and archiving other information such as water temperature, wet/dry events and barometric pressure. When geolocators are retrieved, light-level data are downloaded and directed into astronomical equations that estimate spatial locations based on the timing of twilight events (i.e. sunrises and sunsets). Geolocator data can be interpolated into one or two positions per day with latitude estimated by day length, and longitude estimated by the timing of local midday or midnight relative to Greenwich Mean Time and Julian day (Hill 1994). Geolocators were first applied to tracking the movements of marine vertebrates including elephant seals (Delong et al. 1992), fish (Block et al. 1998), seabirds (Tuck et al. 1999; Croxall et al. 2005; Phillips et al. 2006; Shaffer et al. 2006; González-Solís et al. 2007; Guilford et al. 2009; Egevang et al. 2010) and sea turtles (Fuller et al. 2008).

Recently, geolocators have undergone considerable miniaturisation and improvements to onboard storage capacity, which has stimulated an increase in studies that use light-level data to infer spatial information about both marine and terrestrial species that were otherwise too small to be burdened with tracking devices (Bridge et al. 2011). The number of ecologists using geolocators to study seabird movements has increased in tandem with these sensor improvements and newly designed geolocation methods implemented in several R packages for processing and analysing light-level data (e.g. Sumner et al. 2016; Rakhimberdiev et al. 2017).

Despite the growing volume of geolocator data, the spatial accuracy of geolocators used on seabirds has to-date been empirically tested relative to more precise technologies only on three species of albatross with limited latitudinal breadth (Phillips et al. 2004; Shaffer et al. 2005). These studies employed older geolocator sensors that recorded light levels more infrequently and previous threshold method geolocation software that, unlike modern methods, did not incorporate movement models or probabilistic algorithms. These studies measured the distances of satellite Platform Terminal Transmitter (PTT) locations to corresponding geolocation estimates and assessed mean accuracies ± Standard Deviation (SD) of 186 ± 114 km (Phillips et al. 2004) to 202 ± 171 km (Shaffer et al. 2005). These estimations of geolocation accuracy are coarse relative to those obtained from satellite loggers that fix positions from orbiting Advanced Research and Global Observation Satellites (ARGOS), which have a typical 1–3 km accuracy (Burger and Shaffer 2008) or the Global Positioning System (GPS), which regularly has average location accuracies of less than 10 m (Hulbert and French 2001) to ~15 m (Forin-Wiart et al. 2015). However, tracking instruments that use satellites tend to be too large for many species and may be prohibitively expensive. Satellite tracking instruments typically have limited power capacity and on-board memory

storage, and depending on the species, can place unreasonable burdens on birds in terms of wing-loading and hydrodynamic drag (Phillips et al. 2004; Shaffer et al. 2005). Furthermore, attaching satellite instruments to feathers for long-term deployments is not suitable for most seabirds because they periodically moult. For many seabird species the use of harness attachment to remedy this constraint is not recommended (Phillips et al. 2003) and may increase mortality and device-induced behaviours (Barron et al. 2010). Light-level geolocation has therefore offered an attractive year-round alternative to satellite tracking that tackles many of the constraints associated with using larger, more spatially accurate technology.

Light-level geolocation is inherently prone to coarse spatial accuracy, particularly for estimates of latitude which are generally considered to become less accurate under increasingly "equatorial" solar profiles; that is, either nearer the Equator (spatial variation) or solar equinox (temporal variation) where and when day length changes more shallowly with latitude (Hill 1994; Ekstrom 2004; Lisovski et al. 2020). The inherent accuracy of latitudinal geolocations fluctuates by date, even if the amount of sensor shading remains constant (Lisovski et al. 2012). Weather (e.g. cloud cover) and behavioural patterns such as roosting at twilight periods can induce errors in estimates of day or night length and are thus thought to affect accuracy in geolocation (Lisovski et al. 2012). In addition, light-level data collected during breeding stages are often thought to have reduced spatial accuracy due to specific behaviours that might affect light curves (Lisovski et al. 2012; Lisovski et al. 2020). For example, some species roost on the ground (Schreiber and Chovan 1986; Corre and Jouventin 1997), brood their young at twilights (Howell and Bartholomew 1969) which can shade sensors, or nest underground in burrows (Shaffer et al. 2006). Geolocators fitted on birds that

go to roost before last light or depart nest sites after first light could therefore exhibit

abnormal transitions between light and dark at twilight times in light curve data (Gow 2016).

Another typical behaviour of seabirds is wide-ranging movement that can occur

within a single day or night (McDuie et al. 2015; Clay et al. 2018). Such large-scale

movement between twilights can impact interpolations of longitude by shifting the solar

noon, or latitude by compressing or elongating day length, all depending on the speed and

direction of travel and time of year (Lisovski et al. 2012). Furthermore, data collected by

geolocators fitted to wide-ranging seabirds, generally on leg rings, are likely to have

idiosyncratic differences relative to being collected at a stationary location (Lisovski et al.

2012, Welch and Eveson 1999). Accordingly, it has been suggested that the performance of

geolocators might be species-dependent (Shaffer et al. 2005) and that the choice of

geolocation algorithm might affect the accuracy of position estimates (Musyl et al. 2001).

Despite the well-known and hypothesized limitations of light-level geolocation,

geolocators have generally been considered satisfactory for studying foraging ranges (Phillips

et al. 2004), and habitat preferences and distributions of pelagic seabirds (Shaffer et al. 2006;

González-Solís et al. 2007; Guilford et al. 2009; Egevang et al. 2010; Pollet et al. 2014;

Lascelles et al. 2016; McDuie and Congdon 2016; Quillfeldt et al. 2017; Halpin et al. 2018).

Here, we sought to evaluate for the first time the accuracy of modern geolocation algorithms

on a large and diverse sample of free-flying seabirds and assess whether accuracy is affected

by the species being tracked and movement behaviours. Past studies of geolocation accuracy

have used older technology and/or geolocation algorithms (e.g., Phillips et al. 2004, Shaffer

et al. 2005), evaluated static deployments of tags either carried by resident birds or fixed in

the environment (e.g., Fudickar et al. 2012), or been carried out on single species with sample

sizes that are likely too small to have adequate statistical power to disentangle patterns in accuracy (e.g., Rakhimberdiev et al. 2016).

Our objectives were to 1) investigate if the spatial accuracy typically reported in geolocation studies of seabirds is applicable in the context of a large-scale, multi-species study; 2) test uncertainty estimates of more advanced geolocation models; 3) test whether sea-surface temperature (SST) interpolation improved average accuracy in these new methods; and 4) model which situational factors most affected geolocator spatial accuracy. To address these aims, we conducted a field test using synchronous deployments of GPS loggers and geolocators fitted to individual seabirds from around the world. We measured the spatial accuracy of geolocator-interpolated routes from GPS tracks, tested for effects of species and individuals, and whether the inter-twilight distances travelled by birds affected the spatial accuracy of geolocation.

3.3 Materials and methods

3.3.1 Study Species & Locations

We analysed synchronous location data from 151 chick-provisioning individual seabirds that were tracked concurrently with GPS and light-level geolocator loggers (i.e., "double-tagged") using the geolocation packages, FlightR (Rakhimberdiev et al. 2017) and probGLS (Merkel et al. 2016). Tracking data represent 200 deployments across five species from 11 separate seabird colonies between 2011 – 2019 (Table 1). We originally had access to 278 double-tagged deployments (some individuals were tagged more than once within and between years), but we reduced the dataset to 200 deployments after excluding those with insufficient data to produce stationary calibrations, or where light curve transitions were poor. Breeding colonies were located in several marine regions including in Southern Europe (Mediterranean

Sea), West Africa (east Atlantic Ocean) and Australia (south Pacific Ocean). In the northern hemisphere, we analysed double-tagged deployments from Cape Verde Shearwaters (*Calonectris edwardsii*, *n* = 11; 2014 and 2018), Cory's Shearwaters (*C. borealis*, *n* = 100; 2011 and 2013–2018), Scopoli's Shearwaters (*C. diomedea*, *n* = 61; 2014–2018) and Red-billed Tropicbirds (*Phaethon aethereus*, *n* = 7; 2017–2018) on 10 breeding colonies between latitudes 15°N – 40°N. In the southern hemisphere, we analysed double-tagged deployments from White-necked Petrels *(Pterodroma cervicalis, n* = 21; 2018 and 2019) on a single colony at latitude 29°S.

Colony Name	Latitude	Country	Marine Region	Species (*n* individuals)	Number of Geolocations	
					FLightR	probGLS
Cala Morell (Menorca)	40.1°N	Spain	Mediterranean	Scopoli's Shearwater (52)	574	626
Islas Columbretes	39.9°N	Spain	Mediterranean	Scopoli's Shearwater (4)	73	77
Isla de Cabrera	39.2°N	Spain	Mediterranean	Scopoli's Shearwater (2)	24	26
Isla de las Palomas	37.6°N	Spain	East Atlantic	Scopoli's Shearwater (3)	41	44
Islote de Montaña Clara	29.3°N	Spain	East Atlantic	Cory's Shearwater (32)	441	501
Timanfaya (Lanzarote)	29.0°N	Spain	East Atlantic	Cory's Shearwater (6)	92	43
Veneguera (Gran Canaria)	27.8°N	Spain	East Atlantic	Cory's Shearwater (62)	598	1206
Ilhéu Raso	16.6°N	Cabo Verde	East Atlantic	Red-billed Tropicbird (2)	8	10
Ilha Boa Vista	16.2°N	Cabo Verde	East Atlantic	Red-billed Tropicbird (5)	48	52
Ilhéu de Curral Velho	15.9°N	Cabo Verde	East Atlantic	Cape Verde Shearwater (11)	189	199
Phillip Island (Norfolk Island)	29.1°S	Australia	South Pacific	White-necked Petrel (21)	993	410

Table 1. The species, individuals, regions, and respective colonies tracked synchronously with light-level geolocators and GPS loggers. The sample size of geolocation estimates used in analyses of each geolocation algorithm is provided. *Note*: The number of geolocations per package (i.e., FLightR or probGLS) differs depending on the suitability of the data for analysis in a given package. For example, whether the geolocator recorded water temperature exclusively when immersed, and calibration data from a stationary location.

3.3.2 Double-tagging

We fitted birds with one of five light-level geolocator immersion sensors: BAS_MK19 (British Antarctic Survey) or Biotrack_MK3005 [formerly BAS_MK19] (Biotrack Ltd), which sample light intensity every minute and record the maximum value every 5 min with water temperature recorded when the sensor is immersed continuously for 25 min; and Intigeo-C330, Intigeo-C250, or C65-SUPER (Migrate Technology Ltd), which sample light intensity every minute, storing the maximum value every 5 min and record water temperature when the sensor is immersed continuously for 20 min. The conductivity (wet/dry) sensor sampling rate was 6 s for all models. Devices were leg-mounted and fitted to the tarsus by mounting to either a darvic or metallic ring using a plastic cable tie, or a Velcro© (38 mm, Paskal, Braeside, Vic, Australia) hook-and-loop harness. GPS loggers were fitted to birds using Tesa© tape (4651, Tesa Tape Inc., Charlotte, NC, USA) by taping either to contour feathers between scapulae, or at the base of the two to four central rectrices on shearwaters and petrels and six rectrices on tropicbirds.

3.3.3 Data preparation and analysis

All data were processed in the statistical software environment R, version 3.5.1 (R Core Team 2020), and spatial measurements were calculated on the World Geodetic System (WGS 1984) ellipsoid. The processing of geolocation data was carried out by an analyst who had no knowledge of the spatial attributes of the paired GPS tracking data so that decisions about parameterising geolocation algorithms were not influenced by prior knowledge of the birds' underlying movements. This was done to ensure that geolocation positions in our study would be comparable to those of other geolocation studies for which practitioners typically have no knowledge of where the bird travelled. GPS tracks were standardized using the package adehabitatLT (Calenge 2006) by resampling all GPS locations to an equal 10 min

interval because the GPS sample rates varied among species and colonies. We gap-filled GPS tracks except when periods of more than 1 h occurred between fixes. To account for erroneous positions that may have been caused by poor satellite reception, we applied a standard maximum allowable flight velocity of 27.8 m/s^{-1} (100 km/h^{-1}) between consecutive locations for all seabird taxa. We considered this to be a maximum realistic speed for wide-ranging seabirds (Lascelles et al. 2016).

Depending on the brand of geolocator, we first imported raw light-level data using the functions readMTlux in the package TwGeos (Wotherspoon et al. 2016) or ligTrans in the package GeoLight (Lisovski and Hahn 2012). We then automated twilight event (i.e., sunrises and sunsets) annotation in raw light-level data using the function preprocessLight in the package TwGeos (Wotherspoon et al. 2016) with a threshold level of 1, which presented as a suitable level above which to differentiate twilights from night time noise in log-transformed data. Following guidelines in Lisovski et al. (2020), we visually reviewed raw light data to identify any areas of the time series affected by shading and manually inspected each twilight event, subsequently deleting such events that we deemed to be falsely annotated in the automated procedure, or those with poor transitions between dark and light. Indistinguishable or unclear transitions between dark and light can occur due to the light sensors becoming shaded by weather, individual bird behaviours, or bird plumage. This procedure resulted in an average rate of transition exclusion of 33.6% for Cape Verde Shearwaters, 29.1% for Cory's Shearwaters, 33.9% for Red-billed Tropicbirds, 32% for Scopoli's Shearwaters and 14% for White-necked Petrels. We expected to see a greater proportion of twilights excluded in these data because birds were in their breeding phase. Contrary to non-breeding, migratory seabirds, those in their breeding phase regularly visit

nests, or raft on the water before visiting nests which can cause obscured light curves at twilight times.

We used two geolocation analysis packages to estimate the spatial locations of tracked seabirds: FlightR and probGLS. Using the annotated twilight data, we produced "TAGS" files using the TwGeos2TAGS function in the FLightR package in preparation for light-level analyses. We analysed light-level data from 171 deployments in FLightR and 185 deployments in probGLS, which included 156 of the same datasets used in FLightR (15 deployments analysed in FLightR were excluded from probGLS because they did not collect SST data exclusively when the device was immersed in water). Data from sensors that recorded light and temperature, but did not have light data recorded from a stationary location were included in probGLS but excluded from FLightR analyses. While on-bird geolocator calibration is possible for some centrally placed species (see Rakhimberdiev et al. 2017), we considered that it may not be suitable for seabirds due to the large distances travelled during foraging. Calibrations were therefore conducted as 'rooftop calibrations' (see Lisovski et al. 2012). All species reported were included in analyses by both geolocation packages.

3.3.4 Estimating spatial locations from light-level data

We parameterised both geolocation algorithms (FlightR and probGLS) to calculate seabird locations within a bounding box extending from the breeding colony by 35° of longitude in each direction, and 25° of latitude in the direction of the nearest pole and 50° of latitude in the direction of the Equator.

The geolocation analysis package, FLightR was used first to estimate the spatial likelihood of locations from annotated light-level data. To model movements, FLightR uses a hidden Markov model with the true location as the unobserved state. Inference is performed using a particle filter, with a template-fit method to allow the algorithm to use all available light measurements around annotated twilight events (Rakhimberdiev et al. 2017). FLightR also incorporates biologically-relevant behavioural parameters to improve location estimates. To function, FLightR requires calibration data from each geolocator with which it measures the relationship between observed light levels (i.e., calibration data) and theoretical light levels estimated from current solar elevation angles (Ekstrom 2004; Rakhimberdiev et al. 2017). When executing the FLightR algorithm, we included only data from geolocators that were calibrated by measuring light-levels at a stationary location prior to deployment on a seabird. Analyses in FLightR were run with and without spatial masks to explore how land-masking affected accuracy. We set the algorithm to allow maximum daily flight distances of 1,500 km on a 50 km grid. To estimate locations, we ran the FLightR particle filter with 1 million particles and used the median of the posterior probability distribution as the estimates of daily seabird relocations.

For light-level data from geolocators that also recorded SST, we analysed the same annotated twilights with the package, probGLS (Merkel et al. 2016), to investigate whether SST interpolation improved the spatial accuracy of geolocations. The probGLS algorithm estimates locations using an iterative forward step selection process, computing a weighted probability cloud of potential locations (10,000 particles for each point cloud) and producing the most likely movement path with 200 iterations for each track (Merkel et al. 2016). We included flight speed parameters for when the loggers were dry (probable maximum and SD (ms^{-1}), see supplementary metadata) based on Spear and Ainley (1997) and a maximum

allowable dry-logger flight speed of 27.8 ms^{-1}, thus matching the speed used to filter GPS

relocations; and wet speed parameters to allow for modest drift on the ocean if the bird was

roosting on the water for long periods (fastest most likely = 1 ms^{-1}, SD = 1.3 ms^{-1}, maximum

= 5 ms^{-1}). Geolocations were estimated using probGLS with a land-mask to prevent the

algorithm from estimating locations more than 1 km inland of coasts. We also used the daily

median SST encountered by each bird, which was computed from that recorded by

geolocators every 4 h (Merkel et al. 2016) and matched this to satellite-derived SST (0.25° ×

0.25°, NOAA OI SST V2 High-Resolution Dataset). We also ran probGLS both with and

without SST matching and land-masking.

3.3.5 Measuring and modelling spatial accuracy

To measure the spatial discrepancy between geolocations and GPS positions, we calculated

the distance between the geographic mean of all GPS fixes that occurred within ± 30 min,

respectively, of a given pair of twilights (i.e., sunset-sunrise or vice versa) and the geolocator-

estimated solar noon/midnight position for that same period. This measure of accuracy is

expressed as the great-circle distance in kilometres from an individual's GPS location to its

corresponding geolocation for a given set of twilight events. To investigate the potentially

non-linear effects of predictor variables on the spatial accuracy of geolocation estimates, we

constructed Generalized Additive Mixed-effects Models (GAMM) with a gamma distribution

and a log link function. We separately modelled geolocation accuracy in position estimates

computed by both the FLightR and probGLS analysis packages.

We considered two predictors of geolocation accuracy: spatial displacement as the

great-circle distance (kilometres) between successive twilight locations (from GPS) for

individuals, and the expected inter-twilight period as the expected duration of day or night

calculated from day of year and GPS latitude using the daylength function in the package geosphere (Hijmans 2019). We modelled these as non-linear effects using univariate thin-plate regression splines. We initially considered two other potential predictors of geolocation error: latitudinal position and closeness in time to the March and September equinoxes; but we could not consider these as independent variables due to strong concurvity with the inter-twilight period predictor, which we considered an equatorial solar profile index and the more proximate mechanism governing geolocation accuracy. We included the model of geolocator as a fixed effect. To account for potential effects of species and individuals, we also included the identity of each tracked individual nested under species type as random effects in the model.

Both geolocation packages contain spatial masking functions to avoid the algorithms estimating positions over land. In our data, this would likely have masked the effects of modelled covariates on spatial error, particularly for birds restricted to the relatively small Mediterranean Sea. Therefore, we modelled the effects of covariates on geolocation accuracy only on the position estimates produced without a land-mask (both packages), SST (probGLS) or inbuilt outlier detection (FLightR). We used a correlogram to examine for residual autocorrelation in the time series of geolocations. Some evidence of autocorrelation was evident at the first time lag, but thinning the dataset to include only every second or third observation had no effect on the overall model results. Thus, we did not thin time series of geolocations.

We fitted the models by Restricted Maximum Likelihood using the package mgcv (Wood 2011). We used the inbuilt checks of the mgcv package to ensure that the models converged and that the basis dimension was sufficiently large (using a permutation test for

the presence of a residual pattern along predictors). The residuals of the fitted models were inspected to ensure that residuals followed the gamma distribution assumption and that there was no evident structure or heterogeneity of variances against candidate predictors.

3.4 Results

Our initial geolocation results were implemented without applying land-masks or SST interpolation and produced mean spatial accuracy ($\pm$ SD) of 432 ± 460 and 372 ± 290 km for FLightR and probGLS, respectively (Table 2). When we applied land-masks (for both analysis packages), and SST (probGLS only) mean accuracies were improved to 408 ± 473 and 304 ± 413 km, for FLightR and probGLS, respectively (Table 2). As an additional test to investigate the effect of equinoxes on location accuracy, when we excluded from accuracy measurements the locations within 3 weeks (21 d) of the March or September equinoxes the mean spatial accuracies (km $\pm$ SD) were reduced to 227 ± 250 and 290 ± 369 for FLightR and probGLS, respectively (Table 2).

GPS-derived latitude was within package-specific geolocation uncertainty estimates 38.6% and 84.5% of the time for FLightR (parameter set 4, see Table 2) and probGLS (parameter set 3, see Table 2), respectively, and GPS-derived longitude fell within uncertainty estimates for 23.7% and 88.8% of geolocations, for FLightR and probGLS, respectively. Estimated uncertainties derived from package functions for each geolocation produced by each method are provided as supplementary material. We also provide as supplementary material the spatial accuracies for individual species within (i.e. ≤ 21 d) and outside (i.e. ≥ 21 d) of equinox periods. Results outputs with different parameters from the geolocation analyses are also provided as supplementary material.

Geolocation package	Parameter set	Number of deployments included	Land mask[1]	SST[2]	Outlier Detection[3]	Mean absolute latitudinal accuracy ± SD (º)	Mean absolute longitudinal accuracy ± SD (º)	Mean great-circle accuracy (km ± SD)		
								All data	Equinox periods (< 21 days)	Non-equinox periods (> 21 days)
FLightR	1	171	No	N/A	No	2.9 ± 3.7	2.1 ± 3.1	432 ± 460	670 ± 564	286 ± 300
	2	171	Yes	N/A	No	2.9 ± 4.1	2.1 ± 3.2	430 ± 508	707 ± 635	260 ± 305
	3	171	No	N/A	Yes	2.7 ± 3.8	2.2 ± 3.2	416 ± 474	659 ± 576	267 ± 318
	4	171	Yes	N/A	Yes	2.7 ± 3.7	2.3 ± 3.2	408 ± 473	702 ± 587	227 ± 250
probGLS	1	185	No	No	N/A	3.0 ± 2.6	1.2 ± 1.3	372 ± 290	484 ± 388	344 ± 253
	2	185	Yes	No	N/A	3.7 ± 3.5	1.3 ± 1.3	449 ± 381	713 ± 465	384 ± 325
	3	185	Yes	Yes	N/A	2.4 ± 3.7	1.1 ± 1.5	304 ± 413	364 ± 554	290 ± 369

Table 2. Spatial accuracy for each geolocation algorithm with specified package parameters. Accuracy is expressed as the great-circle distance between the GPS position and corresponding geolocator-derived position for a given twilight. GPS position was defined as the geographic mean of all GPS positions recorded within ±30 min of the given twilight.

[1]Spatial mask restricting estimation of locations > 1 km inland; [2]Sea-surface temperature (not currently available in FLightR); [3]Inbuilt outlier detection is not currently a function in probGLS.

We found strong evidence of a bell-shaped effect of expected inter-twilight period on the spatial accuracy of geolocations (Figure 1(A), FLightR: $F_{6.47} = 993$, $p < 0.001$; Figure 2(A), probGLS: $F_{7.1} = 718$, $p < 0.001$). Results demonstrated that spatial accuracy in both FLightR and probGLS drastically declines as expected inter-twilight periods approach 12 h (i.e., closer to an equinox or the Equator) and best at approximately 9 h and 15 h (Figs. 1(A), 2(A)). Mean spatial accuracy ($\pm$ SD) calculated on geolocation results associated with inter-twilight periods $\leq$ 10 h and $\geq$ 14 h were reduced to 243 ± 232 and 202 ± 239 km ($\pm$ SD) for probGLS (with spatial land-mask and SST) and FLightR (with spatial mask and outlier detection), respectively.

We found significant effects of differences among species and individuals on the spatial accuracy of geolocations when individuals were fitted as random effects nested within their respective species type (Figure 1(C), FLightR: $F_{154.7} = 25.7$, $p < 0.001$; Figure 2(C), probGLS: $F_{158.2} = 11.8$, $p < 0.001$). The model of geolocator used also affected the accuracy (Figure 1(D), FLightR: $F_{4.0} = 5$, $p < 0.001$; Figure 2(D), probGLS: $F_{4.0} = 16.8$, $p < 0.001$). We found that there was an effect of an individual's spatial displacement within expected inter-twilight periods on the accuracy of geolocations when using FLightR (Figure 1(B), $F_{2.3} = 40.3$, $p < 0.001$), but not for probGLS (Figure 2(B), $F_{0.5} = 0.35$, $p = 0.111$).

Figure 1. Response curves for spatial accuracy in FLightR geolocations as a function of expected inter-twilight period (a) and spatial displacement (b) with individual identity nested within species (c) and geolocator model as a fixed effect (d). Tick marks on the horizontal axis of the expected inter-twilight period (a) and displacement (b) plots are observed datapoints. For each predictor with a smooth term (a and b), the effect on spatial accuracy is shown on the y-axis and represented as a spline (s) of the predictor variable with the estimated degrees of freedom. Shaded grey areas in the expected inter-twilight period (a) and displacement (b) plots indicate 95% confidence intervals.

Figure 2. Response curves for spatial accuracy in probGLS geolocations as a function of expected inter-twilight period (a) and spatial displacement (b) with individual identity nested within species (c) and geolocator model as a fixed effect (d). Tick marks on the horizontal axis of the expected inter-twilight period (a) and displacement (b) plots are observed datapoints. For each predictor with a smooth term (a and b), the effect on spatial accuracy is shown on the *y*-axis and represented as a spline (s) of the predictor variable with the estimated degrees of freedom. Shaded grey areas in the expected inter-twilight period (a) and displacement (b) plots indicate 95% confidence intervals.

The average spatial accuracy differed depending on species and geolocation package (Figure 3), with Red-billed Tropicbirds producing the poorest accuracy between GPS and corresponding geolocator positions in the probGLS results, whereas White-necked Petrel geolocations had the poorest accuracy in the FLightR results. Scopoli's Shearwater geolocations had consistently better spatial accuracy relative to other species (Figure 3) in all model runs of both geolocation packages, including when SST and spatial masks were not applied.
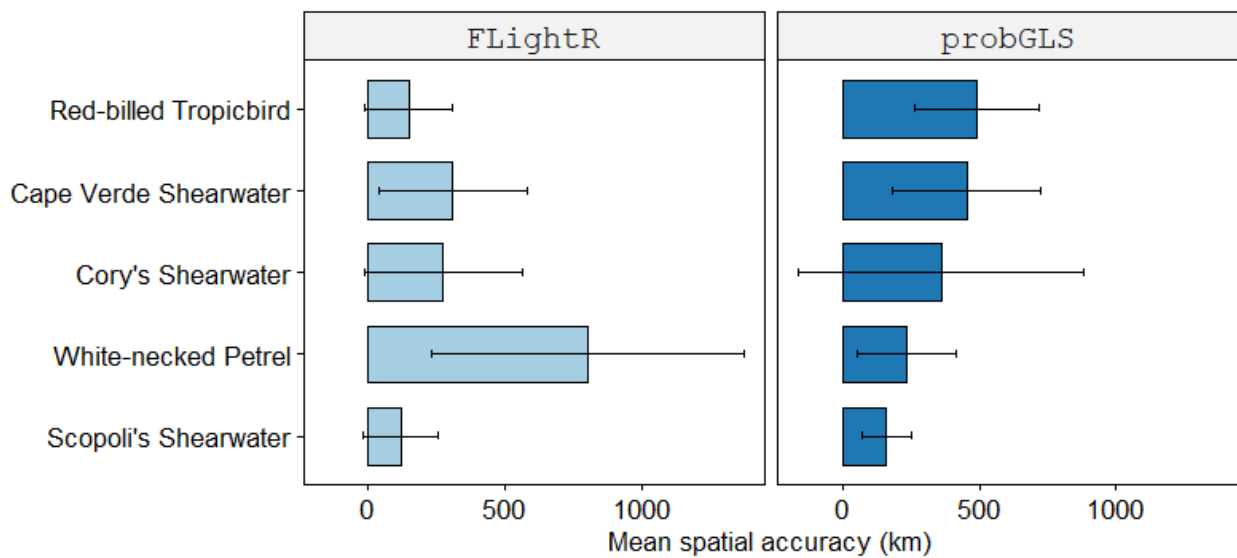
Figure 3. Mean spatial accuracy for each double-tagged seabird species as derived from the FLightR package (left) with a spatial land mask applied (parameter set 4, see Table 2) and probGLS package (right) using SST correction and a spatial land mask (parameter set 3, see Table 2). Accuracy is expressed as the great-circle distance between the GPS position and corresponding geolocator-derived position for a given twilight. GPS position was defined as the geographic mean of all GPS positions recorded within ±30 min of the given twilight. Distances were measured on the WGS 1984 ellipsoid. Error bars represent the standard deviation

3.5 Discussion

We provide the first large-scale assessment of the spatial accuracy of modern geolocation algorithms under field conditions. The advance in understanding our findings provide contextualises the results and hypotheses of past tests of geolocation accuracy that have until now been limited in field testing (e.g. static tags, small sample sizes, single species studies, outdated methods). Our results emphasize the need for practitioners to account for species and spatiotemporal effects on geolocation accuracy by considering both when (i.e., temporal effects) and where (i.e., equatorial effects) they might expect a species to travel. If the former is either a wandering, circuitous or tropical path, the practitioner should be adequately aware of what scale their data could be analysed. This is particularly true of land birds, which do not have the luxury of using SST to enhance the accuracy of interpolation.

We observed lower mean spatial accuracy in light-level geolocation of seabirds than what is typically reported as the expected accuracy in studies that use this tracking method. Moreover, the true location of a seabird was often outside of package-specific uncertainty estimates (as much as 76.3% of the time for FLightR and 15.5% of the time for probGLS). We also observed that the spatial accuracy in light-level geolocation of seabirds varies among species. As previously suggested by Lisovski et al. (2020) and Shaffer et al. (2005), it is likely that inconsistent accuracy is the result of species-dependent geolocator performance, which relates to the way in which the geolocator light sensors are affected by a combination of species-specific behaviour, morphology, plumage and habitat use. It is possible that smaller geolocator models are more prone to sensor shading than larger models, but we could not reliably test this hypothesis due to the confounding effects of species and individuals.

The method and quality of calibration can influence geolocation accuracy (see Lisovski et al. 2012 for a detailed discussion), so it is important that geolocation practitioners carefully consider

calibration when planning their study. In particular, the calibration period should capture the complete variability in twilight transitions and care must be taken to ensure that the calibration method is suitable for the focal species (Lisovski et al. 2012). It is possible that calibration effects contributed to the poor accuracy seen in the FLightR results of some of the species we tracked – particularly in the case of White-necked Petrels due to their very long-distance, looping trips away from the colony whence the geolocators were calibrated. However, we used standard 'rooftop' calibration methods that are commonly used by seabird biologists. Therefore, we expect our geolocation accuracies to be directly comparable to those obtained by seabird biologists in other geolocation studies.

Our modelling results showed that differences in species and individuals affected how accurate geolocations were. For example, in probGLS geolocation, Red-billed Tropicbirds had the poorest mean spatial accuracy. This could be explained by the species' morphology (i.e. extremely short tarsi) and nesting habits, which often include returning to the nest before or during sunset and sunrise, affecting geolocator performance. Conversely, White-necked Petrels had the poorest mean spatial accuracy in FLightR geolocation, which our models suggest is explained by their wide-ranging movement habits and large spatial displacement between twilights. The vastly different performance between FLightR and probGLS for this species supports the assertion that using SST correction is important for geolocation of wide-ranging marine species (Shaffer et al. 2005). Mean spatial accuracy in Scopoli's Shearwater geolocations was good relative to other species possibly due to the species being restricted to a relatively small marine area (i.e., the Mediterranean Sea) compared to the other open-ocean foraging species that we tracked in this study.

Spatial displacement of individuals between sunrises and sunsets affected the accuracy of geolocations produced by both packages, but was strongest in FLightR. Scopoli's Shearwaters made short-range movements within a small marine basin, and hence displacement did little to

diminish their geolocation accuracy in either package. In the case of probGLS, the application of a land-mask will have forced the algorithm to produce these geolocations within a small marine area, thus improving the latitudinal accuracy when using a spatial land-mask. However, the species still had the highest mean spatial accuracy when a land-mask was not applied. The spatial displacement of individuals between sunrises and sunsets appeared to be weakest in its effect on accuracy of geolocations estimated by the probGLS package, which suggests that the accuracies we observed for this package are not only applicable to breeding seabirds that exhibit central place foraging behaviour, but also for non-breeding or migratory seabirds. For these reasons, researchers working on coastal-foraging seabirds or seabirds in small marine basins will likely achieve useful results using either the FLightR or probGLS packages, whereas probGLS seems most suitable for researchers working on open ocean-foraging seabirds.

The FLightR package sometimes did not produce uncertainty estimates at the start of deployments, or for short-term deployments. This may have occurred because, for a given geolocation, FLightR determined low probability of movement between twilights (Rakhimberdiev et al. 2017). It is important to recognize that FLightR was designed to track migratory paths, therefore the algorithm may not calculate a probability of movement away from a capture location when tracking duration is short and when the tracked individual is in a state of central place foraging.

Our results suggest that the effect of spatial displacement on FLightR geolocations was driven by White-necked Petrels, which had the largest mean spatial displacement between twilights (more than double that of all other included species). This effect was likely due to the inbuilt Bayesian priors of the movement model incorporated by the FLightR algorithm. For geolocation of marine species, the FLightR package may benefit from the inclusion of SST as an optional model prior.

We found that the strongest predictor of accuracy was the duration of day or night between twilight events, with this pattern broadly consistent between expected day or night length (i.e. expected inter-twilight period calculated from GPS latitude) contrasted with the empirical geolocator-observed duration of day or night (i.e., calculated from raw light-level data). Our results empirically demonstrate why those using light-level geolocators should not only expect spatial accuracy to be lower during periods of solar equinox when day and night length is similar across the globe, but also as tracked animals move nearer the Equator where day and night length changes ever more shallowly per degree of latitude (Hill 1994; Ekstrom 2004; Lisovski et al. 2012). Our results imply that practitioners should adopt variable spatial uncertainties by estimating a relative spatial accuracy based on observed inter-twilight period calculated from geolocator data, rather than by excluding data from an arbitrary duration either side of the March and September equinox dates, as is done in many geolocation studies (e.g., Fayet et al. 2016; Van Bemmelen et al. 2017; Jones et al. 2020). This approach not only tackles the issue of reduced spatial accuracy during solar equinoxes, but also of equatorial solar profiles and is a particularly important advance for geolocation of animals that migrate to or reside on or near the Equator. The spatial accuracy of geolocation differs between species and inference method, but the relationship between geolocator-observed inter-twilight period and relative accuracy is consistent between periods of 9 h and 15 h, and closely follows a Gaussian function. We can therefore provide a rule-of-thumb for estimating the relative spatial accuracy of geolocations depending on the apparent inter-twilight period, which can be computed directly from geolocator data. The equation:

$\exp(-0.5\left(\frac{d-12}{1.2}\right)^2)$, where d is the duration in hours between the first and second twilight, gives the spatial accuracy in an estimate, relative to the accuracy with a duration of 12 h. For example, when $d = 12$ the relative accuracy is 1, but at $d = 9$ or $d = 15$, the relative accuracy is 0.044, a 95.6% improvement in accuracy relative to when the duration of an inter-twilight period is 12 h and accuracy is at its worst. When $d > 15$ or $d < 9$, this rule is not generalizable (see supplementary material).

Our results present mean spatial accuracies that are within the order of magnitude of the reported average spatial errors (94–1,043 km) in studies of other marine vertebrates (Delong et al. 1992; Hull 1999; Beck et al. 2002; Teo et al. 2004), but, in some species, are considerably larger than those that have previously measured accuracy in geolocation of pelagic seabirds (186–202 km, Phillips et al. 2004; Shaffer et al. 2005; Merkel et al. 2016). Based on our results and considering previous studies that improved geolocations with SST (Delong et al. 1992; Gunn 1994; Hill 1994; Le Boeuf et al. 2000; Teo et al. 2004; Shaffer et al. 2005), we suggest that for pelagic seabirds, using SST as a prior in geolocation models might be essential to achieve better results and to increase spatial accuracy in light-level geolocation. Furthermore, the variation we observed between geolocation packages and geolocator types, and among outputs resulting from differently parametrised geolocation analyses (e.g., use of a land-mask, SST interpolation etc.) validate the recommendations of Lisovski et al. (2020) concerning reporting of study parameters. Specifically, practitioners should clearly and unambiguously report assumptions and package-specific model parameters used to compute geolocations along with estimates of uncertainty associated with the data.

Light-level geolocation and geolocators are unquestionably important tools for studying the movement ecology and behaviour of marine organisms, and in many cases are the only available options to track small or sensitive species. Based on our results, we urge greater caution and consideration of the limitations of light-level geolocation when using geolocator data to draw inferences about regional spatial use and behaviour of wide-ranging marine species. Light-level geolocation is not an exact science and different combinations of geolocation packages, parameterisation, study species and data quality can yield different results and uncertainties. The key message in this study is not a criticism of light-level geolocation due to its inherent spatial uncertainty, but a demonstration that this can be reduced if practitioners adopt a dynamic approach to estimating uncertainty using duration of the inter-twilight period. While the spatial accuracy of

geolocation may vary between packages, species and the quality of calibration data, the influence of the inter-twilight period on relative accuracy will be valid irrespective of the geolocation package chosen, or the species tracked. In particular, practitioners should make use of dynamic uncertainty estimates based on equatorial solar profiles and be aware that the average accuracy that one can expect will vary by species and might be greater than what is typically reported in seabird geolocation studies. This is especially important in the context of using geolocator-derived tracking data when precise, spatially-explicit conservation or management actions are to be implemented.

3.6 Acknowledgements

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3.7 Supplementary materials

Supplementary materials associated with the published version of this chapter are freely available for download from the publication url:

https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210X.13698

3.8 Data and code accessibility

Data and code used in these analyses are archived on the Dryad Digital Repository https://doi.org/10.5061/dryad.gb5mkkwpf (Halpin et al., 2021).

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CHAPTER 4

Arthropod predation of vertebrates structures trophic dynamics in island ecosystems

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4.1 Abstract

On isolated islands, large arthropods can play an important functional role in ecosystem dynamics. On the Norfolk Islands group, South Pacific, we monitored the diet and foraging activity of an endemic chilopod, the Phillip Island centipede (*Cormocephalus coynei*), and used a stable isotope mixing model to estimate dietary proportions. Phillip Island centipede diet is represented by vertebrate animals (48%) and invertebrates (52%), with 30.5% consisting of squamates, including the Lord Howe Island skink (*Oligosoma lichenigera*) and Günther's island gecko (*Christinus guentheri*); 7.9% consisting of black-winged petrel (*Pterodroma nigripennis*) nestlings; and 9.6% consisting of marine fishes scavenged from regurgitated seabird meals. Centipede predation was the principal source of petrel nestling mortality, with annual rates of predation varying between 11.1% and 19.6% of nestlings. This means that 2,109–3,724 black-winged petrel nestlings may be predated by centipedes annually. Petrels produce a single offspring per year; therefore, predation of nestlings by centipedes represents total breeding failure for a pair in a given year. Our work demonstrates that arthropods can play a leading role in influencing vertebrate reproductive output and modifying trophic structures and nutrient flow in island ecosystems.

4.2 Introduction

Predator-prey interactions are important processes that regulate the structure of ecological communities, population dynamics, and nutrient transfer in food webs (Paine 1966; Sih et al. 1985; Krebs 2011; Ripple and Beschta 2012). These processes are central to many ecological studies and provide a foundation to better understand how ecosystems function, including how natural systems can maintain critical function in the face of anthropogenic disturbance and environmental change (Yodzis 1988; Johnson et al. 1996). Interactions between vertebrate predators and their prey have been described in a great diversity of phyla (Mclaren and Peterson 2008; Krebs 2011). Whereas invertebrates have been relatively well-documented as important predators of vertebrate animals in marine (Terlau et al. 1996; Brodeur et al. 2008; Wangvoralak et al. 2011) and freshwater systems

(Brodie Jr and Formanowicz Jr 1983; Mori 2004; Van Buskirk et al. 2004; Ohba et al. 2008), examples of terrestrial invertebrate–vertebrate predation are comparatively scarce (Toledo 2005; Nyffeler and Knörnschild 2013; Nyffeler et al. 2017; Nordberg et al. 2018*a*; Emery et al. 2020). Among invertebrates, arthropods are especially well-suited to vertebrate predation because they are often larger than many potential vertebrate prey and have evolutionary adaptations that increase their predatory efficiency such as venoms and toxins to incapacitate prey (Undheim et al. 2015; Luo et al. 2018).

Systematic reviews have revealed widespread reports of arthropod–vertebrate predation with arthropods in six classes and 83 families observed to prey upon vertebrates in five classes and 162 families (McCormick and Polis 1982; Valdez 2020). However, these reports generally result from opportunistic observations (McCormick and Polis 1982; Valdez 2020), and few arthropod-vertebrate predation systems have been the focus of *in situ* study (e.g., Kopp et al. 2006; Nordberg et al. 2018*a*) with most conducted in laboratory settings (e.g., Pearman 1995; Wizen and Gasith 2011).

Few studies (e.g. Emery et al. 2020) have established or quantified arthropod prey choice because it is challenging to study in a natural context. While it may be relatively easy to observe, identify and quantify foraging in large mammals, birds and reptiles that kill large prey, it can be more difficult to observe invertebrates foraging *in situ* because their behaviour tends to be cryptic, nocturnal and concealed in leaf litter or subterranean (Symondson 2002; Nordberg et al. 2018*a*). Classifying and quantifying invertebrate diet is also acutely challenging because most invertebrates are fluid feeders such that ingested prey cannot easily be identified using traditional methods such as gastric dissection (Shine 1977), gastric lavage (Antonelis Jr. et al. 1987) or pellet/faecal sampling (Southern 1954; Nordberg et al. 2018*b*). Moreover, laboratory simulations are unlikely to replicate conditions that produce natural behaviour in both predator and prey (Symondson 2002). Many of

these challenges can be resolved with relatively new technologies and forensic methods such as stable isotope analysis (Fry 2006; Layman et al. 2012) and molecular screening, including the use of polymerase chain reaction (PCR)-based methods for detecting prey DNA (Symondson 2002). Here we use a stable isotope approach paired with systematic *in situ* observations of foraging in a population of a large endemic arthropod to explore the hypotheses that A) vertebrates can form significant proportions of arthropod diet; and B) arthropod–vertebrate predation is capable of reducing reproductive output in a vertebrate population. Using a subtropical island system as an exemplar, we show that vertebrates, including reptiles, fish and seabirds form an important dietary component for a large, endemic chilopod, the ground-dwelling Phillip Island Centipede (*Cormocephalus coynei*, Figure 1). Our results illustrate that arthropods play a major role in structuring trophic dynamics and nutrient flow in an island ecosystem.

Figure 1. Phillip Island Centipede (*Cormocephalus coynei*, foreground) with an adult Black-winged Petrel (*Pterodroma nigripennis*, background). Image: L. Halpin (2018). Some foreshortening effect exists in this image with the largest Phillip Island Centipede measured at 23.5 cm (this study), and the combined head and body length of an adult Black-winged Petrel (*Pterodroma nigripennis*) estimated as 28-30 cm (Marchant and Higgins 1990).

4.3 Methods

4.3.1 Study area

Phillip Island (29°07'S, 167°57'E, Figure 2) is a small (207 ha), uninhabited subtropical island located approximately 6 km south of Norfolk Island in the South Pacific. Phillip Island supports breeding populations of 13 seabird species, the most abundant being the Black-winged Petrel (15,000-19,000 pairs) (Priddel et al. 2010; N. Carlile, unpublished data). The island also supports native reptiles and invertebrates, including Lord Howe Island Skink (*Oligosoma lichenigera*), Günther's Island Gecko (*Christinus guentheri*), endemic Phillip Island Centipede (*Cormocephalus coynei*), endemic Phillip Island Cricket (*Nesitathra phillipensis*), and native flightless crickets including *Dictyonemobius pacificus* and *D. lateralis* (Koch 1984; Otte and Rentz 1985; Rentz 1988). In addition to these native species, introduced populations of rabbits, pigs, and goats occurred on the island until the 1980s, causing widespread degradation and vegetation denudation. Following the successful eradication of these introduced species the island's vegetation has steadily been recovering (Coyne 2010; Figure 2).

Figure 2. Phillip Island (bottom) location within the Australasian region (top left) and the Norfolk Island Group (top right) where Phillip Island Centipede (*Cormocephalus coynei*) foraging behaviour was studied. Points represent survey plot locations.

4.3.2 Systematic observation of predation events

To identify and document the range of centipede prey, we searched for foraging centipedes nocturnally in six 100 m² survey plots in four habitat types known to be used by Phillip Island Centipedes and on five approximately 300 m long transects interconnected between each survey plot. Three survey plots were in woodland dominated by White Oak (*Lagunaria patersonia*) and one each in Red-leg Grass (*Bothriochloa macra*) grassland, Norfolk Pine (*Araucaria heterophylla*) forest and exposed soil habitat (Figure 2). Each of the six plots was surveyed in randomized order for 30 minutes per night over 17 nights (total 51 hours) between 27 February–29 March, 2019. A further 81 h was spent opportunistically searching for foraging centipedes on transects between

plots. During each survey, we searched for centipedes on the forest floor and on or around any habitat features such as rocks, logs and small trees using a 400 lm white LED light. We did not disturb ground features such as rocks and logs due to the high density of active seabird burrows and risk of crushing them. Upon detection of a centipede, the light source was switched to a red LED to minimise disturbance. We recorded the body length of each individual centipede and the species of prey if the individual was actively hunting (striking at prey) or feeding.

4.3.4 Predation of seabird nestlings

We monitored Black-winged Petrel (2018 $n = 56$, 2019 $n = 45$) and White-necked Petrel (*P. cervicalis*; 2018 $n = 22$; 2019 $n = 19$) nestlings over two breeding seasons and recorded nestling body weight at ~3 d intervals from near hatch date to ~45 d. Where direct predation of nestlings by centipedes was not witnessed, it was inferred from a consistent pattern of predation pathology that was directly observed in instances of centipedes consuming nestlings. In these cases, centipedes had specifically targeted the hind neck, rasping away flesh from this region, the head and soft tissue at the lower mandible (Figure 3 *A–D*). This pattern of predation is consistent with anecdotal reports of Scolopendrid centipede predation (Cloudsley-Thompson 1968; Molinari et al. 2005).

Figure 3. Black-winged Petrel (*Pterodroma nigripennis*) nestlings that have been preyed upon by Phillip Island Centipedes (*Cormocephalus coynei*). Images: L. Halpin (2018, 2019).

4.3.5 Tissue sampling

Tissue samples from centipedes and their prey were collected from February–April in 2018 and 2019 and January–February 2020 (Table 1). We sampled down feathers from Black-winged Petrel nestlings in the first week after hatching. This species was chosen because it is the only seabird species on the island that met the following criteria, which we believe contribute to its importance in the diet of centipedes: 1) breeding population > 1000 pairs; 2) burrow-nesting; 3) small-bodied (adults < 250 g); and 4) nests in summer when centipedes are likely to be most active. Samples of freshly deceased centipedes, geckos, skinks, *Dictyonemobius* sp. crickets; and fish spilled from

regurgitated meals of tree-nesting Black Noddies (*Anous minutus*) were collected opportunistically from within the seabird colony.

Species		n	δ¹³C Values			δ¹⁵N Values		
			Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.
Phillip Island Centipede	*Cormocephalus coynei*	20	-23.9 ± 0.9	-25.3	-21.8	16.9 ± 1.3	15.1	20.8
Crickets	*Dictyonemobius* sp.	10	-24.8 ± 1.3	-26.3	-22.5	14.4 ± 1.8	11.0	16.9
Günther's Island Gecko	*Christinus guentheri*	5	-23.2 ± 1.1	-24.1	-21.4	17.3 ± 2.5	13.5	20.4
Lord Howe Island Skink	*Oligosoma lichenigera*	7	-21.7 ± 1.6	-23.7	-19.4	16.0 ± 4.0	11.9	21.2
Black-winged Petrel	*Pterodroma nigripennis*	92	-18.8 ± 0.5	-19.7	-15.7	13.8 ± 0.5	12.5	15.2
Australian Anchovy	*Engraulis australis*	5	-21.7 ± 2.4	-25.2	-19.7	11.4 ± 4.6	7.3	18.9

Table 1. Sample sizes and stable isotope values (mean ± standard deviation, minimum and maximum) of Phillip Island Centipedes and their main prey species used to inform the dietary source mixing model. δ¹⁵N and δ¹³C values provided are not corrected for trophic enrichment factor (TEF).

4.3.6 Sample processing and analysis

Samples were first cleaned of potential contaminant lipids by washing in a 2:1 chloroform:methanol solution followed by two successive rinses in methanol (Cherel et al. 2008; Giménez et al. 2017). The samples were then dried in a fume hood to a constant weight for 5 d, pulverised and homogenized, before being weighed into tin capsules to an average of 1.06 mg. Stable isotope analysis was conducted at the Water Studies, Monash University, Australia. Samples were analysed on an ANCA GSL2 elemental analyser interfaced to a Hydra 20 – 22 continuous-flow isotope ratio mass-spectrometer (Sercon Ltd. UK). Our quality assurance/ quality control was carried out using four internal standards (ammonium sulfate, sucrose, gelatine and bream) which were calibrated against internationally-recognised reference materials including USGS 40, USGS 41, IAEA N1, USGS 25, USGS 26 and IAEA C-6. The internal standards were used to correct for any variations as results of peak size linearity and instrumental drift with typical reproducibility of ± 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$. Based on these internal standards, the accuracy of our data was calculated to fall within ± 0.3‰ for $\delta^{15}N$ and ± 0.2‰ for $\delta^{13}C$. Isotope ratios are expressed as conventional delta (δ) notation in parts per mil (‰) deviation relative to international standards according to the following equation: $\delta X = [(R_{sample} / R_{standard}) - 1 \times 1000]$; where X is ^{13}C or ^{15}N and R is the corresponding ratio of the heavy isotope to light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) in the sample or standard. International standards Vienna Pee Dee Belemnite (VPDB) Atmospheric Nitrogen (AIR) were used for $\delta^{13}C$ and $\delta^{15}N$, respectively.

4.3.7 Dietary source mixing model

To investigate the contribution of different prey items to the diet of Phillip Island Centipedes (*Cormocephalus coynei*), we used a Bayesian dietary source mixing model with the package, SIMMR (Parnell and Inger 2020) implemented in R (R Core Team 2021). We applied a SIMMR model with diet-to-tissue trophic enrichment factors (TEF). Published TEFs from laboratory feeding experiments for centipedes are unavailable, so we used TEFs ($\delta13C = -0.4 \pm SD 0.1‰; \delta15N = 2.1$

± SD 0.4‰) from an ex situ feeding experiment of a generalist invertebrate predator, lycosid spiders that were fed a carnivorous diet (Oelbermann and Scheu 2002). We incorporated concentration dependence means and standard deviations for dietary sources derived from the % weights of carbon and nitrogen in prey samples. The model was run with four Markov chain Monte Carlo (MCMC) chains (iterations = 50,000, burn in = 5,000, thinning = 10) and checked for convergence using Gelman diagnostic values and by plotting posterior predictive distributions.

Bayesian mixing models estimate proportional dietary contributions regardless of whether models satisfy the point-in-polygon assumptions (Figure 4) for every consumer (i.e. consumer isotopic signatures must be positioned within a polygon bounded by the mean isotope signatures of the source mixtures) (Phillips and Gregg 2003; Parnell et al. 2010). Therefore, to test the suitability of selected TEFs we used a mixing polygon simulation (5,000 iterations) approach following the method described by Smith et al. (2013) to ensure that the consumer isotopic signatures could be explained by our proposed model.
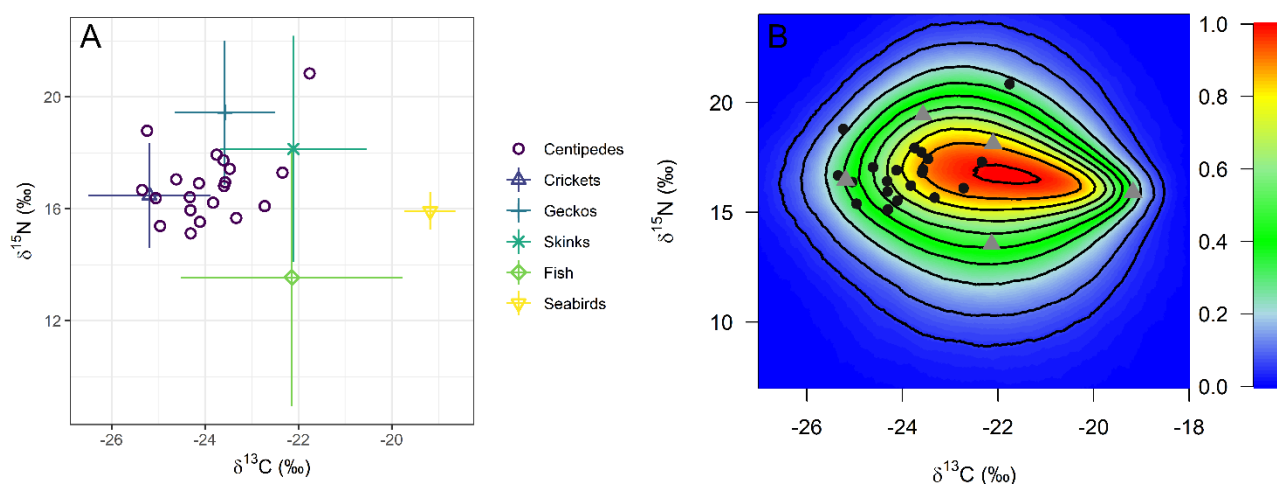
Figure 4. (A) δ^{15}N and δ^{13}C bivariate plot of the isotopic signatures for consumers (centipedes) and dietary sources (mean ± SD) from Phillip Island, South Pacific, corrected for trophic enrichment factors (δ^{15}N: 2.1 ± 0.4 SD; δ^{13}C: –0.4 ± 0.1 SD). (B) Simulated mixing region for the bivariate isospace plot (A). Positions of the centipede consumers (black dots) and the average isotope values

for dietary source signatures (grey triangles). Probability contours are drawn at the 5% (outermost contour) and at each 10% level. The simulation was run with 5,000 iterations. Prey cluster analysis revealed five clearly distinguished source clusters in isotopic space (A). The mixing polygon simulation following Smith et al. (2013) confirmed the suitability of prey sources within the model to explain centipede tissue isotopic values, with all consumers falling within the 95% contour of the mixing region (B).

4.4 Results

4.4.1 Centipede foraging

During 132 h of *in situ* foraging surveys, we observed Phillip Island Centipedes hunting or consuming a range of invertebrate, reptile, fish and bird prey, from 32 observed strikes and 21 observed feeding events (Table 2). Phillip Island Centipedes are large scolopendrids (median body length: 19 cm, range: 1–23.5 cm, $n = 440$). In 2018 and 2019, respectively, 19.6% (11 of 56 nests) and 11.1% (5 of 45 nests) of regularly-monitored Black-winged Petrel nestlings were preyed upon by centipedes. During the same periods, none of the monitored White-necked Petrel nestlings were preyed upon by centipedes. Prior to predation, Black-winged Petrel nestlings appeared healthy and were being provisioned by parents as indicated by an average mass gain (± SD) of 23.5 ± 14.7 g in the approximate 3 d interval immediately prior to predation (Figure 5). The mean body mass (± SD) of nestlings at the last measurement prior to their predation was 87.7 ± 33 g (range: 44–147 g) (Figure 5). In 2018 and 2019, respectively, there were only one and two nestling mortalities that did not exhibit signs of centipede predation and were attributed to other causes. We observed one instance of envenomation of a Black-winged Petrel nestling by a centipede (Video S1[1]) in an

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[1] **Video S1.** Phillip Island centipede (*Cormocephalus coynei*) attacking a small, downy black-winged petrel (*Pterodroma nigripennis*) nestling inside a burrow nest. During this predation event, the centipede climbed onto the nestling's back and embedded its forcipules into the nape while it gripped onto the nestling's body with its walking legs. After approximately 5 min, the centipede moved deeper into the burrow, while the nestling moved to the entrance of the burrow, shaking its head repeatedly while breathing heavily. At approximately 20 min after the initial encounter, the centipede once again attacked the nestling, dragging it into the burrow by its leg and embedding its forcipules into the thigh region. After another 6 min, the centipede released the nestling, but it returned for a third bite ~19 min later, again targeting the nape. The nestling was found breathing but otherwise unresponsive inside the burrow at 14:00 the following day. A subsequent inspection after a further 4 h revealed that the nestling had died, indicating a period of 16–20 h between envenomation and death. The nestling was not consumed by any centipede over a further 5 days of observation. It is unclear whether torch light had interrupted the predation event. Image and video by D. Terrington,2019. Video URL: https://www.journals.uchicago.edu/doi/video_original/10.1086/715702/VideoS1.mp4

exposed burrow that ultimately resulted in nestling death, where the centipede did not consume the nestling at the time of observation. We also observed a centipede consuming a nestling (Video S2[2]) from the group of study nests that, earlier on the same day, was observed alive and well, and was regularly being fed by its parents.

Crickets were the most frequently targeted and consumed prey item. Hunting strike success rates were low for frequently-targeted species, including observations of five strikes at Günther's Island Geckos where all focal individuals evaded capture. All six observations of vertebrates being consumed on the forest floor were presumably the result of scavenging. These included four instances of fish consumption, one Black Noddy nestling presumed to have fallen from an arboreal nest and one Günther's Island Gecko in a state of advanced decomposition (Figure 6).

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[2] **Video S2.** Phillip Island centipede (*Cormocephalus coynei*) consuming a black-winged petrel (*Pterodroma nigripennis*) nestling inside its burrow nest. The centipede's head is consuming flesh around the neck and at the base of the lower mandible. Image and video by L. Halpin, 2018. Video URL: https://www.journals.uchicago.edu/doi/video_original/10.1086/715702/VideoS2.mov

Prey Class	Species	Strikes (%)	Successful strikes (%)	Feeding (%)
Insecta	ant sp.	6.3	100	9.5
	Crickets (*Dictyonemobius pacificus, D. lateralis, Nesitathra phillipensis*)	65.6	19	28.6
	beetle sp.	0		4.8
	moth sp.	0		4.8
Arachnida	spider sp.	0		4.8
Diplopoda	*Oxidus gracilis*	3.1	100	9.5
Chilopoda	*Cormocephalus coynei*	3.1	0	4.8
Osteichthyes	*Engraulis australis*, fish sp.	-		19
Reptilia	*Christinus guentheri*	15.6	0	4.8
Aves	*Anous minutus*	0		4.8
	Pterodroma nigripennis	6.3	50	0

Table 2. Proportion of prey strikes, successful strikes and feeding events by Phillip Island Centipedes.

Note: Strikes ($n = 32$) are defined as the percentage of the total number ($n = 32$) of strikes accounted for by strikes at that prey taxon. Successful strikes are the percentage of those strikes that resulted in successful capture. Feeding is the percentage of the total number of feeding observations ($n = 21$) where a centipede was observed consuming a given prey taxon. Fish are deceased and discarded from tree-nesting seabird nests.
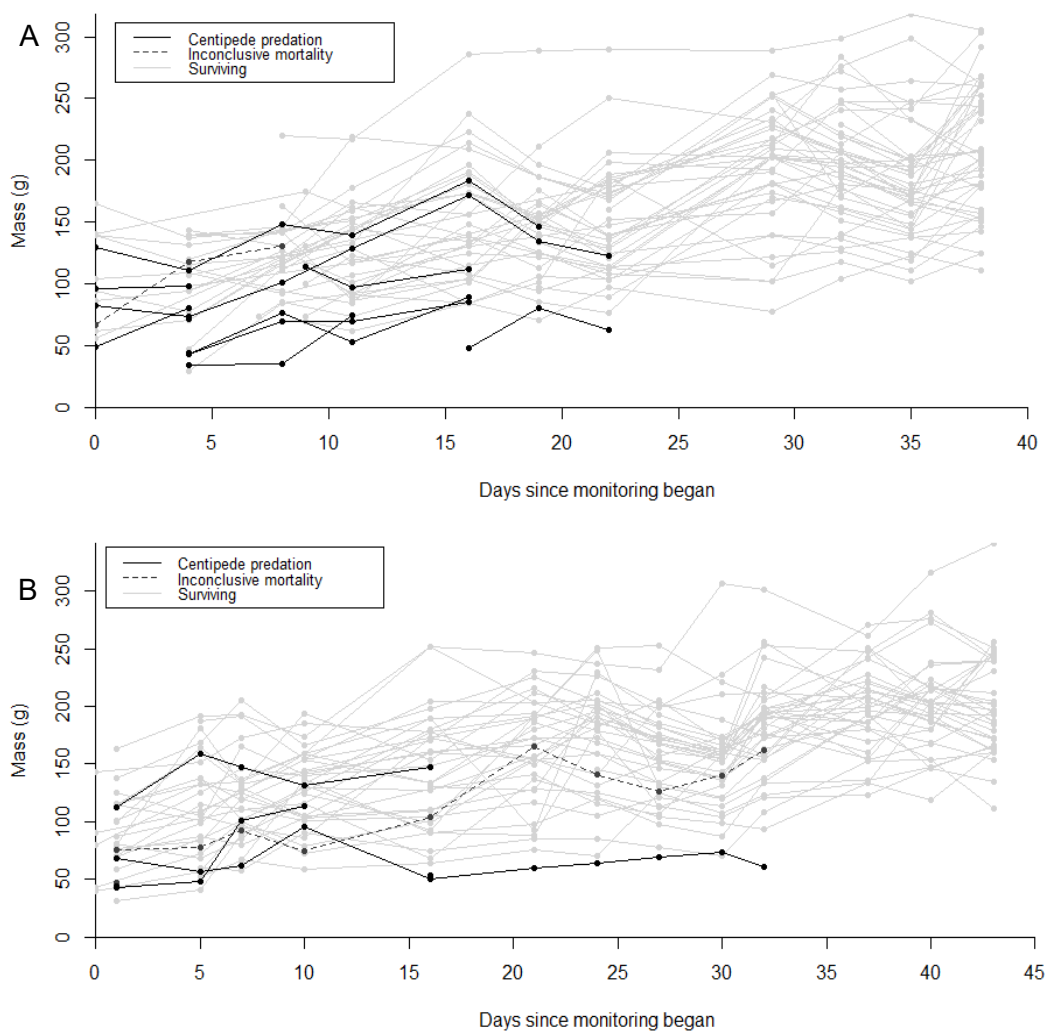
Figure 5. Black-winged Petrel nestling growth in 2018 (A, *n* = 56) and 2019 (B, *n* = 45) as a function of days since monitoring began. In 2018 and 2019, there were 11 and five mortalities, respectively, showing physical injuries consistent with centipede predation and one and two, inconclusive mortalities, respectively, that did not exhibit signs of centipede predation.

Figure 6. A Phillip Island Centipede (*Cormocephalus coynei*) consuming a scavenged Günther's Island Gecko (*Christinus guentheri*). Image: D. Terrington (2019).

4.4.2 Bayesian dietary source model results

The Bayesian dietary source mixing model (Figure 7) estimated that vertebrates form a large proportion (48%) of centipede diet with 38.4% of the diet consisting of terrestrial vertebrates: geckos (17.7%, 95% credibility interval (CI) [2.8, 38.6]), skinks (12.8%, 95% CI [1.8, 31.2]) and seabird nestlings (7.9%, 95% CI [1.6, 16.9]). Fish scavenged from regurgitated meals of seabirds formed 9.6% (95% CI [1.6, 22.5]) of centipede diet. The remainder of the Phillip Island Centipede diet (52.1%, 95% CI [33.2, 69.2]) consisted of invertebrates (crickets). While skinks were not directly observed being hunted or consumed by Phillip Island Centipedes, similarly sized giant centipedes are known to prey upon skinks in other systems (e.g. Emery et al. 2020, 2021). It is likely that Phillip Island Centipedes prey on skinks below ground or under loose leaf litter, thus skinks were included in the dietary mixing model.
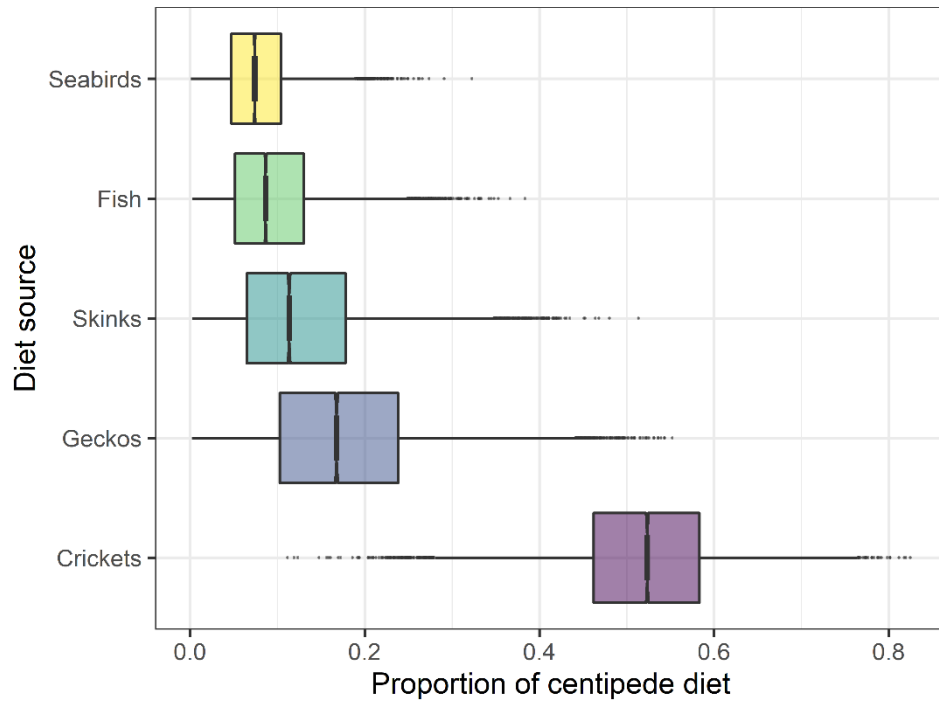
Figure 7. Estimated contribution of prey items in the diet of Phillip Island centipedes. Results present the relative proportions of dietary source contributions to centipede tissue predicted by the Bayesian dietary source mixing model (median, interquartile range, and maximum/minimum values of the posterior probability distribution). Our results demonstrate a system in which the exchange of nutrients is largely driven by arthropod predation. A schematic diagram (Figure 8) depicts the direction and strength of the trophic linkages predicted by the model, hypothesized linkages and the general flow of nutrients. Marine fish enter this terrestrial food web as discards from seabirds.
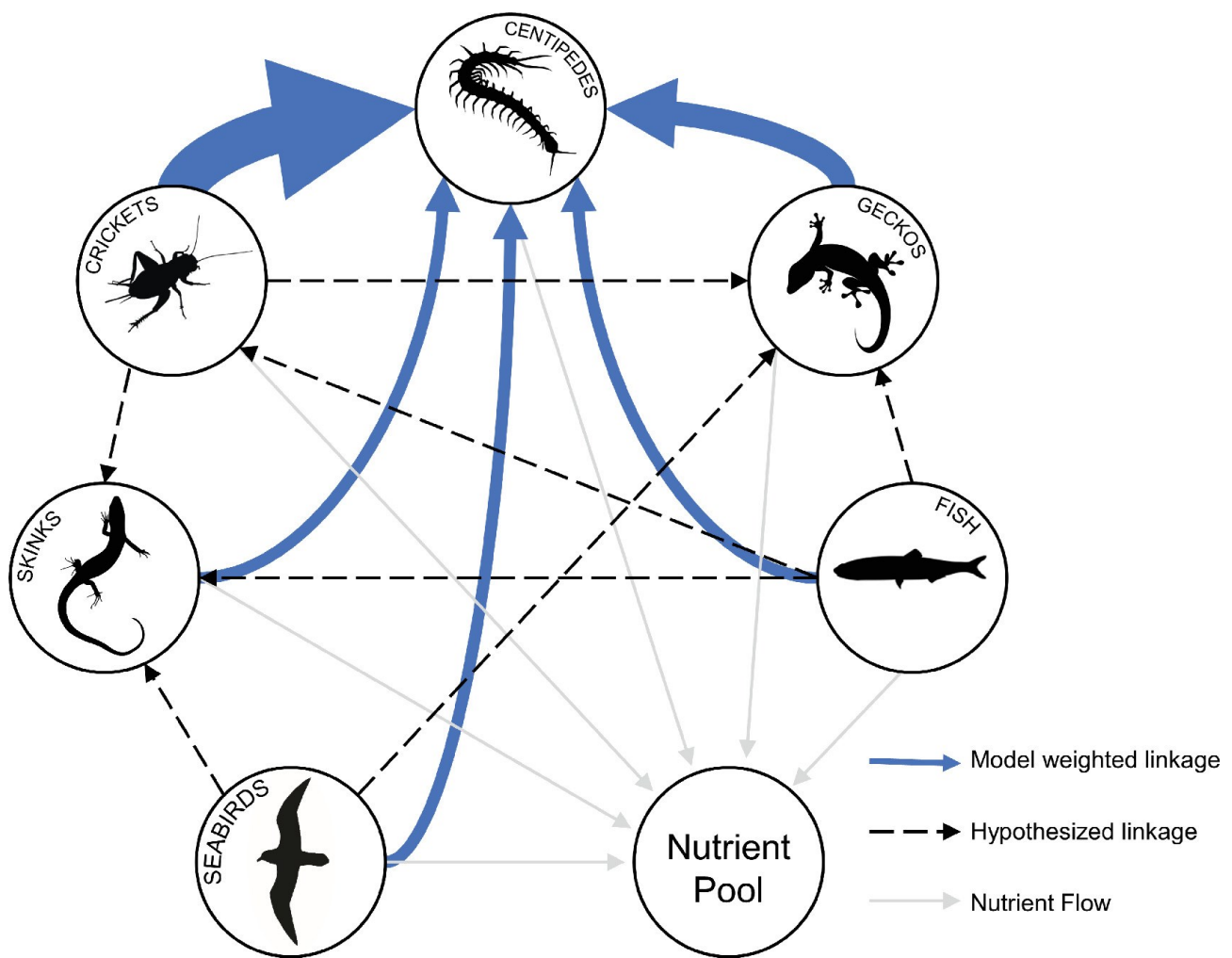
Figure 8. Schematic diagram of the general Phillip Island food web with the thickness of dietary linkages to centipedes weighted according to proportional contributions of centipede prey taxa to centipede tissue isotopic values.

4.5 Discussion

Our results demonstrate that through high rates of predation on vertebrates, arthropods can play an important role in structuring ecosystem nutrient cycling in island ecosystems. On Phillip Island, centipedes that prey on seabirds increase enrichment of the nutrient pool with marine derived nutrients by consuming seabird nestlings that are nourished by their parents exclusively with pelagic fish and squid. Predation by centipedes likely produces a more homogenous nutrient landscape. Nutrient deposition in seabird colonies is typically patchy and localised, with nutrients accumulating around nest sites via spilled food, dead nestlings and adults, abandoned eggs, and

deposition of guano (Gillham 1956; Heatwole 1971; Anderson and Polis 1999; Sánchez-Piñero and Polis 2000; Harding et al. 2004). Predation of nestlings by centipedes means that centipedes are likely to actively translocate nutrients around the island (Schmitz et al. 2010). On an island depauperate of vertebrate predators, this is a potentially important process that could expand the regeneration of the island's vegetation into degraded areas (e.g. if centipedes roam into degraded environments that are unsuitable for burrow-nesting petrels).

Our observations revealed that centipedes targeted seabird nestlings with small body sizes reflective of a young and relatively defenseless age class. By extrapolating the observed rates of centipede predation on monitored petrel nestlings, which differed between years (19.6% in 2018 and 11.1% in 2019), to the upper bound of the most recent Black-winged Petrel population estimate (19,000 breeding pairs in 2017, N. Carlile, unpublished data), we estimate that Phillip Island Centipedes consume between 2,109–3,724 seabird nestlings annually. Black-winged Petrels are long-lived (> 30 y) seabirds that produce a single offspring per year (Hutton and Priddel 2002). This means that each centipede predation of a seabird nestling represents total reproductive failure for a breeding pair in a given year. Arthropods are therefore able to reduce the lifetime reproductive output of long-lived, K-selected vertebrates. Our results not only suggest that predatory arthropods are important trophic engineers that structure nutrient flow on islands, but also verifies that they are important predators of terrestrial vertebrates in some ecosystems (Nordberg et al. 2018*a*; Valdez 2020).

Our results are consistent with reports of scolopendrid centipedes preying on vertebrates including amphibians (Forti et al. 2007), bats (Molinari et al. 2005; Noronha et al. 2015; Lindley et al. 2017), lizards (Nordberg et al. 2018*a*; Emery et al. 2020) and snakes (Smart et al. 2010; Arsovski et al. 2014). Remarkably, however, seabirds have not previously been reported as centipede prey despite centipedes and seabirds co-occurring on many islands. Our study appears to

be a rare documented example in which seabirds have been identified as direct prey of an arthropod, thereby demonstrating a novel pathway for transfer of nutrients from the marine to terrestrial environment.

The dietary source mixing model we used cannot differentiate between prey that is captured and killed, or scavenged. However, results of our *in situ* observations demonstrate that the Phillip Island Centipede is both an active predator that was the principal driver of seabird nestling mortality, and an opportunistic scavenger of other species including geckos and Black Noddy nestlings that fall from tree nests. Our foraging surveys were limited in scope (conducted on only the surface of the forest floor) and were therefore unlikely to have detected centipedes foraging under deep leaf litter or in subterranean cavities. Therefore, prey items captured and consumed underground (e.g. predation of burrow-nesting Black-winged Petrels) are likely to be underrepresented by our monitoring. Results of the dietary mixing model indicate a larger squamate contribution to centipede diet than we observed in foraging surveys, which suggests that centipedes may be more successful at preying on geckos and skinks underground.

Further supporting the conclusion that Black-winged Petrel nestlings were actively preyed upon rather than scavenged is our observation that no White-necked Petrel nestlings were consumed by Phillip Island Centipedes during nest monitoring. White-necked Petrel body mass is almost three times larger (Marchant and Higgins 1990), with their nestlings reaching a larger body mass more quickly than Black-winged Petrel nestlings and presumably they are able to defend themselves from centipedes at a younger age. This accords with our observation that Phillip Island Centipedes preyed predominantly on smaller sized Black-winged Petrel nestlings. Vulnerability to predation by rats (*Rattus* spp.) shows a similar age-dependent pattern in Grey-faced Petrels (*Pterodroma macroptera gouldi*) with predation risk declining to very low levels at ~three weeks after hatching

(Imber et al. 2000). Nevertheless, centipedes are generalists and will likely consume any deceased vertebrates encountered during foraging.

Although nestlings of other seabird species may also have contributed to the isotopic signature of Phillip Island Centipedes, we believe that Black-winged Petrel chicks are the major seabird diet constituent based on our foraging observations and aspects of the ecology of the breeding seabird community. For example, Black-winged Petrels are the only small-bodied, burrow-nesting seabird that breeds in summer (coincident with the timing of stable isotope tissue sampling) on Phillip Island. They are also the most abundant breeding seabird on the island with an abundance one to two orders of magnitude greater than nine of the 12 other breeding seabird species.

We observed a single cannibalism event among Phillip Island Centipedes, which is otherwise common in many food webs (Ings et al. 2009). We did not attempt to quantify the dietary contribution of cannibalism in the dietary mixing model given the challenges of distinguishing cannibalism from other forms of intraguild predation (Greenwood et al. 2010; Traugott et al. 2013). Large scolopendrid centipedes have been introduced to many islands, especially in tropical and subtropical regions (Shelley 2004; Shelley et al. 2014; Waldock and Lewis 2014) and have recently been implicated in the extinction of an endemic island vertebrate (Emery et al. 2020). Systems slated for conservation efforts (e.g. reintroductions of extirpated species) where large introduced centipedes, or other predatory arthropods, are present will likely require innovative solutions or centipede control to minimise impacts to recovering or colonising species targeted for conservation (e.g., Emery et al. 2020). By contrast, innovative approaches may be necessary in disturbed systems given potential interactions between native predatory arthropods and potential prey of conservation importance (e.g., Fehrer 2019; Valdez 2019).

We provide a novel understanding of the role of predatory arthropods in structuring trophic dynamics on islands. We demonstrated that arthropods can increase the flow of marine nutrients in an island ecosystem by preying on the offspring of vertebrates that forage exclusively in pelagic environments. We demonstrate how predatory arthropods can exert top-down pressure on vertebrate populations through predation-mediated reductions in reproductive output. This could have important consequences for understanding trophic structures on islands and how vertebrate communities are shaped. Perhaps especially so on islands, where arthropod gigantism is common and evolutionary processes have allowed invertebrates to occupy novel niches.

4.6 Acknowledgements

4.7 Supplementary materials

Supplementary materials associated with the published version of this chapter are freely available

for download from the publication url: https://www.journals.uchicago.edu/doi/10.1086/715702

4.8 Data and Code Accessibility

All data and code have been deposited in the Dryad Digital Repository

(https://doi.org/10.5061/dryad.9kd51c5g2; Halpin et al. 2021).

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CHAPTER 5

General discussion

Understanding the drivers and consequences of animal movements is a central theme in ecology (Stephens and Krebs 1986; Nathan 2008; Tucker et al. 2018). Knowledge of the natural processes that drive animal movement and of the evolutionary strategies that animals adopt to exploit resources allows ecologists to predict how animals might respond to anthropogenic threats and human-induced changes to their environments. Moreover, detailed knowledge about species movements is important for ecologists to gain in-depth understanding of whole-ecosystem structure and function (Nathan et al. 2008) – both being necessary for effective approaches to conservation (Nathan 2008). This is perhaps particularly important in isolated systems that receive limited nutrient input from external sources. Connecting these themes has been the driving focus of my PhD research.

Major scientific discoveries continue to be made in the field of movement ecology, alongside ongoing developments in bio-logging technology that have led to improved spatial accuracy and expansion in the types of information that can be obtained from animal-borne devices (e.g., Weimerskirch et al. 2015; Koster et al. 2021; Fischer et al. 2021). Our capacity to improve conservation outcomes has been strongly influenced by new knowledge gained through bio-logging technology (Ogburn et al. 2017; Fraser et al. 2018). Spatial ecologists are continuing to make ground-breaking discoveries about the breadth and importance of animal movements across the planet.

In marine ecosystems, seabirds are particularly attractive exemplars of animal movement because they exploit resources over large spatial scales and can demonstrate extreme evolutionary adaptations to survive in environments characterized by scarce and unpredictable resources. Moreover, seabirds play important roles in supporting ecosystem function and they are widely regarded as ideal bio-indicators of ecosystem health because seabirds respond behaviourally and demographically to biophysical changes in marine systems. Among animals, seabirds tend to exhibit particularly extreme strategies to maintain individual condition and achieve reproduction, which also makes them highly susceptible to changes in environmental conditions. From a conservation and management perspective, acquiring reliable information about the foraging behaviour and marine distributions of seabirds is crucial if we are to achieve effective conservation outcomes. The central aim of my thesis has been to better understand the movement ecology of a particularly wide-ranging group of seabirds to improve their management and conservation. In so doing, my thesis contributes to our understanding of *Pterodroma* at-sea distribution, improves the methods used by ecologists to track seabirds, and develops our understanding of the important role of seabirds as nutrient vectors in isolated systems.

In Chapter 2, I focused on the particularly wide-ranging foraging behaviour of three long-lived gadfly petrels that breed on a remote island and forage in a relatively oligotrophic marine region. I tested whether gadfly petrel foraging habitat could be predicted from underlying environmental conditions and demonstrated how gadfly petrels integrate resources across almost the entire Tasman Sea. The foraging ranges of the species I studied spanned large areas of the high seas, demonstrating that international efforts are needed to conserve their foraging habitats.

My results showed support for the hypothesis that, rather than targeting reliable and predictable resource patches, the foraging strategies of gadfly petrels are likely centred on opportunistic prey encounters (e.g., Clay et al. 2017; Ventura et al. 2020).

Using a spatially independent habitat modelling approach, I demonstrated that gadfly petrel distribution models cannot reliably be generalized to predict the probability of foraging on new spatial data and environmental conditions given currently available remote sensing data. This is most likely due to the generalist foraging habits (Elith et al. 2006; Andrew and Fox 2020) of these and other tropical seabirds. Diet diversity in tropical seabirds is thought to be low, with most species concentrating foraging on flying fish and squid (Ashmole and Ashmole 1967; Diamond 1983; Harrison et al. 1983; Ballance et al. 1997; Spear et al. 2007). With new information about the diversity and spatio-temporal distributions of squid and flying fish, the predictability of tropical seabird foraging habitat could potentially be improved (i.e., predictive performance of species distribution models for tropical seabirds might then improve).

Climate driven impacts (i.e., warming oceans, ocean acidification and extreme weather events) to marine ecosystems may have major impacts on tropical seabird populations (e.g., Rodríguez et al. 2019). Studies on the impacts of climate change on seabirds are generally biased toward higher latitudes and little is currently known about impacts on tropical species (Poloczanska et al. 2016; Keogan et al. 2018). However, climate change impacts on seabird demography are known to occur through climate-mediated predator-prey dynamics (Sydeman et al. 2015). Unabated impacts of climate change, anthropogenic pollution, industrial activity, and commercial fishing will impact the structure and functionality of tropical marine ecosystems – this could mean a reduction in the availability of prey resources for seabirds.

My research showed that breeding gadfly petrels need to travel enormous distances to obtain enough resources to maintain their own condition as well as that of their offspring. Breeding petrels need to make decisions about resource allocation which becomes a trade-off between meeting their own nutritional requirements and that of their offspring (e.g., Weimerskirch et al. 1994; Mauck and Grubb 1995). If prey availability is reduced across the Tasman Sea, gadfly petrels are likely to

transfer the costs of reproduction to their offspring (e.g., Mauck and Grubb 1995). Over time, this could result in reduced reproductive output substantial declines in tropical seabird populations. Biological diversity in the oceans generally helps to increase, maintain, and promote functional marine ecosystems (Sala and Knowlton 2006; Worm et al. 2006; Hector and Bagchi 2007).

The spatial extent of foraging in gadfly petrels coupled with their currently unpredictable foraging preferences present challenges for implementing even spatially dynamic conservation measures (e.g., Hobday et al. 2011; Maxwell et al. 2015). However, this research did demonstrate some areas of high foraging activity by multiple individual petrels between years of study, which suggests that further tracking study may reveal that some areas do represent higher foraging value than others. Such an approach to testing for repeated area use in subsequent years may be of more value to conservation practitioners that need to identify important foraging areas for gadfly petrels and other species that lack predictable foraging preferences. Furthermore, that the species tracked all exhibited dual foraging strategies offers some potential for conservation strategies to provide protection measures for the different trip types. For example, shorter foraging trips occur over much smaller areas which means that spatially explicit marine protections may be feasible at this scale (Oppel et al. 2018). However, the vast extent covered by longer foraging trips in self-provisioning gadfly petrels means that policy-based methods such as fisheries regulation (e.g., quotas and more comprehensive enforcement) or management of marine plastic pollution will likely represent the most effective tools for conserving birds undertaking these long-distance trips (Oppel et al. 2018). Therefore, from the perspective of preserving foraging habitat for gadfly petrels it is crucial for rigorous and globally coordinated efforts to preserve the structure and function marine ecosystems (e.g., Palumbi et al. 2009).

In Chapter 3, my goal was to contribute methodological improvements to deal with spatial uncertainty in a widely used method to track the movements of marine species: light-level

geolocation ("geolocators"). Geolocators are one of the most popular tools used to track the movements of seabirds, with practitioners generally expecting average spatial accuracies ± Standard Deviation (SD) of 186 ± 114 km (Phillips et al. 2004) to 202 ± 171 km (Shaffer et al. 2005). These expected spatial accuracies are derived from older geolocation methods that were tested only on three species of albatrosses. Building on Shaffer's (2005) hypothesis that geolocation accuracy likely varies by species type, I field tested the spatial accuracy of geolocators on a suite of 11 seabird species from colonies at varying latitudes with modern and widely used geolocation algorithms. My results showed that geolocation accuracy can be considerably lower than expected and confirmed Shaffer's (2005) hypothesis that spatial accuracy does indeed vary widely according to the species tracked. Increasingly equatorial solar profiles (i.e., closer temporally to equinoxes and/or spatially to the Equator) led to greater spatial error. I also demonstrated that the strongest predictor of spatial accuracy was the expected duration of day or night (i.e., expected inter-twilight period) between twilight events (i.e., sunrises and sunsets) based on the GPS-derived (i.e., true) position of a bird. This was broadly consistent with the inter-twilight period that is estimated from the data recorded by geolocators. These results present an empirical demonstration of why practitioners using geolocators should not only expect that spatial accuracy will vary according to species, but that it will also be reduced during periods of the solar equinoxes (i.e., when daylength is similar across the planet); and that spatial accuracy is reduced as animals move closer to the equator where daylength is broadly more uniform, changing shallowly per degree of latitude (Hill 1994; Ekstrom 2004; Lisovski et al. 2012).

The results of this chapter led to the development of a simple function that practitioners can implement to assess the relative spatial accuracy in their own geolocation data. The investigation of this chapter suggests that greater caution and consideration of the limitations of light-level geolocation are needed when tracking marine species. This is especially true when geolocator data are used to draw inferences about regional spatial use and behaviour of wide-ranging marine

species; and where it may be used to determine spatially explicit conservation and management actions. For example, when using geolocator derived tracking data to inform the design of marine protected areas or identifying species interactions with anthropogenic threats (e.g., commercial fisheries and resource extraction) it is important to consider that spatial accuracy will differ by species type and according to the location of the tracked species relative to the Equator.

Seabirds are widely recognised as important vectors of nutrient transfer from marine to terrestrial systems (Polis and Hurd 1996; Sánchez-Piñero and Polis 2000; Harding et al. 2004; Ellis et al. 2006; Mulder et al. 2011; Smith et al. 2011). This is perhaps especially important in isolated terrestrial systems (e.g., remote islands) that otherwise receive limited nutrient input from external sources. Seabirds are generally considered top marine predators and have not typically been regarded as important prey species for other predators. In Chapter 4, I revealed a novel role for seabirds as nutrient vectors in which seabirds are the direct prey of a large endemic arthropod, the Phillip Island centipede (*Cormocephalus coynei*). This represents a novel understanding in two important ways.

Firstly, my research demonstrated that arthropods play an important role in structuring nutrient cycling in island ecosystems. Direct predation of seabird nestlings by large arthropods represents a previously unrecognized conduit for marine-derived nutrient transfer into a terrestrial system. Arthropods that prey on island vertebrates are therefore likely to actively translocate nutrients throughout the ecosystem resulting in a more homogenous nutrient distribution (e.g., Schmitz et al. 2010). On islands depauperate of vertebrate predators, this novel predator-prey relationship could represent an important process that is beneficial to the recovery of native plants and animals. This is particularly true of recovering systems like Phillip Island that have undergone extreme topsoil erosion and the associated loss of soil nutrients due to decades of habitat destruction from introduced fauna.

Secondly, my research demonstrates a novel challenge for breeding seabirds: large arthropods can reduce the lifetime reproductive output of long-lived, *K*-selected vertebrates. These results not only confirm that predatory arthropods are important trophic engineers that structure nutrient flow on islands, but also verifies that they are important predators of terrestrial vertebrates in some ecosystems (e.g., Nordberg et al. 2018a; Valdez 2020). While seabirds have not previously been recognized as the prey of centipedes, large centipedes occur across the globe, especially in tropical regions and in sympatry with many seabird species. It is thus likely that centipede predation of seabirds and other vertebrates occurs unnoticed on other islands around the world. In some cases, predation will be naturally occurring, and in other cases predatory centipedes may have been introduced (Shelley 2004; Shelley et al. 2014; Waldock and Lewis 2014) and pose challenges for conservation of native or endemic species (e.g., Emery et al. 2020, 2021).

The Phillip Island centipede itself is a rare and recovering endemic, and its persistence is important for the functionality of the island's ecosystem. Recent colonization of the island by black-winged petrels in 1965 (Schodde et al. 1983), rapid expansion of the population and the recovery of native reptiles and invertebrates together likely contributed critical prey resources that have supported the recovery of the Phillip Island centipede. Fossil records indicate that, prior to anthropogenic disturbance to the island and before colonization by black-winged petrels, at least three other small, burrow-nesting seabirds, including Pycroft's petrel (*P. pycrofti*), were extant and likely abundant up until the early 1800s (Meredith 1991; Holdaway and Anderson 2001; Coyne 2009). Recent establishment of the black-winged petrel colony may have replaced traditional food sources for the Phillip Island centipede, including other now-extirpated petrels that the Phillip Island centipedes may have historically preyed upon.

My research findings have together bridged a gap between the marine and terrestrial realms and empirically demonstrated the importance of understanding ecosystem structure and

multifunctionality in a conservation and management context. The results and conclusions of these studies help improve our understanding of seabird movement ecology and ecosystem function in isolated island systems. In the next section I discuss some recommendations for future research and management.

5.2 Future directions in research and management

5.2.1 Seabird research and conservation

1) In this PhD thesis, I did not assess the non-breeding distributions and migratory patterns of the gadfly petrels of the Norfolk Island Group. Current knowledge of the evolutionary adaptations of tropical seabirds as well as conservation outcomes for gadfly petrels could be improved by studying the migration of these species. This would improve our knowledge of anthropogenic threats at sea (e.g., Grémillet and Boulinier 2009; Rodríguez et al. 2019). This research would likely require the use of geolocators. My results in Chapter 3, including the relative accuracy function, will help to improve assessment of variable spatial accuracy as it relates to equatorial effects and temporal variability.

2) The representativeness of the Kermadec petrel tracking data to the colony-level population was considerably lower (68.5%) than for black-winged (87.5%) and white-necked petrels (93.5%). Therefore, further research is needed to achieve a more representative sample from this species. Throughout the course of my PhD research, I was not able to track Kermadec petrels across multiple years. A more representative sample size of birds tracked as well as tracking occurring over multiple years would be beneficial to gain a better understanding of the species' at-sea distribution, behaviour and to improve our ability to identify and mitigate at-sea threats – our ability to achieve this is reinforced with the availability of seabird tracking data (e.g., González-Solís and Shaffer 2009; Rodríguez et al. 2019).

3) Knowledge of the foraging ranges and at-sea distributions of Procellariform seabirds in the south Pacific has been identified as particularly data deficient (Rodríguez et al. 2019). My research demonstrated that black-winged, white-necked and Kermadec petrels spend large portions of their time integrating resources on the high seas for which no single country holds sovereign jurisdiction. In fact, more than half (55%) of the black-winged petrel foraging range occurred on the high seas, with the figure standing at 35% and 42% for white-necked and Kermadec petrels, respectively. Further research to determine whether foraging site fidelity occurs across different breeding seasons (i.e., years) at the level of populations and individuals (e.g., Weimerskirch 2007; Wakefield et al. 2015) will be beneficial given the low predictive performance of the ESDMs that my research demonstrated. With this information it may become clearer whether some form of spatially explicit conservation measures could be applied across the breeding foraging ranges of these species.

An in-depth assessment of potential at-sea threats to gadfly petrels across their foraging ranges would benefit our ability to protect foraging habitat and mitigate current and emerging anthropogenic threats such as climate change and severe weather, pollution, energy production and mining, and overfishing (González-Solís and Shaffer 2009; Croxall et al. 2012; Rodríguez et al. 2019). Moreover, Phillip Island represents one of only two breeding colonies of white-necked petrels in the world with the other located on Macauley Island in the Kermadec Island group (Priddel et al. 2010; Miskelly et al., 2019). Although small, the colony therefore represents an insurance population and one that is significantly easier to reach, and study given the extreme remoteness of the Kermadec Islands. Given the small population size of white-necked petrels on Phillip Island (i.e., 20–30 breeding pairs; Halpin et al. 2021), to avoid population-level impacts to this colony any research should carefully evaluate the costs and benefits of any disturbance that might be associated with proposed research (Rodríguez et al. 2019).

4) With little known about the diet of gadfly petrels (Spear et al. 2007; Cherel and Bocher 2022), future research could assess the diversity of prey species consumed by the gadfly petrels in this research. Following recommendations by Cherel and Bocher (2022), diet studies in these gadfly petrels could include collection of samples from recently fed large chicks to use these data to test whether DNA metabarcoding-based dietary analysis of faeces can reveal species and proportions of prey (McInnes et al. 2017; Carreiro et al. 2020). Such data could not only provide a better understanding of the diet of these species with implications for their conservation (e.g., Ravache et al. 2020; Huang et al. 2021), but also provide a method for detecting changes in diet over time. Because gadfly petrels travel so widely across the Tasman Sea, tracking changes in diet over time may also provide important information about ecosystem-wide health and/or changes in lower trophic levels (Iverson et al. 2007; Xavier et al. 2011).

5.2.2 Ecosystem conservation on Phillip Island

1) Further study of the diet of the Phillip Island centipede with samples from additional prey (including other small seabirds) using amino acid compound specific stable isotopes (AA-CSIA) may provide a deeper understanding of the role of vertebrates in its diet and clarify its role as a top predator in this system. Laboratories capable of AA-CSIA analysis are less common than those with the capability to analyse traditional bulk-tissues and the cost per sample is higher (Bowes and Thorp 2015). However, AA-CSIA requires fewer sample replicates, more accurately and precisely identifies trophic positions, and there is less variability in mean values for each consumer's trophic level (Wolf et al. 2009; Bowes and Thorp 2015).

2) Future studies could also investigate the role of native arthropods as natural predators of seabirds – *and other vertebrates* – on other island systems (e.g., Laidre 2017), especially in tropical areas. This may have important implications both for improving knowledge of the ecosystem services

provided by seabirds and for island conservation. This research could extend to assess the impacts of introduced, non-native centipedes on seabirds (e.g., Emery 2020).

3) Deeper investigation into the role of the Phillip Island centipede as a trophic engineer may reveal new information about its importance in the context of ecosystem restoration; and could reveal important practical consequences for restoring critically endangered species on the island. Research could investigate whether the Phillip Island centipede is a suitable bio-indicator species (e.g., Powell and Powell 1986; Carignan and Villard 2002) for aspects of the health of the island's ecosystem. This could provide a cost and time-effective means for managers to monitor ecosystem integrity and assess ecosystem changes over time. Many of the target species for conservation on Phillip Island are critically endangered plants (e.g., *Achyranthes margaretarum*, *Abutilon julianae*) (Coyne 2010). Future research could test whether in patches of higher centipede density:

A) soil nutrient load and composition are improved;

B) plant recruitment is higher;

C) plants are more successful, healthier and are more likely to persist, and;

D) reptile and invertebrate abundances are higher.

These questions might best be addressed using structural equation modelling (SEM), a modelling technique that is used to test multivariate causal relationships in complex ecological communities (Grace et al. 2010). SEM can be particularly valuable tool to understand complex ecological relationships where large numbers of predictors and responses occur (Grace et al. 2010; Hopcraft et al. 2012; Strauss et al. 2016; Lind et al. 2017), which is likely to be the case in any attempts to elucidate the impact of centipede foraging on Phillip Island's ecosystem functionality.

Furthermore, reptiles on Phillip Island, which are endemic to the Tasman Sea, appear to be hyperabundant. These populations could now be larger having been released from the predation pressure following extirpation of native predators on the island such as the Norfolk Island boobook (*Ninox novaeseelandiae undulata*) and extinction of the Norfolk rail (*Gallirallus spp.*). The Phillip Island centipede is still recovering and the size of its population before anthropogenic disturbances is unclear. It is therefore uncertain whether at larger population sizes, the Phillip Island centipede would have regulated populations of the native gecko and skink.

4) The Phillip Island centipede is an endemic species that is now thought to only occur on Phillip Island. Given its rarity and its extremely restricted range, a formal assessment of its conservation status and population size would help to direct conservation resources. Moreover, assessing whether Phillip Island centipedes occur on other islands in the Norfolk Island Group (e.g., Nepean Island and Bird Rock) would enable authorities to determine whether insurance populations exist. This would provide secure population(s) in the event that rodents ever reach Phillip Island. If centipedes are not present on other islands and assuming ample prey species exist, translocation could be considered to establish insurance population(s).

5.2.3 Introduced predators

Maintaining a rodent-free Phillip Island is critical for the continued persistence of the island's native and endemic species. From a terrestrial perspective, the principal threat to the survival of many seabird populations on oceanic islands is often posed by introduced predators (Brooke et al. 2010; Croxall et al. 2012). Introduced rodents are also renowned for their deleterious effects on island invertebrates (St Clair 2011), and their presence on Phillip Island would likely trigger the extinction of the Phillip Island centipede. Moreover, introduced rodents would likely pose a threat to ongoing revegetation and persistence of healthy populations of reptiles, which together with seabirds and invertebrates on Phillip Island, are likely also important to sustain the recovery of the Phillip Island centipede. Phillip Island remains free of introduced rodents (Coyne 2010; Priddel et

al. 2010), but neighbouring Norfolk Island has introduced Pacific rats (*Rattus exulans*) and black rats (*R. rattus*) and house mice (*Mus musculus*) (Matisoo-Smith et al. 2001; Brett and Ortiz-Catedral 2021). Continued efforts by authorities to ensure that rodents do not reach Phillip Island are critically important to the survival of the island's globally important gadfly petrel populations as well as its native reptiles and the endemic centipede.

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Appendix A. Halpin et al. (2021) *Methods in Ecology & Evolution* publication

RESEARCH ARTICLE

Methods in Ecology and Evolution — BRITISH ECOLOGICAL SOCIETY
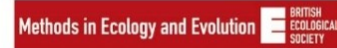
Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles

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Abstract

1. Light-level geolocators are popular bio-logging tools, with advantageous sizes, longevity and affordability. Biologists tracking seabirds often presume geolocator spatial accuracies between 186 and 202 km from previously innovative, yet taxonomically, spatially and computationally limited, studies. Using recently developed methods, we investigated whether assumed uncertainty norms held across a larger-scale, multispecies study.

2. We field-tested geolocator spatial accuracy by synchronously deploying these with GPS loggers on scores of seabirds across five species and 11 Mediterranean Sea, east Atlantic and south Pacific breeding colonies. We first interpolated geolocations using the geolocation package FLightR without prior knowledge of GPS tracked routes. We likewise applied another package, probGLS, additionally testing whether sea-surface temperatures could improve route accuracy.

3. Geolocator spatial accuracy was lower than the ~200 km often assumed. prob-GLS produced the best accuracy (mean ± SD = 304 ± 413 km, $n = 185$ deployments) with 84.5% of GPS-derived latitudes and 88.8% of longitudes falling within resulting uncertainty estimates. FLightR produced lower spatial accuracy (408 ± 473 km, $n = 171$ deployments) with 38.6% of GPS-derived latitudes and 23.7% of longitudes within package-specific uncertainty estimates. Expected inter-twilight period (from GPS position and date) was the strongest predictor of accuracy, with increasingly equatorial solar profiles (i.e. closer temporally to equinoxes and/or spatially to the Equator) inducing more error. Individuals, species and geolocator model also significantly affected accuracy, while the impact of distance travelled between successive twilights depended on the geolocation package.

4. Geolocation accuracy is not uniform among seabird species and can be considerably lower than assumed. Individual idiosyncrasies and spatiotemporal dynamics (i.e. shallower inter-twilight shifts by date and latitude) mean that practitioners

should exercise greater caution in interpreting geolocator data and avoid universal uncertainty estimates. We provide a function capable of estimating relative accuracy of positions based on geolocator-observed inter-twilight period.

1 | INTRODUCTION

Light-level geolocators ('geolocators') are one of the most popular and practical tools available to study animal movement, with well-established, open access standards and techniques available to guide analyses of geolocation data (see Lisovski et al., 2020). However, there can be considerable uncertainty associated with the accuracy of location estimates derived from light-level data. Geolocators are small (i.e. ~0.3–3.3 g) archival data loggers that measure and record solar intensity at regular intervals, some with the capability of measuring and archiving other information such as water temperature, wet/dry events and barometric pressure. When geolocators are retrieved, light-level data are downloaded and directed into astronomical equations that estimate spatial locations based on the timing of twilight events (i.e. sunrises and sunsets). Geolocator data can be interpolated into one or two positions per day with latitude estimated by day length, and longitude estimated by the timing of local midday or midnight relative to Greenwich Mean Time and Julian day (Hill, 1994).

Geolocators were first applied to tracking the movements of marine vertebrates including elephant seals (Delong et al., 1992), fish (Block et al., 1998), seabirds (Croxall et al., 2005; Egevang et al., 2010; González-Solís et al., 2007; Guilford et al., 2009; Phillips et al., 2006; Shaffer et al., 2006; Tuck et al., 1999) and sea turtles (Fuller et al., 2008). Recently, geolocators have undergone considerable miniaturisation and improvements to onboard storage capacity, which has stimulated an increase in studies that use light-level data to infer spatial information about both marine and terrestrial species that were otherwise too small to be burdened with tracking devices (Bridge et al., 2011). The number of ecologists using geolocators to study seabird movements has increased in tandem with these sensor improvements and newly designed geolocation methods implemented in several R packages for processing and analysing light-level data (e.g. Merkel et al., 2016; Rakhimberdiev et al., 2017; Sumner et al., 2009).

Despite the growing volume of geolocator data, the spatial accuracy of geolocators used on seabirds has to-date been empirically tested relative to more precise technologies only on three species of albatross with limited latitudinal breadth (Phillips et al., 2004; Shaffer et al., 2005). These studies employed older geolocator sensors that recorded light levels more infrequently and previous

threshold method geolocation software that, unlike modern methods, did not incorporate movement models or probabilistic algorithms. These studies measured the distances of satellite Platform Terminal Transmitter (PTT) locations to corresponding geolocation estimates and assessed mean accuracies ± standard deviation (*SD*) of 186 ± 114 km (Phillips et al., 2004) to 202 ± 171 km (Shaffer et al., 2005). These estimations of geolocation accuracy are coarse relative to those obtained from satellite loggers that fix positions from orbiting Advanced Research and Global Observation Satellites (ARGOS), which have a typical 1–3 km accuracy (Burger & Shaffer, 2008) or the Global Positioning System (GPS), which regularly has average location accuracies of less than 10 m (Hulbert & French, 2001) to ~15 m (Forin-Wiart et al., 2015). However, tracking instruments that use satellites tend to be too large for many species and may be prohibitively expensive. Satellite tracking instruments typically have limited power capacity and on-board memory storage, and depending on the species, can place unreasonable burdens on birds in terms of wing-loading and hydrodynamic drag (Phillips et al., 2004; Shaffer et al., 2005). Furthermore, attaching satellite instruments to feathers for long-term deployments is not suitable for most seabirds because they periodically moult. For many seabird species the use of harness attachment to remedy this constraint is not recommended (Phillips et al., 2003) and may increase mortality and device-induced behaviours (Barron et al., 2010). Light-level geolocation has therefore offered an attractive year-round alternative to satellite tracking that tackles many of the constraints associated with using larger, more spatially accurate technology.

Light-level geolocation is inherently prone to coarse spatial accuracy, particularly for estimates of latitude which are generally considered to become less accurate under increasingly 'equatorial' solar profiles; that is, either nearer the Equator (spatial variation) or solar equinox (temporal variation) where and when day length changes more shallowly with latitude (Ekstrom, 2004; Hill, 1994; Lisovski et al., 2020). The inherent accuracy of latitudinal geolocations fluctuates by date, even if the amount of sensor shading remains constant (Lisovski et al., 2012). Weather (e.g. cloud cover) and behavioural patterns such as roosting at twilight periods can induce errors in estimates of day or night length and are thus thought to affect accuracy in geolocation (Lisovski et al., 2012). In addition, light-level data collected during breeding stages are often thought to have reduced spatial accuracy due to specific behaviours that

might affect light curves (Lisovski et al., 2012, 2020). For example, some species roost on the ground (Corre & Jouventin, 1997; Schreiber & Chovan, 1986), brood their young at twilights (Howell & Bartholomew, 1969) which can shade sensors, or nest underground in burrows (Shaffer et al., 2006). Geolocators fitted on birds that go to roost before last light or depart nest sites after first light could therefore exhibit abnormal transitions between light and dark at twilight times in light curve data (Gow, 2016).

Another typical behaviour of seabirds is wide-ranging movement that can occur within a single day or night (Clay et al., 2018; McDuie et al., 2015). Such large-scale movement between twilights can impact interpolations of longitude by shifting the solar noon, or latitude by compressing or elongating day length, all depending on the speed and direction of travel and time of year (Lisovski et al., 2012). Furthermore, data collected by geolocators fitted to wide-ranging seabirds, generally on leg rings, are likely to have idiosyncratic differences relative to being collected at a stationary location (Lisovski et al., 2012; Welch & Eveson, 1999). Accordingly, it has been suggested that the performance of geolocators might be species dependent (Shaffer et al., 2005) and that the choice of geolocation algorithm might affect the accuracy of position estimates (Musyl et al., 2001).

Despite the well-known and hypothesised limitations of light-level geolocation, geolocators have generally been considered satisfactory for studying foraging ranges (Phillips et al., 2004), and habitat preferences and distributions of pelagic seabirds (Egevang et al., 2010; González-Solís et al., 2007; Guilford et al., 2009; Halpin et al., 2018; Lascelles et al., 2016; McDuie & Congdon, 2016; Pollet et al., 2014; Quillfeldt et al., 2017; Shaffer et al., 2006). Here, we sought to evaluate for the first time the accuracy of modern geolocation algorithms on a large and diverse sample of free-flying seabirds and assess whether accuracy is affected by the species being tracked and movement behaviours. Past studies of geolocation accuracy have used older technology and/or geolocation algorithms (e.g. Phillips et al. 2004; Shaffer et al. 2005), evaluated static deployments of tags either carried by resident birds or fixed in the environment (e.g. Fudickar et al., 2012), or been carried out on single species with sample sizes that are likely too small to have adequate statistical power to disentangle patterns in accuracy (e.g. Rakhimberdiev et al., 2016).

Our objectives were to (a) investigate if the spatial accuracy typically reported in geolocation studies of seabirds is applicable in the context of a large-scale, multi-species study; (b) test uncertainty estimates of more advanced geolocation models; (c) test whether sea-surface temperature (SST) interpolation improved average accuracy in these new methods and d) model which situational factors most affected geolocator spatial accuracy. To address these aims, we conducted a field test using synchronous deployments of GPS loggers and geolocators fitted to individual seabirds from around the world. We measured the spatial accuracy of geolocator-interpolated routes from GPS tracks, tested for effects of species and individuals, and whether the inter-twilight distances travelled by birds affected the spatial accuracy of geolocation.

2 | MATERIALS AND METHODS

2.1 | Study species & locations

We analysed synchronous location data from 151 chick-provisioning individual seabirds that were tracked concurrently with GPS and light-level geolocator loggers (i.e. 'double tagged') using the geolocation packages, `FlightR` (Rakhimberdiev et al., 2017) and `prob-GLS` (Merkel et al., 2016). Tracking data represent 200 deployments across five species from 11 separate seabird colonies between 2011 and 2019 (Table 1). We originally had access to 278 double-tagged deployments (some individuals were tagged more than once within and between years), but we reduced the dataset to 200 deployments after excluding those with insufficient data to produce stationary calibrations, or where light curve transitions were poor. Breeding colonies were located in several marine regions including in Southern Europe (Mediterranean Sea), West Africa (east Atlantic Ocean) and Australia (south Pacific Ocean). In the northern hemisphere, we analysed double-tagged deployments from Cape Verde Shearwaters (*Calonectris edwardsii*, n = 11; 2014 and 2018), Cory's Shearwaters (*C. borealis*, n = 100; 2011 and 2013–2018), Scopoli's Shearwaters (*C. diomedea*, n = 61; 2014–2018) and Red-billed Tropicbirds (*Phaethon aethereus*, n = 7; 2017–2018) on 10 breeding colonies between latitudes 15°N–40°N. In the southern hemisphere, we analysed double-tagged deployments from White-necked Petrels (*Pterodroma cervicalis*, n = 21; 2018 and 2019) on a single colony at latitude 29°S.

2.2 | Double tagging

We fitted birds with one of five light-level geolocator immersion sensors: BAS_MK19 (British Antarctic Survey) or Biotrack_MK3005 [formerly BAS_MK19] (Biotrack Ltd), which sample light intensity every minute and record the maximum value every 5 min with water temperature recorded when the sensor is immersed continuously for 25 min; and Intigeo-C330, Intigeo-C250 or C65-SUPER (Migrate Technology Ltd), which sample light intensity every minute, storing the maximum value every 5 min and record water temperature when the sensor is immersed continuously for 20 min. The conductivity (wet/dry) sensor sampling rate was 6 s for all models. Devices were leg mounted and fitted to the tarsus by mounting to either a darvic or metallic ring using a plastic cable tie, or a Velcro© (38 mm; Paskal) hook-and-loop harness. GPS loggers were fitted to birds using Tesa© tape (4651; Tesa Tape Inc.) by taping either to contour feathers between scapulae, or at the base of the two to four central rectrices on shearwaters and petrels and six rectrices on tropicbirds.

2.3 | Data preparation and analysis

All data were processed in the statistical software environment R, version 3.5.1 (R Core Team, 2020), and spatial measurements were

TABLE 1 The species, individuals, regions and respective colonies where seabirds were tracked synchronously with light-level geolocators and GPS loggers. The sample size of geolocation estimates used in analyses of each geolocation algorithm isprovided

Colony name	Latitude	Country	Marine Region	Species (no. individuals)	Number of geolocations[a]	
					FLightR	probGLS
Cala Morell (Menorca)	40.1°N	Spain	Mediterranean	Scopoli's Shearwater (52)	574	626
Islas Columbretes	39.9°N	Spain	Mediterranean	Scopoli's Shearwater (4)	73	77
Isla de Cabrera	39.2°N	Spain	Mediterranean	Scopoli's Shearwater (2)	24	26
Isla de las Palomas	37.6°N	Spain	East Atlantic	Scopoli's Shearwater (3)	41	44
Islote de Montaña Clara	29.3°N	Spain	East Atlantic	Cory's Shearwater (32)	441	501
Timanfaya (Lanzarote)	29.0°N	Spain	East Atlantic	Cory's Shearwater (6)	92	43
Veneguera (Gran Canaria)	27.8°N	Spain	East Atlantic	Cory's Shearwater (62)	598	1,206
Ilhéu Raso	16.6°N	Cabo Verde	East Atlantic	Red-billed Tropicbird (2)	8	10
Ilha Boa Vista	16.2°N	Cabo Verde	East Atlantic	Red-billed Tropicbird (5)	48	52
Ilhéu de Curral Velho	15.9°N	Cabo Verde	East Atlantic	Cape Verde Shearwater (11)	189	199
Phillip Island (Norfolk Island)	29.1°S	Australia	South Pacific	White-necked Petrel (21)	993	410

[a]The number of geolocations per package (i.e. `FLightR` or `probGLS`) differs depending on the suitability of the data for analysis in a given package. For example, whether the geolocator recorded water temperature exclusively when immersed, and calibration data from a stationary location.

calculated on the World Geodetic System (WGS 1984) ellipsoid. The processing of geolocation data was carried out by an analyst who had no knowledge of the spatial attributes of the paired GPS tracking data so that decisions about parameterising geolocation algorithms were not influenced by prior knowledge of the birds' underlying movements. This was done to ensure that geolocation positions in our study would be comparable to those of other geolocation studies for which practitioners typically have no knowledge of where the bird travelled. GPS tracks were standardised using the package `adehabitatLT` (Calenge, 2006) by resampling all GPS locations to an equal 10 min interval because the GPS sample rates varied among species and colonies. We gap-filled GPS tracks except when periods of more than 1 hr occurred between fixes. To account for erroneous positions that may have been caused by poor satellite reception, we applied a standard maximum allowable flight velocity of 27.8 m/s (100 km/hr) between consecutive locations for all seabird taxa. We considered this to be a maximum realistic speed for wide-ranging seabirds (Lascelles et al., 2016).

Depending on the brand of geolocator, we first imported raw light-level data using the functions `readMTlux` in the package `TwGeos` (Wotherspoon et al., 2016) or `ligTrans` in the package `GeoLight` (Lisovski & Hahn, 2012). We then automated twilight event (i.e. sunrises and sunsets) annotation in raw light-level data using the function `preprocessLight` in the package `TwGeos` (Wotherspoon et al., 2016) with a threshold level of 1, which presented as a suitable level above which to differentiate twilights from night time noise in log-transformed data. Following guidelines in Lisovski et al. (2020), we visually reviewed raw light data to identify any areas of the time series affected by shading and manually inspected each twilight event, subsequently deleting such events that we deemed to be falsely annotated in the automated

procedure, or those with poor transitions between dark and light. Indistinguishable or unclear transitions between dark and light can occur due to the light sensors becoming shaded by weather, individual bird behaviours or bird plumage. This procedure resulted in an average rate of transition exclusion of 33.6% for Cape Verde Shearwaters, 29.1% for Cory's Shearwaters, 33.9% for Red-billed Tropicbirds, 32% for Scopoli's Shearwaters and 14% for White-necked Petrels. We expected to see a greater proportion of twilights excluded in these data because birds were in their breeding phase. Contrary to non-breeding, migratory seabirds, those in their breeding phase regularly visit nests, or raft on the water before visiting nests which can cause obscured light curves at twilight times.

We used two geolocation analysis packages to estimate the spatial locations of tracked seabirds: `FlightR` and `probGLS`. Using the annotated twilight data, we produced 'TAGS' files using the `TwGeos2TAGS` function in the `FLightR` package in preparation for light-level analyses. We analysed light-level data from 171 deployments in `FLightR` and 185 deployments in `probGLS`, which included 156 of the same datasets used in `FLightR` (15 deployments analysed in `FLightR` were excluded from `probGLS` because they did not collect SST data exclusively when the device was immersed in water). Data from sensors that recorded light and temperature, but did not have light data recorded from a stationary location were included in `probGLS` but excluded from `FLightR` analyses. While on-bird geolocator calibration is possible for some centrally placed species (see Rakhimberdiev et al., 2017), we considered that it may not be suitable for seabirds due to the large distances travelled during foraging. Calibrations were therefore conducted as 'rooftop calibrations' (see Lisovski et al., 2012). All species reported were included in analyses by both geolocation packages.

2.4 | Estimating spatial locations from light-level data

We parameterised both geolocation algorithms (FlightR and probGLS) to calculate seabird locations within a bounding box extending from the breeding colony by 35° of longitude in each direction, and 25° of latitude in the direction of the nearest pole and 50° of latitude in the direction of the Equator.

The geolocation analysis package, FLightR was used first to estimate the spatial likelihood of locations from annotated light-level data. To model movements, FLightR uses a hidden Markov model with the true location as the unobserved state. Inference is performed using a particle filter, with a template-fit method to allow the algorithm to use all available light measurements around annotated twilight events (Rakhimberdiev et al., 2017). FLightR also incorporates biologically relevant behavioural parameters to improve location estimates. To function, FLightR requires calibration data from each geolocator with which it measures the relationship between observed light levels (i.e. calibration data) and theoretical light levels estimated from current solar elevation angles (Ekstrom, 2004; Rakhimberdiev et al., 2017). When executing the FLightR algorithm, we included only data from geolocators that were calibrated by measuring light levels at a stationary location prior to deployment on a seabird. Analyses in FLightR were run with and without spatial masks to explore how land masking affected accuracy. We set the algorithm to allow maximum daily flight distances of 1,500 km on a 50 km grid. To estimate locations, we ran the FLightR particle filter with 1 million particles and used the median of the posterior probability distribution as the estimates of daily seabird relocations.

For light-level data from geolocators that also recorded SST, we analysed the same annotated twilights with the package, probGLS (Merkel et al., 2016), to investigate whether SST interpolation improved the spatial accuracy of geolocations. The probGLS algorithm estimates locations using an iterative forward step selection process, computing a weighted probability cloud of potential locations (10,000 particles for each point cloud) and producing the most likely movement path with 200 iterations for each track (Merkel et al., 2016). We included flight speed parameters for when the loggers were dry (probable maximum and SD (m/s), see supplementary metadata) based on Spear and Ainley (1997) and a maximum allowable dry-logger flight speed of 27.8 m/s, thus matching the speed used to filter GPS relocations; and wet speed parameters to allow for modest drift on the ocean if the bird was roosting on the water for long periods (fastest most likely = 1 m/s, SD = 1.3 m/s, maximum = 5 m/s). Geolocations were estimated using probGLS with a land mask to prevent the algorithm from estimating locations more than 1 km inland of coasts. We also used the daily median SST encountered by each bird, which was computed from that recorded by geolocators every 4 hr (Merkel et al., 2016) and matched this to satellite-derived SST (0.25° × 0.25°, NOAA OI SST V2 High-Resolution Dataset). We also ran probGLS both with and without SST matching and spatial masks.

2.5 | Measuring and modelling spatial accuracy

To measure the spatial discrepancy between geolocations and GPS positions, we calculated the distance between the geographic mean of all GPS fixes that occurred within ±30 min, respectively, of a given pair of twilights (i.e. sunset–sunrise or vice versa) and the geolocator-estimated solar noon/midnight position for that same period. This measure of accuracy is expressed as the great-circle distance in kilometres from an individual's GPS location to its corresponding geolocation for a given set of twilight events. To investigate the potentially nonlinear effects of predictor variables on the spatial accuracy of geolocation estimates, we constructed generalised additive mixed-effects models (GAMM) with a gamma distribution and a log link function. We separately modelled geolocation accuracy in position estimates computed by both the FLightR and probGLS analysis packages. We considered two predictors of geolocation accuracy: spatial displacement as the great-circle distance (kilometres) between successive twilight locations (from GPS) for individuals, and the expected inter-twilight period as the expected duration of day or night calculated from day of year and GPS latitude using the daylength function in the package geosphere (Hijmans, 2019). We modelled these as nonlinear effects using univariate thin-plate regression splines. We initially considered two other potential predictors of geolocation error: latitudinal position and closeness in time to the March and September equinoxes; but we could not consider these as independent variables due to strong concurvity with the inter-twilight period predictor, which we considered an equatorial solar profile index and the more proximate mechanism governing geolocation accuracy. We included the model of geolocator as a fixed effect. To account for potential effects of species and individuals, we also included the identity of each tracked individual nested under species type as random effects in the model.

Both geolocation packages contain spatial mask functions to avoid the algorithms estimating positions over land. In our data, this would likely have masked the effects of modelled covariates on spatial error, particularly for birds restricted to the relatively small Mediterranean Sea. Therefore, we modelled the effects of covariates on geolocation accuracy only on the position estimates produced without a land mask (both packages), SST (probGLS) or inbuilt outlier detection (FLightR). We used a correlogram to examine for residual autocorrelation in the time series of geolocations. Some evidence of autocorrelation was evident at the first time lag, but thinning the dataset to include only every second or third observation had no effect on the overall model results. Thus, we did not thin time series of geolocations.

We fitted the models by restricted maximum likelihood using the package mgcv (Wood, 2011). We used the inbuilt checks of the mgcv package to ensure that the models converged and that the basis dimension was sufficiently large (using a permutation test for the presence of a residual pattern along predictors). The residuals of the fitted models were inspected to ensure that residuals followed the gamma distribution assumption and that there was no

evident structure or heterogeneity of variances against candidate predictors.

3 | RESULTS

Our initial geolocation results were implemented without applying land masks or SST interpolation and produced mean spatial accuracy ($\pm SD$) of 432 ± 460 and 372 ± 290 km for `FLightR` and `probGLS`, respectively (Table 2). When we applied land masks (for both analysis packages), and SST (`probGLS` only) mean accuracies were improved to 408 ± 473 and 304 ± 413 km, for `FLightR` and `probGLS` respectively (Table 2). As an additional test to investigate the effect of equinoxes on location accuracy, when we excluded from accuracy measurements the locations within 3 weeks (21 days) of the March or September equinoxes the mean spatial accuracies (km $\pm SD$) were reduced to 227 ± 250 and 290 ± 369 for `FLightR` and `probGLS` respectively (Table 2).

GPS-derived latitude was within package-specific geolocation uncertainty estimates 38.6% and 84.5% of the time for `FLightR` (parameter set 4, see Table 2) and `probGLS` (parameter set 3, see Table 2), respectively, and GPS-derived longitude fell within uncertainty estimates for 23.7% and 88.8% of geolocations, for `FLightR` and `probGLS` respectively. Estimated uncertainties derived from package functions for each geolocation produced by each method are provided as supplementary material. We also provide as supplementary material the spatial accuracies for individual species within (i.e. ≤21 days) and outside (i.e. ≥21 days) of equinox periods. Results outputs with different parameters from the geolocation analyses are also provided as Supporting Information.

We found strong evidence of a bell-shaped effect of expected inter-twilight period on the spatial accuracy of geolocations (Figure 1a, `FLightR`: $F_{6.47} = 993$, $p < 0.001$; Figure 2a, `probGLS`: $F_{7.1} = 718$, $p < 0.001$). Results demonstrated that spatial accuracy in both `FLightR` and `probGLS` drastically declines as expected inter-twilight periods approach 12 hr (i.e. closer to an equinox or the Equator) and best at approximately 9 and 15 hr (Figures 1a and 2a). Mean spatial accuracy ($\pm SD$) calculated on geolocation results associated with inter-twilight periods ≤10 and ≥14 hr was reduced to 243 ± 232 and 202 ± 239 km ($\pm SD$) for `probGLS` (with spatial land mask and SST) and `FLightR` (with spatial land mask and outlier detection) respectively.

We found significant effects of differences among species and individuals on the spatial accuracy of geolocations when individuals were fitted as random effects nested within their respective species type (Figure 1c, `FLightR`: $F_{154.7} = 25.7$, $p < 0.001$; Figure 2c, `probGLS`: $F_{158.2} = 11.8$, $p < 0.001$). The model of geolocator used also affected the accuracy (Figure 1d, `FLightR`: $F_{4.0} = 5$, $p < 0.001$; Figure 2d, `probGLS`: $F_{4.0} = 16.8$, $p < 0.001$). We found that there was an effect of an individual's spatial displacement within expected inter-twilight periods on the accuracy of geolocations when using `FLightR` (Figure 1b, $F_{2.3} = 40.3$, $p < 0.001$), but not for `probGLS` (Figure 2b, $F_{0.5} = 0.35$, $p = 0.111$).
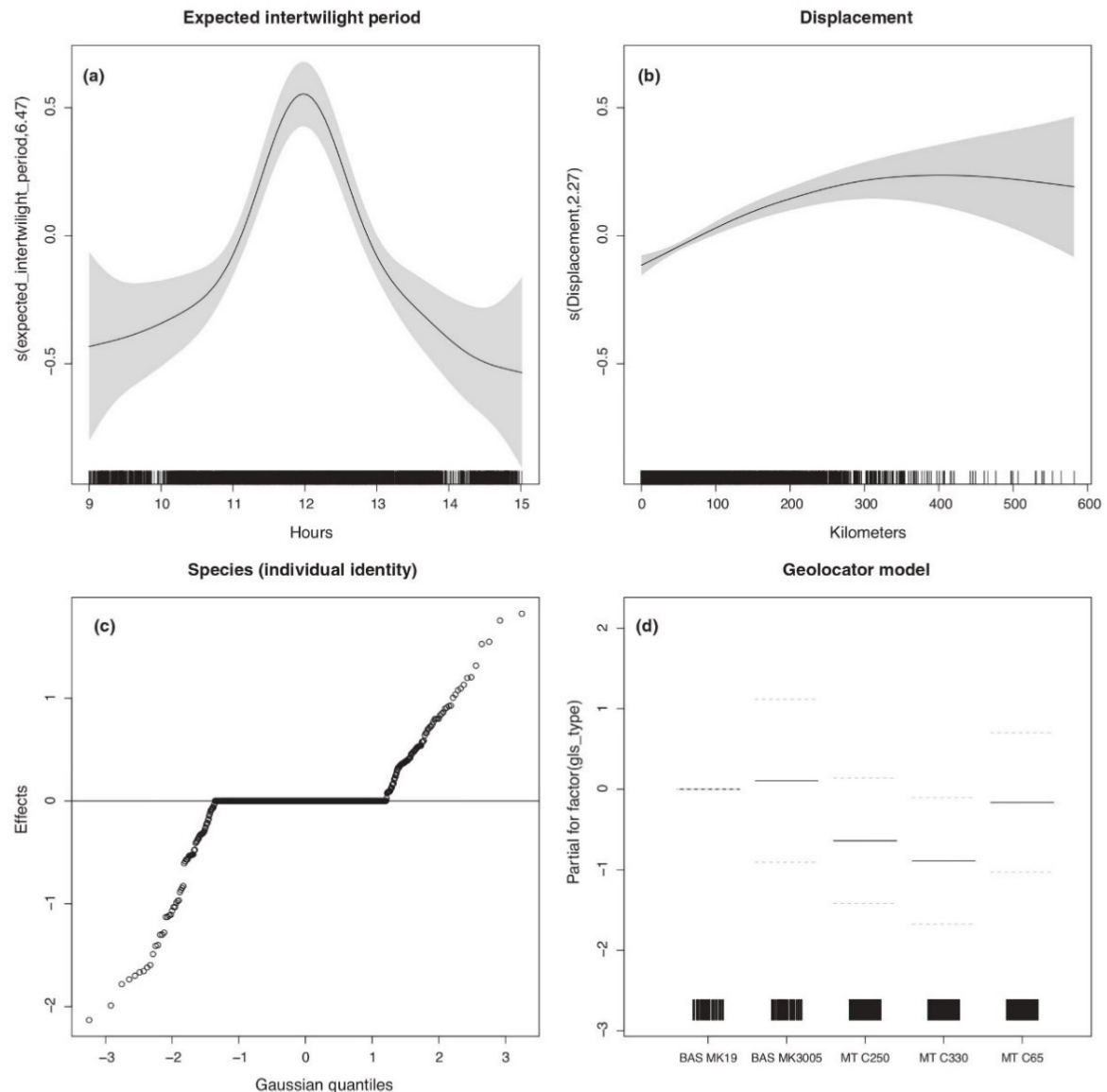
TABLE 2 Spatial accuracy for each geolocation algorithm with specified package parameters. Accuracy is expressed as the great-circle distance between the GPS position and corresponding geolocator-derived position for a given twilight. GPS position was defined as the geographic mean of all GPS positions recorded within ±30 min of the given twilight

Geolocation package	Parameter set	Number of deployments included	Land mask[a]	SST[b]	Outlier detection[c]	Mean absolute latitudinal accuracy ± SD (°)	Mean absolute longitudinal accuracy ± SD (°)	Mean great-circle accuracy (km ± SD)		
								All data	Equinox periods (<21 days)	Non-equinox periods (>21 days)
`FLightR`	1	171	No	N/A	No	2.9 ± 3.7	2.1 ± 3.1	432 ± 460	670 ± 564	286 ± 300
	2	171	Yes	N/A	No	2.9 ± 4.1	2.1 ± 3.2	430 ± 508	707 ± 635	260 ± 305
	3	171	No	N/A	Yes	2.7 ± 3.8	2.2 ± 3.2	416 ± 474	659 ± 576	267 ± 318
	4	171	Yes	N/A	Yes	2.7 ± 3.7	2.3 ± 3.2	408 ± 473	702 ± 587	227 ± 250
`probGLS`	1	185	No	No	N/A	3.0 ± 2.6	1.2 ± 1.3	372 ± 290	484 ± 388	344 ± 253
	2	185	Yes	No	N/A	3.7 ± 3.5	1.3 ± 1.3	449 ± 381	713 ± 465	384 ± 325
	3	185	Yes	Yes	N/A	2.4 ± 3.7	1.1 ± 1.5	304 ± 413	364 ± 554	290 ± 369

[a]Spatial mask restricting estimation of locations >1 km inland;
[b]Sea-surface temperature (not currently available in `FLightR`);
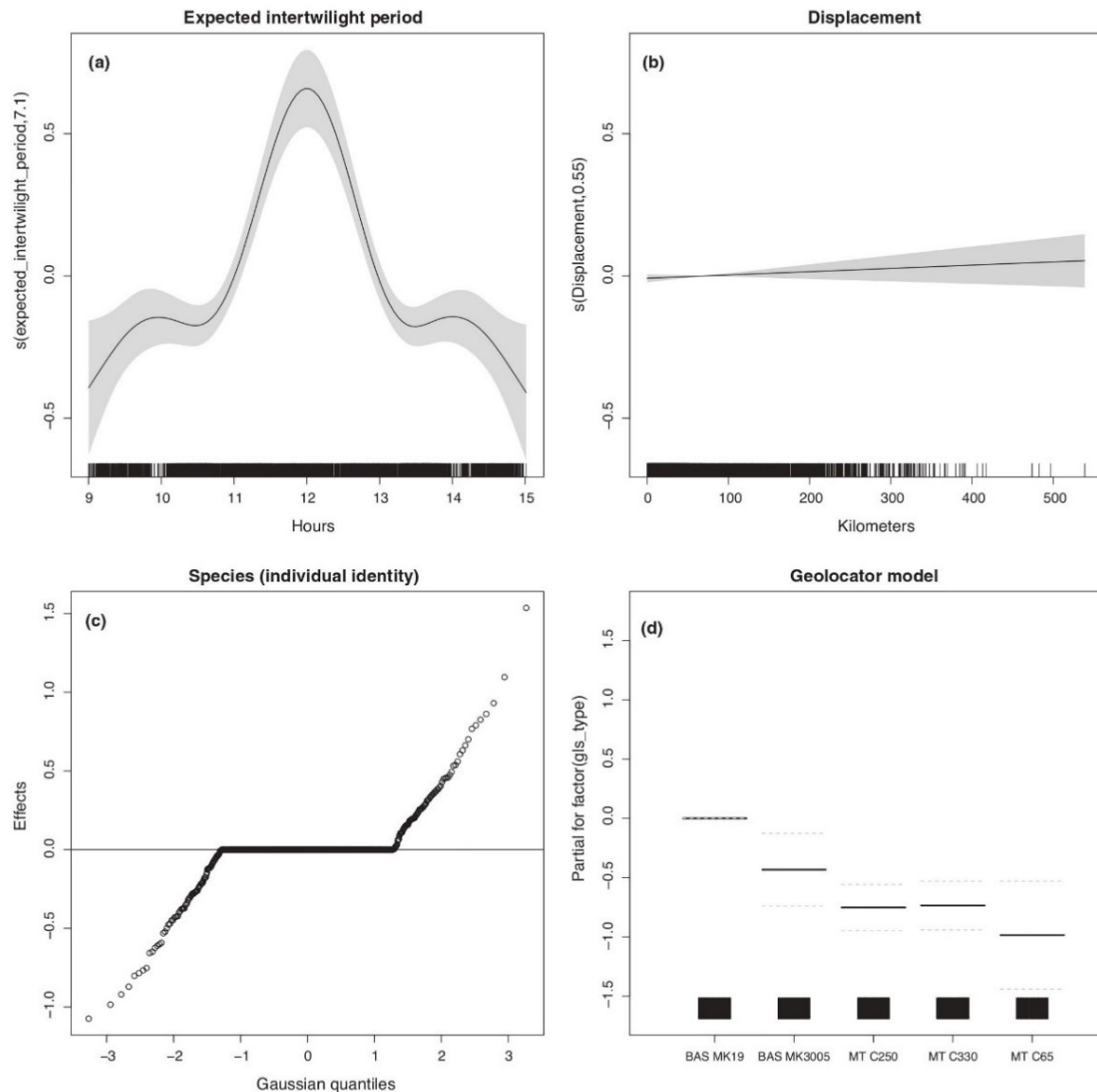[c]Inbuilt outlier detection is not currently a function in `probGLS`.

FIGURE 1 Response curves for spatial accuracy in `FLightR` geolocations as a function of expected inter-twilight period (a) and spatial displacement (b) with individual identity nested within species (c) and geolocator model as a fixed effect (d). Tick marks on the horizontal axis of the expected inter-twilight period (a) and displacement (b) plots are observed datapoints. For each predictor with a smooth term (a and b), the effect on spatial accuracy is shown on the y-axis and represented as a spline (s) of the predictor variable with the estimated degrees of freedom. Shaded grey areas in the expected inter-twilight period (a) and displacement (b) plots indicate 95% confidence intervals

The average spatial accuracy differed depending on species and geolocation package (Figure 3), with Red-billed Tropicbirds producing the poorest accuracy between GPS and corresponding geolocator positions in the `probGLS` results, whereas White-necked Petrel geolocations had the poorest accuracy in the `FLightR` results. Scopoli's Shearwater geolocations had consistently better spatial accuracy relative to other species (Figure 3) in all model runs of both geolocation packages, including when SST and spatial land masks were not applied.

4 | DISCUSSION

We provide the first large-scale assessment of the spatial accuracy of modern geolocation algorithms under field conditions. The advance in understanding our findings provide contextualises the results and hypotheses of past tests of geolocation accuracy that have until now been limited in field testing (e.g. static tags, small sample sizes, single species studies and outdated methods). Our results

Expected intertwilight period

Displacement

Species (individual identity)
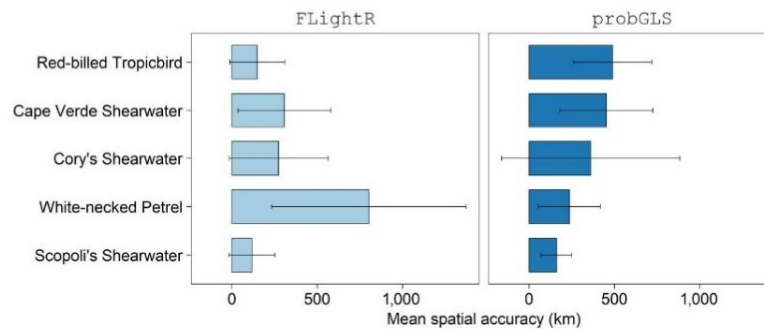

Geolocator model

FIGURE 2 Response curves for spatial accuracy in probGLS geolocations as a function of expected inter-twilight period (a) and spatial displacement (b) with individual identity nested within species (c) and geolocator model as a fixed effect (d). Tick marks on the horizontal axis of the expected inter-twilight period (a) and displacement (b) plots are observed datapoints. For each predictor with a smooth term (a and b), the effect on spatial accuracy is shown on the y-axis and represented as a spline (s) of the predictor variable with the estimated degrees of freedom. Shaded grey areas in the expected inter-twilight period (a) and displacement (b) plots indicate 95% confidence intervals

emphasise the need for practitioners to account for species and spatiotemporal effects on geolocation accuracy by considering both when (i.e. temporal effects) and where (i.e. equatorial effects) they might expect a species to travel. If the former is either a wandering, circuitous or tropical path, the practitioner should be adequately aware of what scale their data could be analysed. This is particularly true of land birds, which do not have the luxury of using SST to enhance the accuracy of interpolation. We observed lower mean

spatial accuracy in light-level geolocation of seabirds than what is typically reported as the expected accuracy in studies that use this tracking method. Moreover, the true location of a seabird was often outside of package-specific uncertainty estimates (as much as 76.3% of the time for `FLightR` and 15.5% of the time for `probGLS`). We also observed that the spatial accuracy in light-level geolocation of seabirds varies among species. As previously suggested by Lisovski et al. (2020) and Shaffer et al. (2005), it is likely that inconsistent

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FIGURE 3 Mean spatial accuracy for each double-tagged seabird species as derived from the `FLightR` package (left) with a spatial land mask applied (parameter set 4, see Table 2) and `probGLS` package (right) using SST correction and a spatial land mask (parameter set 3, see Table 2). Accuracy is expressed as the great-circle distance between the GPS position and corresponding geolocator-derived position for a given twilight. GPS position was defined as the geographic mean of all GPS positions recorded within ±30 min of the given twilight. Distances were measured on the WGS 1984 ellipsoid. Error bars represent the standard deviation

accuracy is the result of species-dependent geolocator performance, which relates to the way in which the geolocator light sensors are affected by a combination of species-specific behaviour, morphology, plumage and habitat use. It is possible that smaller geolocator models are more prone to sensor shading than larger models, but we could not reliably test this hypothesis due to the confounding effects of species and individuals.

The method and quality of calibration can influence geolocation accuracy (see Lisovski et al., 2012 for a detailed discussion), so it is important that geolocation practitioners carefully consider calibration when planning their study. In particular, the calibration period should capture the complete variability in twilight transitions and care must be taken to ensure that the calibration method is suitable for the focal species (Lisovski et al., 2012). It is possible that calibration effects contributed to the poor accuracy seen in the `FLightR` results of some of the species we tracked—particularly in the case of White-necked Petrels due to their very long distance, looping trips away from the colony whence the geolocators were calibrated. However, we used standard 'rooftop' calibration methods that are commonly used by seabird biologists. Therefore, we expect our geolocation accuracies to be directly comparable to those obtained by seabird biologists in other geolocation studies.

Our modelling results showed that differences in species and individuals affected how accurate geolocations were. For example, in `probGLS` geolocation, Red-billed Tropicbirds had the poorest mean spatial accuracy. This could be explained by the species' morphology (i.e. extremely short tarsi) and nesting habits, which often include returning to the nest before or during sunset and sunrise, affecting geolocator performance. Conversely, White-necked Petrels had the poorest mean spatial accuracy in `FLightR` geolocation, which our models suggest is explained by their wide-ranging movement habits and large spatial displacement between twilights. The vastly different performance between `FLightR` and `probGLS` for this species supports the assertion that using SST correction is important for geolocation of wide-ranging marine species (Shaffer et al., 2005).

Mean spatial accuracy in Scopoli's Shearwater geolocations was good relative to other species possibly due to the species being restricted to a relatively small marine area (i.e. the Mediterranean Sea) compared to the other open ocean-foraging species that we tracked in this study. Spatial displacement of individuals between sunrises and sunsets affected the accuracy of geolocations produced by both packages, but was strongest in `FLightR`. Scopoli's Shearwaters made short-range movements within a small marine basin, and hence displacement did little to diminish their geolocation accuracy in either package. In the case of `probGLS`, the application of a land mask will have forced the algorithm to produce these geolocations within a small marine area, thus improving the latitudinal accuracy when using a spatial land mask. However, the species still had the highest mean spatial accuracy when a land mask was not applied. The spatial displacement of individuals between sunrises and sunsets appeared to be weakest in its effect on accuracy of geolocations estimated by the `probGLS` package, which suggests that the accuracies we observed for this package are not only applicable to breeding seabirds that exhibit central place foraging behaviour, but also for non-breeding or migratory seabirds. For these reasons, researchers working on coastal-foraging seabirds or seabirds in small marine basins will likely achieve useful results using either the `FLightR` or `probGLS` packages, whereas `probGLS` seems most suitable for researchers working on open ocean-foraging seabirds.

The `FLightR` package sometimes did not produce uncertainty estimates at the start of deployments, or for short-term deployments. This may have occurred because, for a given geolocation, `FLightR` determined low probability of movement between twilights (Rakhimberdiev et al., 2017). It is important to recognise that `FLightR` was designed to track migratory paths, therefore the algorithm may not calculate a probability of movement away from a capture location when tracking duration is short and when the tracked individual is in a state of central place foraging.

Our results suggest that the effect of spatial displacement on `FLightR` geolocations was driven by White-necked Petrels, which

had the largest mean spatial displacement between twilights (more than double that of all other included species). This effect was likely due to the inbuilt Bayesian priors of the movement model incorporated by the `FLightR` algorithm. For geolocation of marine species, the `FLightR` package may benefit from the inclusion of SST as an optional model prior.

We found that the strongest predictor of accuracy was the duration of day or night between twilight events, with this pattern broadly consistent between expected day or night length (i.e. expected inter-twilight period calculated from GPS latitude) contrasted with the empirical geolocator-observed duration of day or night (i.e. calculated from raw light-level data). Our results empirically demonstrate why those using light-level geolocators should not only expect spatial accuracy to be lower during periods of solar equinox when day and night length is similar across the globe, but also as tracked animals move nearer the Equator where day and night length changes ever more shallowly per degree of latitude (Ekstrom, 2004; Hill, 1994; Lisovski et al., 2012).

Our results imply that practitioners should adopt variable spatial uncertainties by estimating a relative spatial accuracy based on observed inter-twilight period calculated from geolocator data, rather than by excluding data from an arbitrary duration either side of the March and September equinox dates, as is done in many geolocation studies (e.g. Van Bemmelen et al., 2017; Fayet et al., 2016; Jones et al., 2020). This approach not only tackles the issue of reduced spatial accuracy during solar equinoxes, but also of equatorial solar profiles and is a particularly important advance for geolocation of animals that migrate to, or reside on or near the Equator. The spatial accuracy of geolocation differs between species and inference method, but the relationship between geolocator-observed inter-twilight period and relative accuracy is consistent between periods of 9 and 15 hr, and closely follows a Gaussian function. We can therefore provide a rule-of-thumb for estimating the relative spatial accuracy of geolocations depending on the apparent inter-twilight period, which can be computed directly from geolocator data. The equation:

$$\exp\left(-0.5\left(\frac{d-12}{1.2}\right)^2\right)$$

where d is the duration in hours between the first and second twilight, gives the spatial accuracy in an estimate, relative to the accuracy with a duration of 12 hr. For example, when $d = 12$ the relative accuracy is 1, but at $d = 9$ or $d = 15$, the relative accuracy is 0.044, a 95.6% improvement in accuracy relative to when the duration of an inter-twilight period is 12 hr and accuracy is at its worst. When $d > 15$ or $d < 9$, this rule is not generalisable.

Our results present mean spatial accuracies that are within the order of magnitude of the reported average spatial errors (94–1,043 km) in studies of other marine vertebrates (Beck et al., 2002; Delong et al., 1992; Hull, 1999; Teo et al., 2004), but, in some species, are considerably larger than those that have previously measured accuracy in geolocation of pelagic seabirds (186–202 km; Merkel et al., 2016;

Phillips et al., 2004; Shaffer et al., 2005). Based on our results, and considering previous studies that improved geolocations with SST (Delong et al., 1992; Gunn et al., 1994; Hill, 1994; Le Boeuf et al., 2000; Shaffer et al., 2005; Teo et al., 2004), we suggest that for pelagic seabirds, using SST as a prior in geolocation models might be essential to achieve better results and to increase spatial accuracy in light-level geolocation. Furthermore, the variation we observed between geolocation packages and geolocator types, and among outputs resulting from differently parametrised geolocation analyses (e.g. use of a land mask, SST interpolation etc.) validate the recommendations of Lisovski et al. (2020) concerning reporting of study parameters. Specifically, practitioners should clearly and unambiguously report assumptions and package-specific model parameters used to compute geolocations along with estimates of uncertainty associated with the data.

Light-level geolocation and geolocators are unquestionably important tools for studying the movement ecology and behaviour of marine organisms, and in many cases are the only available options to track small or sensitive species. Based on our results, we urge greater caution and consideration of the limitations of light-level geolocation when using geolocator data to draw inferences about regional spatial use and behaviour of wide-ranging marine species. Light-level geolocation is not an exact science and different combinations of geolocation packages, parameterisation, study species and data quality can yield different results and uncertainties. The key message in this study is not a criticism of light-level geolocation due to its inherent spatial uncertainty, but a demonstration that this can be reduced if practitioners adopt a dynamic approach to estimating uncertainty using duration of the inter-twilight period. While the spatial accuracy of geolocation may vary between packages, species and the quality of calibration data, the influence of the inter-twilight period on relative accuracy will be valid irrespective of the geolocation package chosen, or the species tracked. In particular, practitioners should make use of dynamic uncertainty estimates based on equatorial solar profiles and be aware that the average accuracy that one can expect will vary by species and might be greater than what is typically reported in seabird geolocation studies. This is especially important in the context of using geolocator-derived tracking data when precise, spatially explicit conservation or management actions are to be implemented.

work. Pacific tracking data were collected under Monash University Animal Ethics Permit BSCI/2017/42 and Parks Australia wildlife research approvals. Tracking data from the Atlantic and Mediterranean were gathered with valuable help from many students and volunteers to whom we are enormously grateful. These data were collected under the following permits: Cabildo de Lanzarote num. I-15-16-T, Cabildo Gran Canaria num. 1169, Excmo. Cabildo de Lanzarote 2107, Excmo. Cabildo de Lanzarote num. 1948, Excmo. Cabildo de Lanzarote num. 2018/2290, Generalitat Valenciana num. 249-18 SGENP, Gobierno de Canarias num. 2011/0795, Gobierno de Canarias num. 2015/1170 & 2016/9887, Gobierno de Canarias num. 2018/6432, Govern Balear num. ANE-02/2017, Govern Balear num. ANE-05/2016, Govern Balear num. CEP-24/2015, Govern Balear num. CEP-30/2016, Govern Balear num. CEP-31/2014, Parque Nacional num. 160/15, Parque Nacional num. RES-AUT I03/2015, Región de Murcia num. AUF20140056.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

L.R.H. and J.D.R. conceived the project idea and co-designed the research; L.R.H. acquired funding and scientific permits, collected Pacific data, analysed the data and led the writing of the manuscript; J.D.R. generated positions of geolocator data, performed data analysis and contributed to writing the manuscript; R.M. helped with data analysis and contributed to project development and writing the manuscript; N.C. contributed to project development and ideas, permit acquisition and funding and assisted with Pacific data collection and writing the manuscript; N.G. helped with data analysis and contributed to writing the manuscript; R.R. was responsible for collating the Atlantic and Mediterranean tracking data; R.R. and J.G.-S. acquired funding and scientific permits, collected Atlantic and Mediterranean data, and assisted with writing the manuscript; J.M.R.-G., T.M., Z.Z., M.C.-F., S.S., V.M.-P., and L.Z. collected Atlantic data; F.D.F. and L.N.-H. collected Mediterranean data; R.H.C. contributed to project development, acquisition of scientific permits and funding and assisted with Pacific data collection and writing the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code used in these analyses are archived on the Dryad Digital Repository https://doi.org/10.5061/dryad.gb5mkkwpf (Halpin et al., 2021).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

Appendix B. Halpin et al. (2021) *The American Naturalist* publication

Arthropod Predation of Vertebrates Structures Trophic Dynamics in Island Ecosystems

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ABSTRACT: On isolated islands, large arthropods can play an important functional role in ecosystem dynamics. On the Norfolk Islands group, South Pacific, we monitored the diet and foraging activity of an endemic chilopod, the Phillip Island centipede (*Cormocephalus coynei*), and used a stable isotope mixing model to estimate dietary proportions. Phillip Island centipede diet is represented by vertebrate animals (48%) and invertebrates (52%), with 30.5% consisting of squamates, including the Lord Howe Island skink (*Oligosoma lichenigera*) and Günther's island gecko (*Christinus guentheri*); 7.9% consisting of black-winged petrel (*Pterodroma nigripennis*) nestlings; and 9.6% consisting of marine fishes scavenged from regurgitated seabird meals. Centipede predation was the principal source of petrel nestling mortality, with annual rates of predation varying between 11.1% and 19.6% of nestlings. This means that 2,109–3,724 black-winged petrel nestlings may be predated by centipedes annually. Petrels produce a single offspring per year; therefore, predation of nestlings by centipedes represents total breeding failure for a pair in a given year. Our work demonstrates that arthropods can play a leading role in influencing vertebrate reproductive output and modifying trophic structures and nutrient flow in island ecosystems.

Keywords: seabirds, reptiles, centipedes, insects, trophic estimation, stable isotopes.

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Introduction

Predator-prey interactions are important processes that regulate the structure of ecological communities, population dynamics, and nutrient transfer in food webs (Paine 1966; Sih et al. 1985; Krebs 2011; Ripple and Beschta 2012). These processes are central to many ecological studies and provide a foundation to better understand how ecosystems function, including how natural systems can maintain critical function in the face of anthropogenic disturbance and environmental change (Yodzis 1988; Johnson et al. 1996). Interactions between vertebrate predators and their prey have been described in a great diversity of phyla (McLaren and Peterson 2008; Krebs 2011). Whereas invertebrates have been relatively well documented as important predators of vertebrate animals in marine (Terlau et al. 1996; Brodeur et al. 2008; Wangvoralak et al. 2011) and freshwater (Brodie and Formanowicz 1983; Mori 2004; Van Buskirk et al. 2004; Ohba et al. 2008) systems, examples of terrestrial invertebrate-vertebrate predation are comparatively scarce (Toledo 2005; Nyffeler and Knörnschild 2013; Nyffeler et al. 2017; Nordberg et al. 2018*a*; Emery et al. 2020).

Among invertebrates, arthropods are especially well suited to vertebrate predation because they are often larger than many potential vertebrate prey and have evolutionary adaptations that increase their predatory efficiency, such as venoms and toxins to incapacitate prey (Undheim et al. 2015; Luo et al. 2018). Systematic reviews have revealed widespread reports of arthropod-vertebrate predation, with arthropods in six classes and 83 families observed to prey on vertebrates in five classes and 162 families (McCormick and Polis 1982;

Valdez 2020). However, these reports generally result from opportunistic observations (McCormick and Polis 1982; Valdez 2020), and few arthropod-vertebrate predation systems have been the focus of in situ study (e.g., Kopp et al. 2006; Nordberg et al. 2018*a*), with most conducted in laboratory settings (e.g., Pearman 1995; Wizen and Gasith 2011).

Few studies (e.g., Emery et al. 2020) have established or quantified arthropod prey choice because it is challenging to study in a natural context. While it may be relatively easy to observe, identify, and quantify foraging in large mammals, birds, and reptiles that kill large prey, it can be more difficult to observe invertebrates foraging in situ because their behavior tends to be cryptic, nocturnal, and concealed in leaf litter or subterranean (Symondson 2002; Nordberg et al. 2018*a*). Classifying and quantifying invertebrate diet are also acutely challenging because most invertebrates are fluid feeders such that ingested prey cannot easily be identified using traditional methods, such as gastric dissection (Shine 1977), gastric lavage (Antonelis et al. 1987) or pellet/fecal sampling (Southern 1954; Nordberg et al. 2018*b*). Moreover, laboratory simulations are unlikely to replicate conditions that produce natural behavior in both predator and prey (Symondson 2002). Many of these challenges can be resolved with relatively new technologies and forensic methods, such as stable isotope analysis (Fry 2006; Layman et al. 2012) and molecular screening, including the use of polymerase chain reaction–based methods for detecting prey DNA (Symondson 2002).

Here, we use a stable isotope approach paired with systematic in situ observations of foraging in a population of a large, endemic arthropod to explore the hypotheses that (*a*) vertebrates can form significant proportions of arthropod diet and (*b*) arthropod-vertebrate predation is capable of reducing reproductive output in a vertebrate population. Using a subtropical island system as an exemplar, we show that vertebrates, including reptiles, fish, and seabirds, form an important dietary component for a large, endemic chilopod, the ground-dwelling Phillip Island centipede (*Cormocephalus coynei*; fig. 1). Our results illustrate that arthropods play a major role in structuring trophic dynamics and nutrient flow in an island ecosystem.

Methods

Study Area

Phillip Island (29°07′S, 167°57′E; fig. 2) is a small (207 ha), uninhabited subtropical island located approximately 6 km south of Norfolk Island in the South Pacific. Phillip Island supports breeding populations of 13 seabird species, the most abundant being the black-winged petrel (*Pterodroma nigripennis*; 15,000–19,000 pairs; Priddel et al. 2010; N. Carlile, unpublished data). The island also supports native reptiles

and invertebrates, including Lord Howe Island skinks (*Oligosoma lichenigera*), Günther's island geckos (*Christinus guentheri*), endemic Phillip Island centipedes (*Cormocephalus coynei*), endemic Phillip Island crickets (*Nesitathra phillipensis*), and native flightless crickets, including *Dictyonemobius pacificus* and *Dictyonemobius lateralis* (Koch 1984; Otte and Rentz 1985; Rentz 1988). In addition to these native species, introduced populations of rabbits, pigs, and goats occurred on the island until the 1980s, causing widespread degradation and vegetation denudation. Following the successful eradication of these introduced species, the island's vegetation has steadily been recovering (Coyne 2010; fig. 2).

Systematic Observation of Predation Events

To identify and document the range of centipede prey, we searched for foraging centipedes nocturnally in six 100-m² survey plots in four habitat types known to be used by Phillip Island centipedes and in five transects approximately 300 m long interconnected between each survey plot. Three survey plots were in woodland dominated by white oak (*Lagunaria patersonia*), and one each was in red-leg grass (*Bothriochloa macra*) grassland, Norfolk pine (*Araucaria heterophylla*) forest, and exposed soil habitat (fig. 2). Each of the six plots was surveyed in randomized order for 30 min per night over 17 nights (total 51 h) between February 27 and March 29, 2019. A further 81 h was spent opportunistically searching for foraging centipedes on transects between plots. During each survey, we searched for centipedes on the forest floor and on or around any habitat features, such as rocks, logs, and small trees, using a 400-lm white LED light. We did not disturb ground features, such as rocks and logs, because of the high density of active seabird burrows and risk of crushing them. Upon detection of a centipede, the light source was switched to a red LED to minimize disturbance. We recorded the body length of each individual centipede and the species of prey if the individual was actively hunting (striking at prey) or feeding.

Predation of Seabird Nestlings

We monitored black-winged petrel (2018, $n = 56$; 2019, $n = 45$) and white-necked petrel (*Pterodroma cervicalis*; 2018, $n = 22$; 2019, $n = 19$) nestlings over two breeding seasons and recorded nestling body weight at ~3-day intervals from near hatch date to ~45 days. Where direct predation of nestlings by centipedes was not witnessed, it was inferred from a consistent pattern of predation pathology that was directly observed in instances of centipedes consuming nestlings. In these cases, centipedes had specifically targeted the hind neck, rasping away flesh from this region,

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Figure 1: Phillip Island centipede (*Cormocephalus coynei*; *foreground*) with an adult black-winged petrel (*Pterodroma nigripennis*; *background*). Some foreshortening effect exists in this image, with the largest Phillip Island centipede measured at 23.5 cm (this study) and the combined head and body length of an adult black-winged petrel estimated at 28–30 cm (Marchant and Higgins 1990). Image by L. Halpin, 2018.

the head, and soft tissue at the lower mandible (fig. 3). This pattern of predation is consistent with anecdotal reports of scolopendrid centipede predation (Cloudsley-Thompson 1968; Molinari et al. 2005).

Tissue Sampling

Tissue samples from centipedes and their prey were collected from February to April in 2018 and 2019 and January to February in 2020 (table S1, available online). We sampled down feathers from black-winged petrel nestlings in the first week after hatching. The black-winged petrel was chosen because it is the only seabird species on the island that met the following criteria, which we believe contributes to its importance in the diet of centipedes: (1) has a breeding population of >1,000 pairs, (2) nests in burrows, (3) is small bodied (adults <250 g), and (4) nests in the summer, when centipedes are likely to be most active. Samples of freshly deceased centipedes, geckos, skinks, *Dictyonemobius* sp. crickets, and fish spilled from regurgitated meals of tree-nesting black

noddies (*Anous minutus*) were collected opportunistically from within the seabird colony.

Sample Processing and Analysis

Stable isotope analysis was conducted on an ANCA GSL2 elemental analyzer interfaced to a Hydra 20-22 continuous-flow isotope ratio mass spectrometer (Sercon, Cheshire, United Kingdom). We used multiple internal standards calibrated against internationally recognized reference materials for quality control (for detailed methods, see the supplemental PDF, available online).

Proportion of Prey Items in Centipede Diet

We used a Bayesian dietary source mixing model with the package simmr (Parnell and Inger 2020) in R (R Development Core Team 2020). We applied a simmr model with diet-to-tissue trophic enrichment factors (TEFs). Published TEFs from laboratory feeding experiments for centipedes are unavailable, so we used TEFs (δ^{13}C = -0.4‰ $\pm$ 0.1‰ SD;
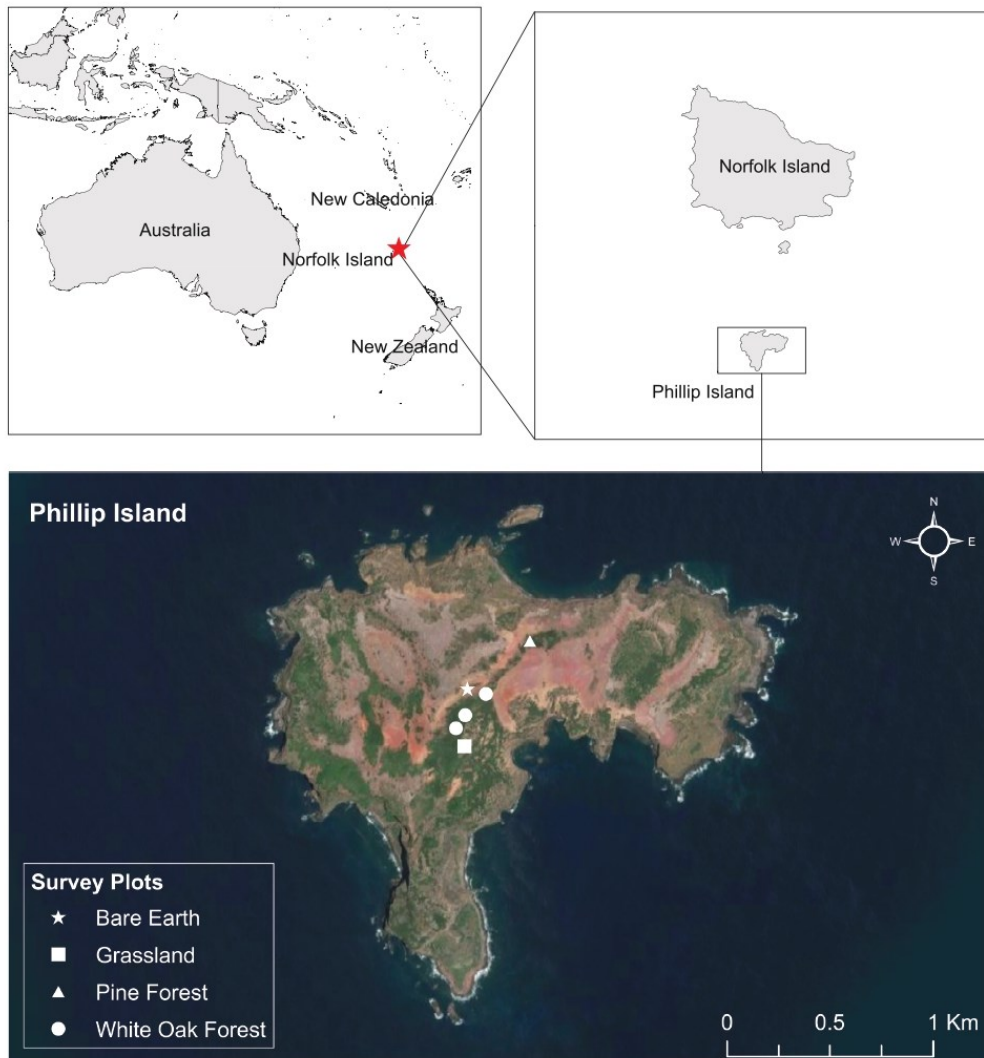
Figure 2: Phillip Island (*bottom*) and its location within the Australasian region (*top left*) and the Norfolk Island group (*top right*), where Phillip Island centipede (*Cormocephalus coynei*) foraging behavior was studied. Points represent survey plot locations.

δ^{15}N = 2.1‰ ± 0.4‰ SD) from an ex situ feeding experiment of a generalist invertebrate predator, lycosid spiders that were fed a carnivorous diet (Oelbermann and Scheu 2002). To test the suitability of selected TEFs, we used a mixing polygon simulation following Smith et al. (2013) to ensure that the consumer isotopic signatures could be explained by our proposed model (fig. S1; figs. S1–S3 are available online). Data and code underlying the Bayesian dietary source mixing model have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.9kd51c5g2; Halpin et al. 2021).

Results

Centipede Foraging

During 132 h of in situ foraging surveys, we observed Phillip Island centipedes hunting or consuming a range of

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Figure 3: Black-winged petrel (*Pterodroma nigripennis*) nestlings that have been preyed on by Phillip Island centipedes (*Cormocephalus coynei*). Images by L. Halpin, 2018, 2019.

invertebrate, reptile, fish, and bird prey from 32 observed strikes and 21 observed feeding events (table 1). Phillip Island centipedes are large scolopendrids (median body length: 19 cm; range: 1–23.5 cm; $n = 440$). In 2018 and 2019, respectively, 19.6% (11 of 56 nests) and 11.1% (5 of 45 nests) of regularly monitored black-winged petrel nestlings were preyed on by centipedes. During the same periods, none of the monitored white-necked petrel nestlings were preyed on by centipedes. Before predation, black-winged petrel nestlings appeared healthy and were being provisioned by parents as indicated by an average mass gain (±SD) of 23.5 ± 14.7 g in the approximate 3-day interval immediately before predation (fig. S2). The mean body mass (±SD) of nestlings at the last measurement before their predation was 87.7 ± 33 g (range: 44–147 g; fig. S2). In 2018 and 2019, respectively, there were only one and two nestling mortalities that did not exhibit signs of centipede predation and were attributed to other causes. We observed one instance of envenomation of

a black-winged petrel nestling by a centipede (video S1; videos S1, S2 are available online) in an exposed burrow that ultimately resulted in nestling death, where the centipede did not consume the nestling at the time of observation. We also observed a centipede consuming a nestling (video S2) from the group of study nests that, earlier on the same day, was observed alive and well and was regularly being fed by its parents.

Crickets were the most frequently targeted and consumed prey item. Hunting strike success rates were low for frequently targeted species, including observations of five strikes at Günther's island geckos where all focal individuals evaded capture. All six observations of vertebrates being consumed on the forest floor were presumably the result of scavenging. These included four instances of fish consumption, one black noddy nestling presumed to have fallen from an arboreal nest, and one Günther's island gecko in a state of advanced decomposition (fig. S3).

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Table 1: Proportion of prey strikes, successful strikes, and feeding events by Phillip Island centipedes

Prey class, species	Strikes (%)	Successful strikes (%)	Feeding (%)
Insecta:			
Ant sp.	6.3	100	9.5
Crickets (*Dictyonemobius pacificus, Dictyonemobius lateralis, Nesitathra phillipensis*)	65.6	19	28.6
Beetle sp.	0	0	4.8
Moth sp.	0	0	4.8
Arachnida:			
Spider sp.	0	0	4.8
Diplopoda:			
Oxidus gracilis	3.1	100	9.5
Chilopoda:			
Cormocephalus coynei	3.1	0	4.8
Osteichthyes:			
Engraulis australis, fish sp.	0	0	19
Reptilia:			
Christinus guentheri	15.6	0	4.8
Aves:			
Anous minutus	0	0	4.8
Pterodroma nigripennis	6.3	50	0

Note: Strikes are defined as the percentage of the total number ($n = 32$) of strikes accounted for by strikes at that prey taxon. Successful strikes are the percentage of those strikes that resulted in successful capture. Feeding is the percentage of the total number of feeding observations ($n = 21$) where a centipede was observed consuming a given prey taxon. Fish are deceased and discarded from tree-nesting seabirds.

Bayesian Dietary Source Model Results

The Bayesian dietary source mixing model (fig. 4) estimated that vertebrates form a large proportion (48%) of centipede diet, with 38.4% of the diet consisting of terrestrial vertebrates: geckos (17.7%; 95% credibility interval [CI]: 2.8–38.6), skinks (12.8%; 95% CI: 1.8–31.2), and seabird nestlings (7.9%; 95% CI: 1.6–16.9). Fish scavenged from regurgitated meals of seabirds formed 9.6% (95% CI: 1.6–22.5) of centipede diet. The remainder of the Phillip Island centipede diet (52.1%; 95% CI: 33.2–69.2) consisted of invertebrates (crickets). While skinks were not directly observed being hunted or consumed by Phillip Island centipedes, similarly sized giant centipedes are known to prey on skinks in other systems (e.g., Emery et al. 2020, 2021). It is likely that Phillip Island centipedes prey on skinks belowground or under loose leaf litter; thus, skinks were included in the dietary mixing model.

Our results demonstrate a system in which the exchange of nutrients is largely driven by arthropod predation. A schematic diagram (fig. 5) depicts the direction and strength of the trophic linkages predicted by the model, hypothesized linkages, and the general flow of nutrients. Marine fish enter this terrestrial food web as discards from seabirds.

Discussion

Our results demonstrate that through high rates of predation on vertebrates, arthropods can play an important role in structuring ecosystem nutrient cycling in island ecosystems. On Phillip Island, centipedes that prey on seabirds increase enrichment of the nutrient pool with marine-derived nutrients by consuming seabird nestlings that are nourished by their parents exclusively with pelagic fish and squid. Predation by centipedes likely produces a more homogenous nutrient landscape. Nutrient deposition in seabird colonies is typically patchy and localized, with nutrients accumulating around nest sites via spilled food, dead nestlings and adults, abandoned eggs, and deposition of guano (Gillham 1956; Heatwole 1971; Anderson and Polis 1999; Sánchez-Piñero and Polis 2000; Harding et al. 2004). Predation of nestlings by centipedes means that centipedes are likely to actively translocate nutrients around the island (Schmitz et al. 2010). On an island depauperate of vertebrate predators, this is a potentially important process that could expand the regeneration of the island's vegetation into degraded areas (e.g., if centipedes roam into degraded environments that are unsuitable for burrow-nesting petrels).

Our observations revealed that centipedes targeted seabird nestlings with small body sizes reflective of a young and relatively defenseless age class. By extrapolating the observed rates of centipede predation on monitored petrel nestlings, which differed between years (19.6% in 2018 and 11.1% in 2019), to the upper bound of the most recent black-winged petrel population estimate (19,000 breeding pairs in 2017; N. Carlile, unpublished data), we estimate that Phillip Island centipedes consume between 2,109 and 3,724 seabird nestlings annually. Black-winged petrels are long-lived (>30 years) seabirds that produce a single offspring per year (Hutton and Priddel 2002). This means that each centipede predation of a seabird nestling represents total reproductive failure for a breeding pair in a given year. Arthropods are therefore able to reduce the lifetime reproductive output of long-lived, *K*-selected vertebrates. Our results not only suggest that predatory arthropods are important trophic engineers that structure nutrient flow on islands but also verify that they are important predators of terrestrial vertebrates in some ecosystems (Nordberg et al. 2018*a*; Valdez 2020).

Our results are consistent with reports of scolopendrid centipedes preying on vertebrates, including amphibians (Forti et al. 2007), bats (Molinari et al. 2005; Noronha et al. 2015; Lindley et al. 2017), lizards (Nordberg et al.

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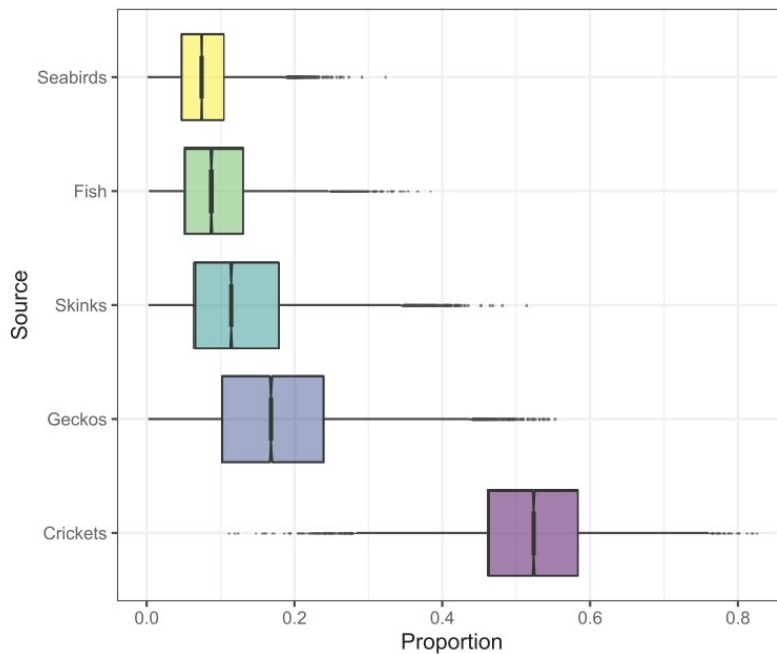
Figure 4: Estimated contribution of prey items in the diet of Phillip Island centipedes. Results present the relative proportions of dietary source contributions to centipede tissue predicted by the Bayesian dietary source mixing model (median, interquartile range, and maximum/minimum values of the posterior probability distribution).

2018*a*; Emery et al. 2020), and snakes (Smart et al. 2010; Arsovski et al. 2014). Remarkably, however, seabirds have not previously been reported as centipede prey despite centipedes and seabirds co-occurring on many islands. Our study appears to be a rare documented example in which seabirds have been identified as direct prey of an arthropod, thereby demonstrating a novel pathway for transfer of nutrients from the marine to terrestrial environment.

The dietary source mixing model we used cannot differentiate between prey that is captured and killed and prey that is scavenged. However, results of our in situ observations demonstrate that the Phillip Island centipede is both an active predator that was the principal driver of seabird nestling mortality and an opportunistic scavenger of other species, including reptiles and black noddy nestlings that fall from tree nests. Our foraging surveys were limited in scope (conducted on only the surface of the forest floor) and were therefore unlikely to have detected centipedes foraging under deep leaf litter or in subterranean cavities. Therefore, prey items captured and consumed underground (e.g., predation of burrow-nesting black-winged petrels) are likely to be underrepresented by our monitoring. Results of

the dietary mixing model indicate a larger squamate contribution to centipede diet than we observed in foraging surveys, which suggests that centipedes may be more successful at preying on geckos and skinks underground.

Further supporting the conclusion that black-winged petrel nestlings were actively preyed on rather than scavenged is our observation that no white-necked petrel nestlings were consumed by Phillip Island centipedes during nest monitoring. White-necked petrel body mass is almost three times larger (Marchant and Higgins 1990), with their nestlings reaching a larger body mass more quickly than black-winged petrel nestlings, and presumably, nestlings are able to defend themselves from centipedes at a younger age. This accords with our observation that Phillip Island centipedes preyed predominantly on smaller-sized black-winged petrel nestlings. Vulnerability to predation by rats (*Rattus* spp.) shows a similar age-dependent pattern in gray-faced petrels (*Pterodroma gouldi*), with predation risk declining to very low levels at ~3 weeks after hatching (Imber et al. 2000). Nevertheless, centipedes are generalists and will likely consume any deceased vertebrates encountered during foraging.
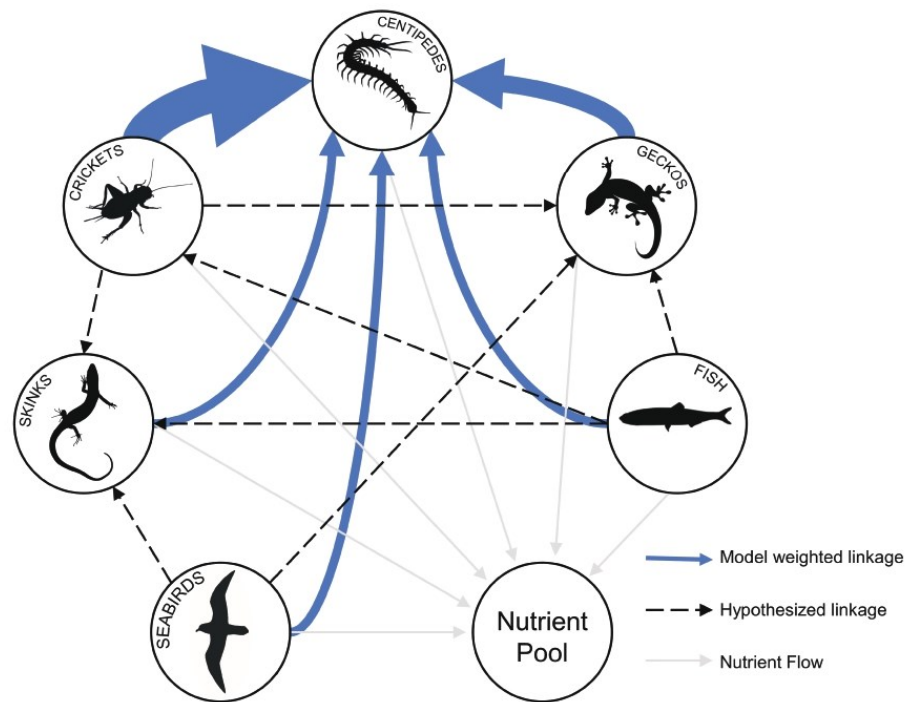
Figure 5: Schematic diagram of the general Phillip Island food web with the thickness of dietary linkages to centipedes weighted according to proportional contributions of centipede prey taxa to centipede tissue isotopic values.

Although nestlings of other seabird species may also have contributed to the isotopic signature of Phillip Island centipedes, we believe that black-winged petrel chicks are the major seabird diet constituent on the basis of our foraging observations and aspects of the ecology of the breeding seabird community. For example, black-winged petrels are the only small-bodied, burrow-nesting seabird that breeds in summer (coincident with the timing of stable isotope tissue sampling) on Phillip Island. They are also the most abundant breeding seabird on the island, with an abundance one to two orders of magnitude greater than nine of the 12 other breeding seabird species.

We observed a single cannibalism event among Phillip Island centipedes, which is otherwise common in many food webs (Ings et al. 2009). We did not attempt to quantify the dietary contribution of cannibalism in the dietary mixing model given the challenges of distinguishing cannibalism from other forms of intraguild predation (Greenwood et al. 2010; Traugott et al. 2013).

Large scolopendrid centipedes have been introduced to many islands, especially in tropical and subtropical regions (Shelley 2004; Shelley et al. 2014; Waldock and Lewis 2014) and have recently been implicated in the extinction of an endemic island vertebrate (Emery et al. 2020). Systems slated for conservation efforts (e.g., reintroductions of extirpated species) where large introduced centipedes or other predatory arthropods are present will likely require innovative solutions or centipede control to minimize impacts to recovering or colonizing species targeted for conservation (e.g., Emery et al. 2020). By contrast, innovative approaches may be necessary in disturbed systems given the potential interactions between native predatory arthropods and potential prey of conservation importance (e.g., Feher 2019; Valdez 2019).

We provide a novel understanding of the role of predatory arthropods in structuring trophic dynamics on islands. We demonstrated that arthropods can increase the flow of marine nutrients in an island ecosystem by preying on

the offspring of vertebrates that forage exclusively in pelagic environments. We demonstrate how predatory arthropods can exert top-down pressure on vertebrate populations through predation-mediated reductions in reproductive output. This could have important consequences for understanding trophic structures on islands and how vertebrate communities are shaped, perhaps especially so on islands, where arthropod gigantism is common and evolutionary processes have allowed invertebrates to occupy novel niches.

Statement of Authorship

L.R.H. conceived the study, acquired funding and scientific permits, collected field data, performed lab analyses, analyzed the data, and led the writing of the manuscript. D.I.T. collected field data and assisted with data analysis. H.P.J. and R.M. contributed to research development and assisted with data analysis. D.C.D. collected field data. W.W.W. conducted stable isotope lab analyses. R.H.C. and N.C. contributed to project development, acquisition of scientific permits, funding, and fieldwork. All authors contributed substantially to the manuscript and gave final approval for publication.

Data and Code Availability

All data and code have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.9kd51c5g2; Halpin et al. 2021).

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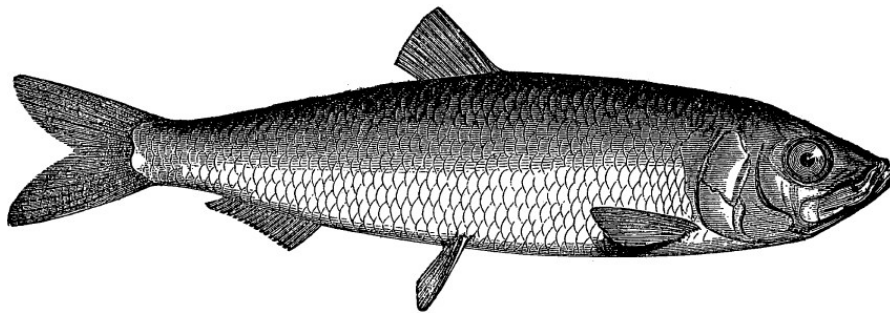
"In respect to our smaller fishes, the Herring (*Clupea elongata*), etc., we observe a considerable decrease in the numbers which now annually visit our shores, as compared with their former numbers." From "The Habits and Migrations of Some of the Marine Fishes of Massachusetts" by James H. Blake (*The American Naturalist*, 1870, 4:513–521).