A CONCEPTUAL FRAMEWORK
FOR THE DRIVERS OF ALBATROSS MOVEMENT

SARAH E. GUTOWSKY

Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada (sarahegutowsky@gmail.com)

ABSTRACT

GUTOWSKY, S.E. 2017. A conceptual framework for the drivers of albatross movement. *Marine Ornithology* 45: 23–38.

The objective of movement ecology is to understand the connections among factors that drive *why, when, where, and how* organisms move. The basic movement ecology framework (MEF) envisions how four major components (internal state, navigation capacity, motion capacity, and external elements) interact to generate an individual's movement path. Empirical studies of movement have become increasingly sophisticated as a result of advancements in animal-attached biologging technologies that estimate movement paths. These tools have been applied extensively in the study of marine animal movement, particularly the highly mobile and threatened albatrosses (Diomedeidae). Despite the volume of albatross-biologging movement research, the complex factors and processes that govern the movements of these birds have not before been unified into a comprehensive framework. This paper aims to accomplish two main objectives: (1) integration of ideas from across disciplines to build a custom MEF for albatross, resulting in the identification of 45 discrete factors and their interactions; and (2) use of this MEF to survey the albatross-biologging movement literature for trends, shortcomings, and future directions. As the sophistication of analytical and biologging tools continues to grow, so too will the breadth and complexity of processes invoked and investigated to explain albatross movements at all spatiotemporal scales.

Key words: albatross, biologging, movement, marine ecology, seabirds, telemetry

INTRODUCTION

Understanding the ecological and evolutionary significance of individual movement is the motivation behind a broad field of research called movement ecology (herein ME; Nathan *et al.* 2008). The collective objective of ME is to understand the connections among the multitude of factors that drive *why*, *when*, *where* and *how* individuals move (Nathan & Giuggioli 2013). By considering all aspects of individual movement together, ME offers a cross-disciplinary framework for conceptualizing the underlying mechanisms of movement patterns, and the interaction of animal movement and evolutionary processes (Nathan *et al.* 2008). The framework is universal to the study of movement, in that it is applicable across taxa, movement phenomena, and methodologies, and at any spatiotemporal scale.

The movements of organisms of all kinds can be explored in the context of the many factors that influence an individual's "movement path," defined as a sequence of locations occupied during some definitive duration within an individual's lifespan (Nathan *et al.* 2008). The factors simultaneously influencing a focal individual's movements can be considered within a basic framework composed of four interacting components (Fig. 1, adapted from Nathan *et al.* 2008): (1) the internal state component encompasses all factors that influence *why* an individual moves along a given movement path by considering intrinsic factors that influence an individual's motivation to move (e.g., age or body condition); (2) the navigation capacity component considers factors relevant to an individual's cognitive and noncognitive "decision-making" of *when and where* to move along a movement path (e.g., olfactory or geomagnetic cues); (3) the motion capacity component covers the biomechanical and morphological traits that allow an individual to move via different modes (e.g., soaring or flapping

flight), thus influencing *how* a movement path is generated; and (4) the external environment component is composed of all abiotic and biotic elements that influence a movement path through interactions with the other three components (e.g., wind or the presence of other individuals could influence *when, where and how* a bird might move). All four components interact through a variety of processes represented in the ME framework (Fig. 1). For example, *why* an individual moves can determine the types of information likely relevant to *when* and *where* it moves (e.g., the age of a bird could determine the cues influencing its movements). This interaction is represented in the ME framework as *navigation processes* acting between the internal state and navigation capacity components. The components and processes influencing movements are inevitably over-simplified in such a framework. Still, identifying key factors within each component and how they interact, is the primary challenge in populating the ME framework to customize it to a particular system or group of organisms under study (Nathan *et al.* 2008).

In this review, I populate the basic ME framework proposed by Nathan *et al.* (2008) for the highly mobile albatrosses (order Procellariiformes, family Diomedeidae, all 22 common and scientific species names in Table 1). There has been a wealth of movement studies conducted on albatross, as a result of a number of traits in these birds, especially their suitability for carrying biologging devices. Their large body size (wingspans ranging from 1.9 to 3.2 m and mass from 1.7 to 11.9 kg; Tickell 2000) was recognized 25 years ago as a robust platform for device attachment by Jouventin & Weimerskirch (1990). Since this seminal study that deployed satellite-tracking devices on Wandering Albatross *Diomedea exulans*, movement paths of individuals of all 22 albatross species have been recorded using the myriad of continually advancing biologging technologies (Taylor *et al.* 2004, Pinaud *et al.*

2005, Wakefield *et al.* 2011; Table 1), and over 100 movement studies have been published in peer-reviewed journals. Further traits contributing to the high number of albatross biologging studies include long lifespans, with high adult survivorship and high site fidelity to their conspicuous surface nests (Warham 1990, 1996, Tickell 2000). This means that adults are generally easy to

capture and re-capture at their nests, as they reliably return to breed throughout their long lives, making them optimal candidates for the deployment and recovery of devices (Burger & Shaffer 2008).

There is also considerable conservation incentive to investigate albatross ME. Fifteen species are currently considered Vulnerable
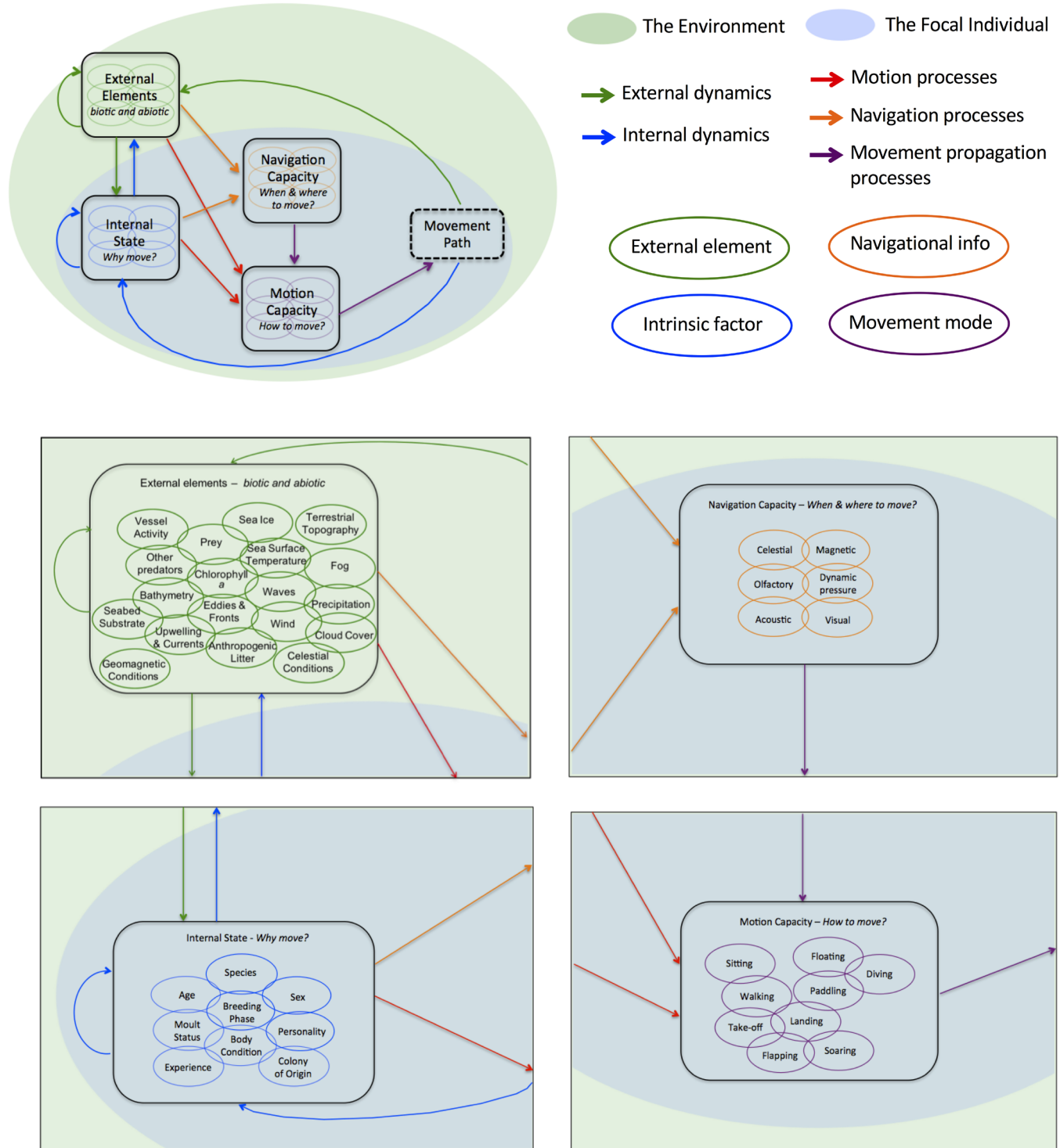

Fig. 1. A custom movement ecology framework for the drivers of albatross movement (adapted from Nathan *et al.* 2008). The basic framework is composed of four interacting components that together determine an individual's movement path (upper left). Arrows indicate the processes acting within and between components. Albatross-specific factors within each component of the full framework are detailed in the four cut-out panes (bottom).

to extinction, Endangered or Critically Endangered, according to the International Union for the Conservation of Nature, and the remaining seven species are considered Near Threatened (Table 1, IUCN 2015). Understanding what drives patterns in range and distributions at sea, especially in relation to overlap with fisheries and other threats such as pollution, is a key component in effective conservation planning for these species (Burger & Shaffer 2008). Conservation concerns, in combination with body size and life-history traits, have led to a significant body of research based on recording individual movement paths of biologger-equipped albatross.

Despite the considerable volume of published albatross-biologging movement research, the complex factors and processes that govern the movements of these birds have not before been unified into a comprehensive framework. Instead, our understanding of the multitude of factors that drive albatross movements remains scattered across disciplines, including spatial, behavioural, physiological, and sensory ecology, as well as neurophysiology, biomechanics, and biological oceanography. Therefore, this paper has two main objectives: (1) to integrate ideas from across disciplines to build a custom conceptual ME framework for albatross; and (2) to use this framework to survey the albatross-biologging movement literature for trends, shortcomings, and future directions in our understanding of the drivers of these species' movement. To meet the first objective, I pull together pieces from the cross-disciplinary body of research that help address *why, when, where, and how* albatross move. I define each component such that discrete and comparable factors within each component can be identified. Throughout, I identify interactions within and among the components, and biotic and abiotic elements in the environment that interact with all other factors to produce a movement path. For the second objective, I then apply the custom framework as a guide for a focused review of published research in which bird-borne biologging devices are used to record sequential location data of individual albatross. I survey the literature for the factors most commonly measured or suggested as important in determining the observed movement patterns. This allows for the recognition of components and factors that have received the most consideration, and those in need of attention, in order to develop a more holistic understanding of albatross movement.

TABLE 1
Published biologging studies of movement for each albatross species (from 1990 to 2015), current IUCN Red List category, and oceanic regions of residence

Common name (all ending in "Albatross")	Scientific name	No. of published biologging movement studies	IUCN Red List category[a]	Oceanic regions of residence[b]
Amsterdam	*Diomedea amsterdamensis*	3	CR	Southern Indian
Antipodean	*Diomedea antipodensis*	2	VU	South Pacific
Atlantic Yellow-nosed	*Thalassarche chlororhynchos*	0[c]	EN	South Atlantic
Black-browed	*Thalassarche melanophris*	25	NT	Southern Indian, South Pacific, South Atlantic
Black-footed	*Phoebastria nigripes*	16	NT	North Pacific
Buller's	*Thalassarche bulleri*	4	NT	South Pacific
Campbell	*Thalassarche impavida*	1	VU	South Pacific
Chatham	*Thalassarche eremita*	2	VU	South Pacific
Grey-headed	*Thalassarche chrysostoma*	14	EN	Southern Indian, South Pacific, South Atlantic
Indian Yellow-nosed	*Thalassarche carteri*	3	EN	Southern Indian, South Pacific
Laysan	*Phoebastria immutabilis*	13	NT	North Pacific
Light-mantled	*Phoebetria palpebrata*	8	NT	Southern Indian, South Pacific, South Atlantic
Northern Royal	*Diomedea sanfordi*	3	EN	Southern Indian, South Pacific, South Atlantic
Salvin's	*Thalassarche salvini*	0[c]	VU	Southern Indian, South Pacific
Short-tailed	*Phoebastria albatrus*	5	VU	North Pacific
Shy	*Thalassarche cauta*	2	NT	Southern Indian
Sooty	*Phoebetria fusca*	1	EN	Southern Indian, South Atlantic
Southern Royal	*Diomedea epomophora*	2	VU	Southern Indian, South Pacific, South Atlantic
Tristan	*Diomedea dabbenena*	2	CR	South Atlantic
Wandering	*Diomedea exulans*	46	VU	Southern Indian, South Pacific, South Atlantic
Waved	*Phoebastria irrorata*	6	CR	Central Pacific
White-capped	*Thalassarche steadi*	2	NT	Southern Indian, South Pacific, South Atlantic

[a] IUCN Red List Categories: Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR).
[b] IUCN 2015.
[c] No biologging research has been published in peer-reviewed journals but biologging studies have been carried out and published in reports.

THE INTERNAL STATE: INTRINSIC FACTORS THAT INFLUENCE WHY TO MOVE

The internal state component of the ME framework includes the factors intrinsic to an individual that drive *why* it moves and thus influence an observed movement path (Nathan *et al.* 2008). The internal state at any given moment could be thought of as a multidimensional vector of intrinsic factors that play a role in determining *why* an individual moves. For example, a bird's movements may be influenced by the effects of age, breeding phase, and body condition (i.e., intrinsic factors) on its need to both forage and rest. Below, I briefly review distinct intrinsic factors likely to play a role in determining an individual's movements (summarized in Fig. 1). These factors are first presented independently, with simple examples of their effects on individual movement. This is followed by discussion of the inter-relatedness of intrinsic factors (i.e., how factors interact within the internal state), how the influence of intrinsic factors depends on the external environment, and how these relationships and processes are represented in the ME framework.

Species: An individual's species is the fundamental intrinsic factor that plays a role in influencing *why* a bird moves along a particular movement path by determining the general species-specific traits and ecological niche. Among albatross species, traits might include for example species-specific wing loading (e.g., Suryan *et al.* 2008) and foraging techniques (e.g., Fernández & Anderson 2000, Weimerskirch & Guionnet 2002). Thus, individuals of different species fill distinct ecological niches in terms of their habitats (both on land and at sea) and diet (e.g., Suryan & Fischer 2010, Kappes *et al.* 2010). An individual's species establishes the foundation for its unique set of intrinsic factors that influence *why* move via a given movement path. For example, the movements of a Laysan Albatross *Phoebastria immutabilis* in the North Pacific Ocean may be driven in part by adaptations associated with its diet of squid acquired from cool deep waters, while the movements of a Black-footed Albatross *Phoebastria nigripes* within the same ocean basin may be driven in part by adaptations associated with its diet of flying fish eggs found in warmer waters (Kappes *et al.* 2010).

Age: Albatross generally exhibit delayed sexual maturity (age of first breeding attempt >5 years) and longevity (>50 years), and they experience senescence (i.e., physical deterioration and reduced reproductive success) in later life (Warham 1990, Tickell 2000, Catry *et al.* 2006, Lecomte *et al.* 2010). The at-sea movements of an immature, pre-breeding bird in its first years are likely driven mostly by the need to feed itself, while the movements of a mid-aged bird could be driven in part by the need to feed itself and also by the demands of breeding, such as finding a mate or feeding a chick (Alderman *et al.* 2010, Riotte-Lambert & Weimerskirch 2013, Gutowsky *et al.* 2014). The movements of an older bird may be driven by similar needs to that of a mid-aged bird as it continues to raise offspring, but with increased self-provisioning demands resulting from declining faculties such as poorer visual acuity or muscular function (e.g., Catry *et al.* 2006, Angelier *et al.* 2006, Lecomte *et al.* 2010, Pardo *et al.* 2013, Froy *et al.* 2015).

Breeding phase: Once an individual has reached breeding age, its breeding cycles are divided into distinct phases, including pre-breeding (courtship, nest building, laying of a single egg), incubation, chick brooding, chick rearing, and overwintering (Warham 1990, Tickell 2000). The overwinter phase can begin following fledging or during any phase of the breeding cycle if the reproductive attempt fails, and can also be extended to a sabbatical year at varying species-specific intervals (Warham 1990, Tickell 2000, Jouventin & Dobson 2002). The movements of an individual in the incubation phase could be driven by the need to feed itself at sea, to recover from fasting and replenish reserves for its next incubation shift, and to return to the nest to relieve its incubating mate. The movements of an individual in the chick-rearing phase could be driven by the need to both feed itself and its growing chick (e.g., Salamolard & Weimerskirch 1993, Shaffer *et al.* 2003, Hedd & Gales 2005, Young *et al.* 2009).

Sex: Males and females can differ in their dietary or habitat needs as a result of reproductive role specialization and foraging niche divergence (e.g., Salamolard & Weimerskirch 1993, Weimerskirch *et al.* 1997c, 2000b, Shaffer *et al.* 2001b, Phillips *et al.* 2004b, 2011). The movements of a female albatross following return from overwintering could be driven in part by the need to recover resources invested into developing an egg (e.g., Frings & Frings 1961), while the movements of a male could be driven by the need to spend time ashore at the colony for courtship and to establish a territory in the hopes of securing a mate or to wait near the same nest site shared with a mate in the previous year (e.g., Fisher 1971a, Pickering 1989). Further, the movements of a chick-rearing bird of a sexually dimorphic species could be driven by an interaction between the individual's sex and the sex of the chick; the movements of a larger male parent may be driven by its own energetic demands and the high demands of rearing a fast-growing and heavy male chick (e.g., Weimerskirch *et al.* 2000b).

Personality (i.e., consistent behavourial tendencies): Albatross have been shown to exhibit distinct personalities, characterized along a shy–bold continuum using standardized tests (i.e., "boldness" toward an approaching human or novel object ranging from consistently shy to aggressive; Patrick *et al.* 2013). The movements of a bolder individual during the incubation and chick-brooding phases may be driven by a personality-related tendency to forage nearer to the colony in shallow areas where competition for abundant resources is high, while a shyer individual would be more likely to forage further from the colony over deeper, less productive waters (Patrick & Weimerskirch 2014).

Body condition (morphological or physiological): Body condition in birds is most often treated as a reflection of energy reserves (Labocha & Hayes 2012), which affect a bird's physiological functions and, in turn, drive it to move. Body condition can be represented by morphometric estimates of energy stores, such as abdominal fat profiles, fat scoring, or body mass (Labocha & Hayes 2012). Other qualititative or quantitative variables can be taken as a proxy for body condition based on expected relationships with energy reserves, including for example the size and time of the last meal (Catry *et al.* 2004b), blood levels of hormones linked to mobilizing energy reserves and coping with energetic stress (Angelier *et al.* 2006, 2011), or parasite loads linked to decreased body fat stores (Langston & Hillgarth 1995). The movements of an individual in poor body condition, measured as any of these variables, may be driven by both the need to forage intensively to meet high immediate energy demands and to increase energy reserves for future use, such as when fasting on the nest.

Moult status: For albatross, maintaining the plumage needed for efficient long-distance flight is an energetically costly process,

necessitating complex multi-year or biennial flight feather moult strategies (e.g., Langston & Rohwer 1996, Edwards 2008). An individual's moult status at any point in time could consist of entirely fresh plumage, mostly old or severely worn plumage, or any combination of new and old, and could also include active replacement of some body or flight feathers. The movements of an adult with flight feathers requiring replacement would be driven in part by a need to build energy, protein, and nutrient stores sufficient for upcoming feather growth while also compensating for reduced flight efficiency from worn plumage (e.g., Gutowsky *et al.* 2014).

Experience: Experience is often measured relative to age or total number of breeding attempts (e.g., Angelier *et al.* 2007). However, experience differs among individuals of the same age and breeding history, as it encompasses a bird's unique history of breeding failures and successes as well as social and competitive interactions, foraging, and exposure to stresses. The learning opportunities (or lack thereof) afforded by an individual's unique cumulative lifetime experiences likely influence its movements. The movements of a less experienced bird may be driven by an increased need to forage owing to low foraging proficiency (i.e., poor choice of foraging areas, poor recognition of suitable prey items, or poor prey handling; Riotte-Lambert & Weimerskirch 2013, Froy *et al.* 2015) or by the need to be present at the colony for courtship practice with other unpaired individuals (Pickering & Berrow 2001).

Colony of origin: Albatross have high natal philopatry (i.e., recruitment of first-time breeders to their birth colony) and near-absolute breeding philopatry (i.e., once it has started breeding, an individual continues to nest at the same colony throughout its lifetime; Tickell 2000). Thus, an individual's colony of origin can be an important factor intrinsic to the individual that may influence its movements. The movements of a breeding bird with an egg or chick will be constrained by its ties to the colony (i.e., central place foraging constraints; Orians & Pearson 1979). The movement path of a bird during breeding is also influenced by the level of competitive pressure for local resources around the colony, which depends on the size and location of the colony (Ashmole 1963, Cairns 1989). The movements of an albatross originating from a large colony (or from a small colony close to a large one) may be driven in part by local competitive pressure during periods of high central place constraint (e.g., Wakefield *et al.* 2011).

Interactions among intrinsic factors: The true impact of any one factor in determining an individual's movement path is more realistically understood when considered in concert with others. The interactions among intrinsic factors are represented in the ME framework as *internal dynamics* acting within the internal state component (Fig. 1). One example is the inter-relation among breeding phase, body condition, and moult status. Moult status is determined in part by breeding phase, and in turn likely influences, and is influenced by, body condition. For example, an albatross will typically actively moult flight feathers only during the non-breeding season (Bridge 2006, Rohwer *et al.* 2011), and an actively moulting bird is likely to have lower body condition in terms of energy stores because of the energetic demands of feather growth and to have reduced ability to forage because of compromised flight dynamics (Edwards 2008, Gutowsky *et al.* 2014). A bird's movements are likely influenced by the combined effect of these three intrinsic factors on *why* a bird would move via a particular path.

Another example is the inter-relation of experience and body condition. The *internal dynamics* acting among these factors could be considered carryover effects, defined by O'Connor *et al.* (2014, p. 2) as "any situation in which an individual's previous history and experience explains their current performance in a given situation." *Why* an individual albatross moves along a particular path is likely influenced in part by carryover effects from past experiences on its present body condition in terms of energy stores, aerobic capacity, and hormonal status (e.g., Crossin *et al.* 2012, 2013). For example, a female albatross returning to the colony after overwinter may skip the opportunity to breed (Tickell 2000) and hence present a movement path atypical of a breeding bird. The movements of this individual will be driven in part by present body condition, which will depend on experiences during recent movements and during the previous overwinter and breeding phases (Crossin *et al.* 2013).

Interactions between the internal state and the external environment

All movement occurs within an environmental context (Fig. 1), and thus the effects of intrinsic factors on movement are related to the external environment in which they act. These interactions are represented in the ME framework as *internal and external dynamics* acting between the internal state and the external environment (Fig. 1). Many of the biotic and abiotic elements in the external environment also co-vary, represented in the ME framework as *external dynamics* acting within the environmental component (Fig. 1). For example, colony of origin can influence *why* an individual moves along a particular movement path. It is also, however, an important determinant of elements within the external environment that a moving bird is likely to encounter, such as density of conspecifics at sea, local colony topography (i.e., nest site substrate or slope), and local species assemblage both at sea and on land (all of which are inter-related). Colony of origin will also in part determine the oceanographic and meteorological conditions likely to be encountered along a movement path, as well as the likelihood of encounters with fishing vessels or anthropogenic litter. Overall, each of the intrinsic factors discussed above will interact in some way with elements in the external environment to influence an individual's movement path.

NAVIGATION CAPACITY: INFORMATION THAT INFLUENCES WHEN AND WHERE TO MOVE

The navigation capacity component of the ME framework is defined here as comprising the sources of navigational information that influence an individual's "decision-making" concerning *when and where* to move (i.e., initiation, cessation, and direction of movement) and thus influence an observed movement path. Similar to an individual's internal state, an individual's navigation capacity at any given moment could be thought of as a multidimensional vector of information inputs that together impact movement decisions at various spatial and temporal scales (Bonadonna *et al.* 2003a, Muheim *et al.* 2006, Mardon *et al.* 2010). An individual's "decisions" in response to information inputs are a combination of non-cognitive processes (i.e., timing or direction determined by inherited traits; Åkesson & Weimerskirch 2005, Åkesson & Hedenström 2007) and true cognitive choices that reflect navigation skills (i.e., aptitude for processing information inputs and sense of current location) learned through experience (e.g., Kenyon & Rice 1958, Fisher 1971b, Riotte-lambert & Weimerskirch 2013). Albatross frequently cross vast expanses of open ocean devoid of

cues detectable by the modern human's eye, yet these birds achieve remarkable precision in navigating back to their colonies (even when experimentally displaced more than 6 000 km; Kenyon & Rice 1958). The navigation capacities of these birds must encompass a diversity of sensory abilities receiving varied information inputs that likely impact movement decisions simultaneously at multiple spatiotemporal scales. Below, I identify a variety of information inputs likely to influence the movement decisions of an albatross and discuss the processes that determine how factors within the internal state and elements in the environment influence the types of navigational information available or relevant to an individual.

Celestial cues (i.e., information from the sky): Both diurnal and nocturnal celestial information, including photoperiod, sun polarization, sun position, stellar orientation, and moon position, are known cues used by long-distance songbird migrants during their large biannual movements (e.g., Able & Able 1996, Gould 1998, Muheim *et al.* 2006). Although there is no direct evidence that celestial cues are important for navigation in albatross, it has been suggested this mechanism is used (Mouritsen *et al.* 2003, Bonadonna *et al.* 2005). The distance covered during annual songbird migrations are often equivalent to the foraging commutes made by albatross dozens of times each breeding season. For example, a Wandering Albatross off-duty from incubation at the nest could travel over 13 000 km over 28 d across a vast pelagic landscape (Weimerskirch *et al.* 1997b). It is reasonable to suggest that individual albatross use celestial information in movement decisions in these routine large-scale movements, similar to that used by migrating songbirds.

Geomagnetic cues (i.e., information from the magnetic field of the earth): Magnetic field strength or inclination can act as a guide to orient general movement direction (reviewed by Wiltschko & Wiltschko 1996, O'Neill 2013). While some experimental evidence suggests that albatross can navigate without geomagnetic cues (e.g., Åkesson & Alerstam 1998, Bonadonna *et al.* 2003b, 2005, Mouritsen *et al.* 2003), their general use cannot be ruled out. Geomagnetic cues may be part of a multi-modal navigation system in which different sources of navigational information can be substituted based on availability, to accomplish the same directional movement (Åkesson & Alerstam 1998, Mouritsen *et al.* 2003). An individual albatross travelling thousands of kilometres across an open ocean landscape is likely to be integrating multiple sources of navigational information to orient its broad-scale movements, and these may include geomagnetic cues.

Dynamic pressure cues: The long-distance movements of albatross and many of their tube-nosed relatives rely on a method of flight called "dynamic soaring" that depends on an ability to detect changes in wind speed and direction, in both the vertical and horizontal plane (Weimerskirch *et al.* 2000a, Pennycuick 2002), likely using an innate internal barometer or "baroreception" that detects small changes in atmospheric pressure (O'Neill 2013). The olfactory neuroanatomy of tubenoses shows strong hypertrophy, occupying *ca.* 37% of the total brain volume, compared with *ca.* 3% in most other birds (Bang 1966, 1971). Pennycuick (2002) proposed that the highly developed nasal sense organ in albatross functions to receive both dynamic pressure information (i.e., to detect changing wind speed and direction by sensing air pressure) and olfactory information (see next section). Dynamic pressure can indicate airspeed relative to wind speed and direction, contributing to individual decisions concerning timing and direction of movement

in response to large-scale meteorological conditions and fine-scale wind and elevation conducive to efficient soaring flight (e.g., Murray *et al.* 2003, Catry *et al.* 2004a, Richardson 2011).

Olfactory cues (i.e. information from odours): Olfaction is likely important for movements toward food resources when foraging and toward the island/colony upon returning. Olfactory information could be produced from phytoplankton (e.g., dimethyl sulfide released in response to grazing krill; Nevitt *et al.* 1995), from prey species (e.g., when macerated during consumption; Nevitt & Bonadonna 2005), or from other birds (e.g., social odours; Nevitt 2008). For albatross, it is unclear to what extent they rely on odours for navigating (e.g., Nevitt *et al.* 1995, Bonadonna *et al.* 2003a), but it is likely that olfactory cues play a role in guiding movement decisions (Nevitt *et al.* 2008, Mardon *et al.* 2010). Albatross and other seabirds have well-documented associations at sea with several inter-related biological and physical oceanographic features that are considered proxies for primary and secondary productivity, including sea surface temperature, chlorophyll *a* concentrations, eddies and fronts, upwelling and currents, and bathymetry (Tremblay *et al.* 2009, Wakefield *et al.* 2009a, Kappes *et al.* 2010). An individual's movement decisions that result from these associations are likely influenced, at least in part, by olfactory cues.

Visual and acoustic cues (i.e. information from sight and sound): At a broad spatial scale, visual detection of wind streaks and ripples may aid in identifying likely areas of buoyant prey aggregation (Nevitt *et al.* 2008). Gatherings of other seabirds and subsurface predators at a fishing vessel or a productive feeding area at sea could provide both visual and acoustic information (e.g., Silverman *et al.* 2004, Sakamoto *et al.* 2009, Collet *et al.* 2015). Visual cues would also play a key role in influencing fine-scale movement decisions when localizing and capturing target prey items upon encountering them, both above and below the water's surface (e.g., Martin 1998, Weimerskirch *et al.* 2007). Upon return to the colony from the open sea, the sight and sound of increasing numbers of sympatric birds nearer the colony, as well as wave and cloud formations influenced by a land mass, likely serve as navigational information used to guide the direction of movement, followed by sight of the colony's physical land mass and familiar landmarks. Low-frequency infrasound emitted when wind blows over physical barriers or when waves break against shore can propagate great distances, perhaps also guiding the movements of individual albatross (Åkesson & Alerstam 1998).

Interactions between navigation capacity and the internal state

The relative contribution of each source of navigational information is determined by a bird's unique vector of intrinsic factors, represented in the ME framework as *navigation processes* acting between navigation capacity and the internal state (Fig. 1). For example, an individual's age and experience play an important role in determining which sources of information contribute to movement decisions. The movement path of a fledgling albatross is most likely influenced by movement "decisions" based on an inherited genetic program for movement bearing relative to geomagnetic or celestial cues, while more fine-scale movement decisions might be made in response to olfactory or visual cues (e.g., Riotte-Lambert & Weimerskirch 2013, Gutowsky *et al.* 2014). Memories and learned navigation skills accumulate and improve with age; thus, experience becomes increasingly important in

influencing cognitive movement decisions over an albatross's long lifespan (Weimerskirch *et al.* 2014).

Interactions between navigation capacity and the external environment

The availability of each source of navigational information is determined by elements in the environment, represented in the ME framework as *navigation processes* acting between navigation capacity and the external environment (Fig. 1). For example, the strength and reliability of geomagnetic cues vary between regions of the planet, and thus the influence of this cue on an individual's movement decisions depends on its availability (Åkesson & Alerstam 1998). Similarly, the presence of olfactory cues depends on the biological and physical features of the environment that produce and concentrate odours, while the detectability of those cues for an individual at any location and time will depend on the transport of odours by wind and water current conditions (Bonadonna *et al.* 2003a, Nevitt *et al.* 2008). Visual and acoustic cues rely directly on elements in the environment, including the presence of prey or other predators, while the detectability of those cues for an individual at any location and time are influenced by meteorological elements of the environment, such as fog, cloud cover, or precipitation. Overall, the multidimensional vector of information inputs that constitutes an individual's navigation capacity at a given moment depends on interactions with both the external environment and its internal state.

MOTION CAPACITY: MODES OF MOVEMENT THAT INFLUENCE HOW TO MOVE

The motion capacity component of the ME framework is composed of the various modes of movement available to an individual that determine *how* a movement path is generated (Nathan *et al.* 2008). The biomechanical and morphological traits of an individual provide a set of "motion machineries," enabling movement. The *movement propagation process*, in which bouts of different modes of movement are strung together to generate a movement path, could be considered the mechanistic bottleneck between all components and processes in the ME framework and the actual movement of the individual (Fig. 1). Below, I briefly review the different movement modes that may be available to an albatross and discuss how an individual's unique motion capacity at any moment depends on its internal state, navigation capacity, and the external environment.

Soaring flight: Dynamic soaring flight is the most iconic and hence widely recognized mode of movement used by albatross. Dynamic soaring flight is sustained flight, powered mainly by the energy of wind gradients (Pennycuick 1982, Arnould *et al.* 1996, Weimerskirch *et al.* 2000a, Suryan *et al.* 2008). The low energetic cost of soaring is made possible by unique anatomy, high wing aspect ratio paired with optimal wing loading, and a shoulder-lock mechanism enabling wings to be outstretched with little muscular contraction (Pennycuick 1982, Meyers & Stakebake 2005). Soaring flight is likely to contribute a high proportion of an individual's movement path when transiting long distances (Wakefield *et al.* 2009b, Mackley *et al.* 2010) but is certainly not the only mode of movement.

Flapping flight: Flapping flight is more energetically demanding than soaring flight but is nonetheless employed by albatross out

of necessity when soaring alone is not possible (Pennycuick 1982, Suryan *et al.* 2008, Sakamoto *et al.* 2013). For Black-browed Albatross *Thalassarche melanophris*, for example, heart rates when flapping have been shown to increase by ~75% compared with soaring, if flapping accounts for half of a flight bout (Sakamoto *et al.* 2013). Albatross are thought to lack the necessary musculature to undertake sustained bouts of flapping flight (Pennycuick 1982, Meyers & Stakebake 2005). Instead, flapping is interspersed with soaring to varying degrees to determine *how* a movement path is generated.

Takeoffs and landings: These are a critical and distinct transitional mode of movement. To take off, an albatross orients into the wind and often runs along the sea or land surface while beating its wings to gain lift (Kabat *et al.* 2007). This is probably the most energetically costly mode of movement, especially under calm or light wind conditions (Weimerskirch *et al.* 2000b, Shaffer *et al.* 2001a, Suryan *et al.* 2008). Similarly, landing (on water or land) requires rapid rotations of the wings about the long axis to stall (Pennycuick 1982) and is also energetically costly (Weimerskirch *et al.* 2000b, Sakamoto *et al.* 2013).

Floating, paddling, sitting, and walking: These are modes of movement with varying degrees of low mobility (or immobility, for sitting). Since a movement path is defined as a sequence of locations occupied by an individual during some definitive duration within its lifespan (Nathan *et al.* 2008), if this encompasses time spent on the colony, sitting as a "mode of movement" could contribute in generating the path. Paddling and walking are leg-propelled modes of movement often associated with a bout of floating or sitting. While out to sea, time spent floating (or drifting) is interspersed with active paddling (Conners *et al.* 2015). While on land, all albatross must cope with the necessity of walking between a destination and the landing or takeoff site, despite their limited terrestrial manoeuvrability (Weimerskirch *et al.* 2000b, Kabat *et al.* 2007).

Diving: Diving is wing- or foot-propelled swimming under the water and is used when target prey is deep enough that submersion of the head from a floating position would be insufficient. Diving as a mode of movement is available to only some species of albatross (e.g., Black-browed, Grey-headed *Thalassarche chrysostoma*, Shy *Thalassarche cauta*, Light-mantled *Phoebetria palpebrata*; Prince *et al.* 1994, Hedd *et al.* 1997, Huin & Prince 1997). These species regularly dive to depths of 2–5 m, with dives up to 12 m recorded for Light-mantled Albatross (Prince *et al.* 1994). For some species, diving as a mode of movement will contribute to *how* an individual's movement path is generated when foraging out to sea.

Interactions between motion capacity and the internal state

The modes of movement available to an albatross depend on its unique intrinsic factors, represented in the ME framework as *motion processes* acting between the internal state and motion capacity (Fig. 1). For example, a bird's breeding phase will influence the relative contribution of flight and sitting that contribute to an observed movement path; during the incubation phase, sitting could contribute a high proportion of a bird's path if the duration included an incubation bout (e.g., Weimerskirch 1995). The modes of movement that generate a movement path have important feedbacks to the internal state, represented in the ME framework as *internal dynamics* acting between the movement path and internal state

component (Fig. 1). Because different modes of movement require different energetic expenditure, the movement path feeds back to a bird's body condition. For example, during the incubation phase, long bouts of sitting are followed by foraging trips requiring all other modes of movement (i.e., sitting followed by walking, takeoff, flapping, soaring, then landings, takeoffs and possibly diving for prey capture, and so on). The relative contribution of each of these movement modes to a movement path will have a net energetic cost to the individual that will feed back to its body condition (Weimerskirch 1995, Weimerskirch *et al.* 2002).

Interactions between motion capacity and navigation capacity

The modes of movement employed by an albatross also depend in part on its navigation capacity, represented in the ME framework as *movement propagation processes* acting between navigation capacity and motion capacity (Fig. 1). An individual's decision to move in a particular direction at a particular time will influence which mode of movement is employed to generate the movement path. For example, if a bird uses olfactory and visual cues to navigate toward an aggregation of foraging conspecifics at a fishing vessel, this movement "decision" will influence which modes of movement contribute to the movement path (i.e., landing, paddling and floating, rather than continued soaring flight).

Interactions between motion capacity and the external environment

The modes of movement available to an albatross also depend on elements in the environment, represented in the ME framework as *motion processes* acting between the environment and motion capacity (Fig. 1). For example, the proportion of a movement path generated by flapping and soaring flight will be closely linked to wind conditions (Weimerskirch *et al.* 2000a, Sakamoto *et al.* 2013). The wind conditions experienced depend on the movement path that resulted in a bird's location (i.e., *external dynamics* acting between the movement path and the external environment). Whether the wind affects the decision of *when* and *where* to move depends on intrinsic factors that influence *why* a bird would move, and ultimately *how* it does so.

APPLYING A CUSTOM ME FRAMEWORK TO A LITERATURE REVIEW

I have demonstrated the feasibility of summarizing and relating cross-disciplinary literature pertaining to movement for a particular system or organism under the ME framework (Fig. 1), despite the breadth of material. By explicitly defining each of the four major components of the basic ME framework, I have identified 45 factors likely to contribute to determining the movement path of any individual albatross. The custom ME framework built here for albatross is admittedly over-simplified, with non-exhaustive coverage of the published literature; a full review of all relevant research to date would entail a book-sized volume. Yet the exercise of populating a custom ME framework is useful in revealing areas that are generally well understood and those where the literature is lacking. As a next step, I conducted a thorough literature review to explicitly evaluate the research in which biologging technologies are used to record the movement paths of individual albatross.

Based on the 45 factors identified in the albatross ME framework, I surveyed the literature for which factors are most commonly

measured or suggested as important in determining observed movement patterns. This allows for the recognition of components and factors within the framework that have received the most consideration and those in need of attention, in order to develop a more holistic understanding of albatross movement through the use of biologging tools.

Literature review methods

This review is based on the analysis of contents from published research articles selected from the ISI Web of Knowledge (Thomson Reuters) database with the search criteria: Topic = (albatross AND (biologging OR biologger OR telemetry OR satellite OR GPS OR GLS OR geolocator)). The results were narrowed to include only peer-reviewed journal articles (i.e., not books or reports) in which bird-borne biologging tools were used to produce positional data for individuals, and in which the movement paths of individuals could be inferred. This yielded a total of 117 papers published in 48 journals between 1990 and 2015 (search truncated on 31 December 2015; a separate bibliography of assessed publications can be found in Appendix 1, available on the website).

To provide a general overview of trends in the albatross-biologging movement literature, each article was assessed for (1) the number of individual birds with recorded movement paths; (2) the study species; and (3) device types used. Because the conceptual ME framework is built from the perspective of explaining individual movement, I also determined for each study whether biologger-derived movement data were used to examine the movement paths of individuals independently (i.e., to explore the drivers of movements at the individual level) or to examine movement paths
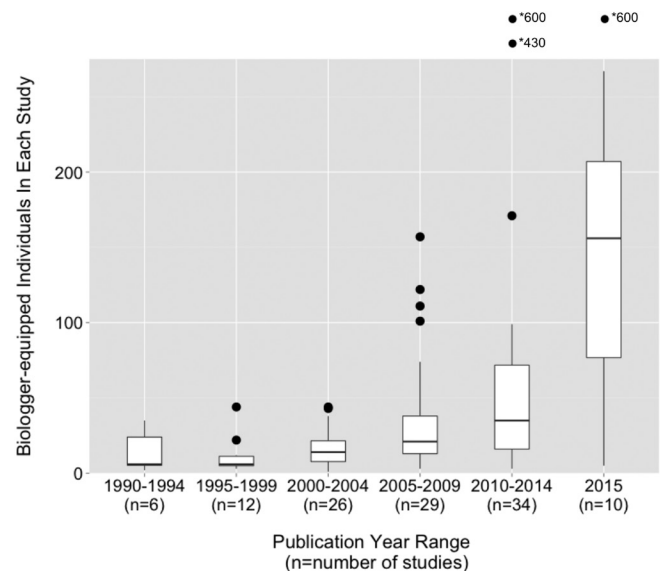

Fig. 2. Temporal trends in albatross-biologging movement research. Boxplots (median line and 1.5 × interquartile range whisker) show the number of individual albatross equipped with positional biologging devices in each of 117 assessed studies. Published articles are grouped into 5-year bins beginning with 1990–2014, and 2015 is shown alone. Outliers are shown as filled circles, and y-values for extreme outliers are reported with an asterisk. The number of published articles (*n*) contributing to each box plot is shown on the x-axis.

of all device-equipped birds collectively (i.e., to describe general movement patterns at the group level). For each article, I then determined which of the 45 factors from the custom ME framework were either measured (quantitatively or qualitatively) or suggested as potential drivers of movements. Because so few published studies investigate specific sources of navigational information, I also assessed whether navigation capacity was discussed in terms of whether albatross use inherited genetic programs in making "decisions" concerning when and where to move, or whether they use cues based on memory and learning experiences.

General trends in albatross-biologging research

Not surprisingly, the number of albatross-biologging movement studies published has increased gradually over the past 25 years, as has the number of individual birds contributing biologger-derived movement data to a given study (Fig. 2). Since 2005, it has become commonplace for a single study to incorporate movement data from 50 or more individuals. Of the 10 studies published in 2015, seven included movement data from >100 individual

birds (mean 180 birds, standard deviation (SD) 170; Fig. 2). This trend is driven by a combination of decreased device costs, accumulation of large datasets over time, increasing collaborations among researchers, and improved online repositories for data sharing. Importantly, studies with low sample sizes continue to contribute to the published literature, albeit to a lesser degree than they did in the earliest days of research in this field. Low sample sizes can be the result of intentional small-scale deployments of multi-sensor or high-resolution devices, often for short durations, to gain a more fine-scale understanding of particular movement processes. Alternatively, small sample sizes can result from cost, time, pilot studies, or device recovery and failure rates. All research efforts should be recognized for their contribution to our greater understanding of the drivers of albatross movement at the appropriate temporal or spatial scale, regardless of sample size.

The albatross-biologging movement literature has been subject to a species bias toward Wandering Albatross since the landmark paper tracking this species 25 years ago (Jouventin & Weimerskirch 1990). Movement paths of biologger-equipped Wandering
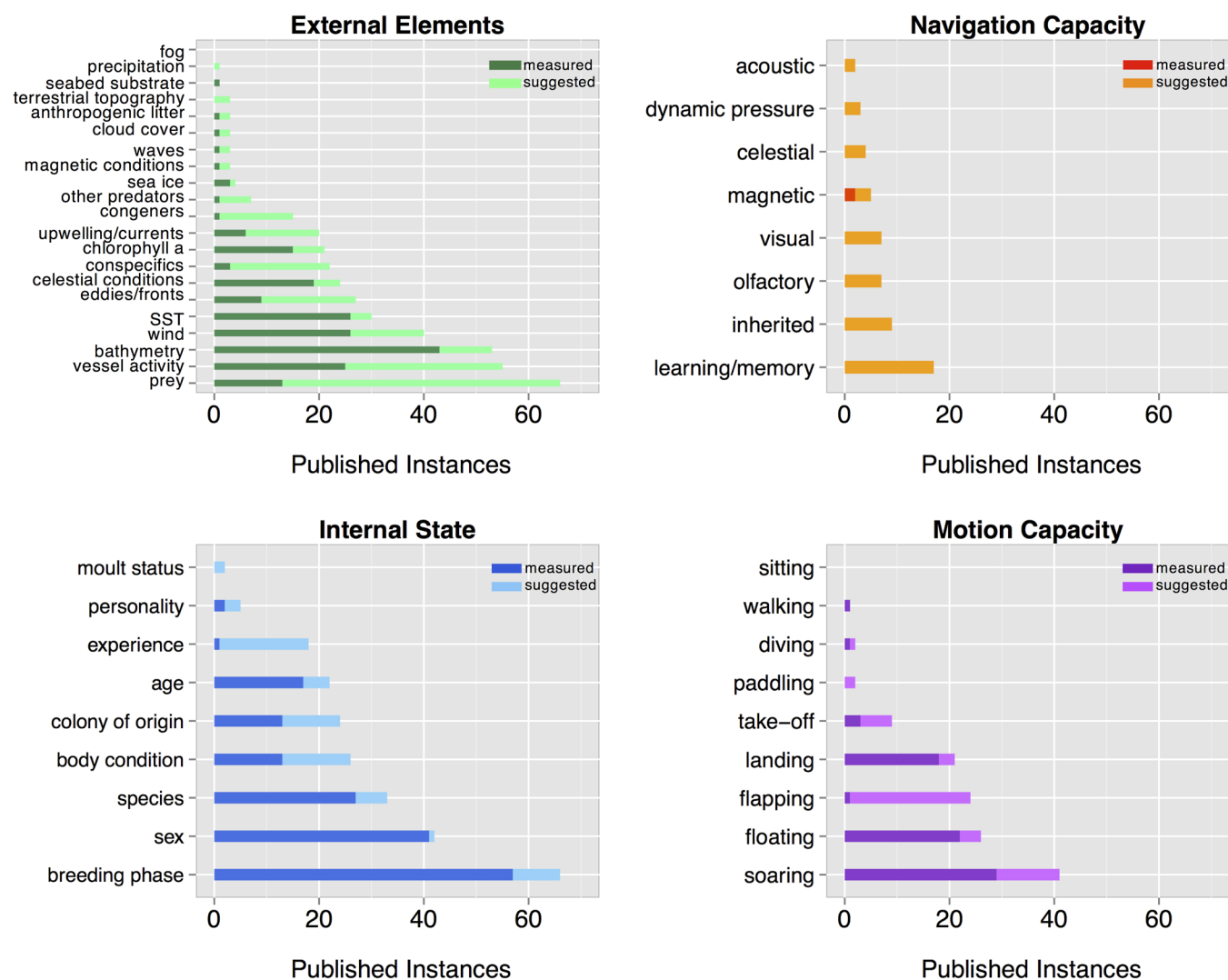

Fig. 3. Results from a survey of factors measured or suggested as drivers of movement in published albatross-biologging research. The custom movement ecology framework was used to conduct a literature survey of the most commonly measured (dark bars) or suggested (light bars) factors in driving movement patterns (where movement paths of individuals are known from biologging devices). A total of 117 studies, published from 1990 to 2015, were assessed.

Albatross were included in 40% (46 of 117) of the articles assessed (including multi-species studies). Twenty-five articles include Black-browed Albatross, while Black-footed, Grey-headed, and Laysan Albatrosses have also been relatively well represented in the movement literature (16, 14, and 13 articles, respectively). Another 46 articles are shared among 15 less-studied species (Table 1). Neither Salvin's *Thalassarche salvini* nor Atlantic Yellow-nosed Albatrosses *Thalassarche chlororhynchos* have been the subject of published articles, although movements of individuals from both species have been tracked with biologging devices (Taylor *et al.* 2004).

Positional data have been derived from three main types of bird-borne biologging devices: satellite transmitters, global positioning system (GPS) receivers, and light-based geolocators (deployed in 84, 31, and 17 articles, respectively; some articles use variations of the three, and some use multiple device types). Ancillary *in situ* data have been recorded by additional sensors or animal-attached devices in 22% of the assessed papers. These include 25 studies incorporating wet/dry state data to identify periods of saltwater immersion, seven employing stomach temperature loggers to infer ingestion events, two using accelerometers for fine-scale three-dimensional movements, two using heart-rate recorders to quantify energetic expenditure, and one using bird-borne cameras to capture images of the surrounding environment.

Regardless of sample size, study species or device type, 87% of published studies use individual-based movement data to describe movement patterns collectively for all birds in a dataset, and to then make inferences regarding movement for a higher-level group that the tracked birds are taken to represent. Only 15 studies (13%) to date have described or compared the movements of the tracked individuals themselves. Of these 15 individual-focused studies, nearly half have been published in the past two years.

Common factors thought to drive movement patterns

Overwhelmingly, factors within the internal state and external environment components are most commonly measured or suggested as probable drivers of observed movements for biologger-equipped albatross (Fig. 3). Within the internal state component, breeding phase is routinely considered as a primary explanation for *why* birds move via a given movement path. Half of all published articles assessed include breeding phase as an explanatory variable, with another 8% speculating on the likely importance of this factor. Sex is also commonly included as a potential driver of movement patterns, with 35% of publications including this factor in analyses. This is likely due in part to the prevalence of studies conducted on Wandering Albatross, in which sexual dimorphism makes sex relatively easy to assign (i.e., genetic sexing is not required). Species is explicitly examined as a factor determining movements in 29% of papers, designed to investigate if and *why* individuals of different species move differently.

Within the external environment component, bathymetry is quantified or qualified in 37% of albatross-biologger research and discussed as a probable abiotic element driving movements in an additional 9%. The next most commonly measured external elements are wind and sea surface temperature (both quantified in 23% of assessed articles), followed closely by fishing vessel activity (quantified in 22% of articles). Overall, the presence of prey and fishing vessels are the two most common elements of the external

environment considered to impact albatross movements, each being empirically or speculatively discussed in approximately half of all published articles (Fig. 3).

Factors less commonly considered

Within the internal state component, age emerged as a topic of interest in albatross movement research beginning in 2005, and has gradually increased in the literature since. There are now 17 published studies (15% of the assessed articles) investigating the role of age in determining movements, and 10 of these were published in the past 5 years. Many focus on individuals from younger age classes, but some also include older, senescent-aged individuals. Personality (i.e., consistent behavioural tendencies) is rarely investigated as an intrinsic factor influencing observed movement paths (Fig. 3), likely owing, at least in part, to the difficulty of quantitatively assessing this factor. Individual moult has never been quantified in the published albatross-biologger movement literature, and has been speculated as potentially important in only four studies.

Within the motion capacity component, flapping as a mode of flight is often suggested as an important contributor to generating movements (20% of published articles), but the proportion of a movement path contributed by flapping has been quantified in only one study (Fig. 3). The two modes of movement used to accomplish short-distance movements at sea (paddling and diving) are rarely, if ever, measured or discussed as important in albatross-biologging movement research. Further, despite recorded movement paths encompassing time spent at the colony, location data while the bird is on land is typically filtered out for analyses, leaving time spent walking or sitting unquantified (Fig. 3).

Overall, navigation capacity has not been commonly discussed as important to movement, nor quantified relative to specific types of navigational information used by individuals (Fig. 3). In more general terms, inherited navigational abilities were suggested to be important in determining movements in nine published articles (<8%), while learned abilities were suggested as important in 17 published articles (<15%). Overall, 20% of assessed studies considered some aspect of navigation capacity in their discussions of potential drivers of observed movement patterns from biologger-equipped albatross.

Limitations in albatross movement research

Many of the weaknesses in our current understanding of albatross ME can be attributed to two limitations, both of which have lessened over time: (1) a tendency to ignore the individual to which biologging devices are attached; and (2) the accessibility of quantifying or qualifying factors. In light of these limitations, I discuss shortcomings in our understanding of what drives a bird to move via a given movement path, identify trends toward change in the drivers we explore with biologging, and recommend future research directions.

The albatross-biologging movement research has tended to generalize the movements of individual equipped birds to represent the movements of a much larger group (Gutowsky *et al.* 2015). Mostly these extrapolations are made at the level of the species, colony, sex, or age class (87% of published articles). The research thus tends to ignore the individuals from which positional data

are derived and fails to identify the unique intrinsic factors that drive individuals to move via a given observed movement path. However, an emerging shift among seabird scientists away from inferring group-level movement patterns and toward investigating individual specialization in movement was reflected at the recent 2nd World Seabird Conference ("WSC2," Cape Town, South Africa, 26–30 October 2015). Three complete WSC2 symposia, in total including 19 oral presentations, were dedicated to showcasing research on the causes and consequences of individual variability and specialization in movement, foraging, and migration strategies. This growing interest in individual seabird movement is likely to be reflected in the albatross-biologging movement literature as well.

Several intrinsic factors unique to an individual are likely to receive increasing attention as studies focus on individual equipped birds. Measures of body condition are becoming more common and sophisticated in terms of the physiological variables considered (e.g., aerobic capacity, energetic, and endocrine state from blood and feather sampling) and are likely to become key in studies of movement and carryover effects. Investigations explicitly examining "personality" may be less common, but are expected to increase beyond the two published papers in which personality is quantified in relation to movement, and the three papers where personality is suggested to exist, all of which have been published in the past five years. In contrast, interest in moult status as an important intrinsic factor in determining individual movements is not yet apparent and represents an area of albatross movement ecology research with great potential for exploration.

Our ability to quantify or qualify each of the 45 factors identified in the custom ME framework outlined earlier present practical limitations to their study. It was only 25 years ago that it became possible to infer individual movement paths from sequential location data, let alone identify multiple intrinsic and extrinsic variables likely to influence the observed patterns. On average, each of the assessed studies attempted to measure *ca.* four of the 45 factors identified (mean 3.9 SD 2.2) and invoked *ca.* three additional factors as potential contributors to observed movement patterns (mean 3.3 SD 2.8). Study designs traditionally have not included measurement of factors relevant to individual movements beyond those easily acquired, such as breeding phase, sex (for sexually dimorphic species), and age-class (i.e., immature or mature), often paired with readily available coarse-scale satellite-derived external elements such as bathymetry, sea surface temperature, wind, and celestial conditions (i.e., moon phase or day versus night). Ideally, study designs in which biologging devices are attached to individual birds would attempt to identify a minimum of sex, age, breeding success and experience, and some measure of body condition and moult status, to allow for future explorations of the role of these internal state factors in determining movements.

As for the external environment, the presence and behaviour of fishing vessels and prey are both commonly discussed as important but are quantified much less often. Cooperation from fisheries operations in recording and providing data on vessel position and activity is paramount in improving quantitative assessments of bird movements relative to fisheries. Historically, national and international fisheries bodies have been reluctant to release data on vessel activities (i.e., vessel monitoring system [VMS] data), but access to VMS data is improving, as is the quality of the data (e.g., Granadeiro *et al.* 2011, Torres *et al.* 2011, 2013, Collet *et al.* 2015, Sugishita *et al.* 2015). Incidental mortality through drowning

on baited longline hooks, entanglement in nets, and collisions with trawl warps are primary threats to albatross populations worldwide. Therefore, determining how vessel activity impacts bird movements is key to effective conservation management solutions.

Gathering reliable data on the availability and behaviour of potential prey in relation to the movements of individuals also remains challenging. Of the 13 studies that had measured prey in some respect, only two quantified the availability and distribution of prey in the environment that individuals moved through (i.e., the prey field or "preyscape"). These studies used acoustic transducers to assess the presence of squid aggregations (Rodhouse & Boyle 2010) or size of krill swarms (Veit & Prince 1997) where birds had been detected. Rather, the majority of studies have measured prey in terms of what birds successfully captured and consumed throughout their movements; seven studies used stomach-temperature loggers to infer ingestion events along the movement path, while three analyzed general prey consumption from stomach contents of biologger-equipped individuals, and one estimated long-term diet using chemical signatures of stable isotopes. Better understanding of movement in relation to the presence and behaviour of prey will require *in situ* measurements of prey fields combined with accurate information on feeding events and dietary composition. Because albatross diets are variable, and prey are patchily dispersed throughout their vast ranges, successfully quantifying prey fields in relation to individual movements remains a great challenge. Regardless, foraging is a central theme throughout the albatross-biologging movement literature, and we need to investigate how prey in the environment interacts with an individual's internal state, navigation capacity, and motion capacity to advance the study of albatross movement.

Quantifying some factors within the framework that could not previously be measured is becoming possible thanks to rapid technological advancements in biologging. Devices are becoming increasingly sophisticated and miniaturized, enabling multiple on-board sensors that have higher precision and sampling rate of positional data, as well as capability to record concurrent ancillary data. High-quality location data, paired with immersion state, depth, or accelerometry data, can allow for investigations of the contribution of all modes of movement, including flapping flight, diving, and paddling on the water's surface. Bird-borne cameras are another promising technology that can provide insight into the external surroundings immediately relevant to an individual. These technologies can reveal important interactions between an individual and various elements of the environment, including conspecifics, congeners, other predators, vessels, and prey. Further, the technologies may also be able to determine important localized abiotic elements that are not readily measured from coarse-scale satellite-derived data, such as waves, cloud cover, precipitation, fog, or celestial conditions. By considering more detailed information on the intrinsic factors and external elements relevant to each biologger-equipped individual, we can begin to disentangle how interactions among the internal state, external environment, and motion capacity of individuals determine an individual's movements.

Empirical study of animal orientation and navigation under natural conditions remains exceedingly challenging, and thus the contribution of an individual's navigation capacity in determining movements recorded by biologgers remains a major "black box" in albatross ME (Fig. 3). Investigations and established hypotheses of

the mechanisms controlling pelagic seabird movement decisions are recognized to be inadequate (e.g., Guilford *et al.* 2011, Åkesson & Weimerskirch 2014). There are recent advancements in animal navigation research, particularly for seabirds and albatross. Qin *et al.* (2015) discovered the likely protein molecule complex that acts as a compass in animals' geomagnetic sense, representing an enormous step toward understanding the role of geomagnetic cues in influencing movement decisions. Wikelski *et al.* (2015) combined biologging, sensory manipulations, and translocations to assess the role of olfactory cues in guiding migratory navigation in gulls. They showed that birds with severed olfactory nerves travelled with clear directional preference but were unable to compensate for displacements, lending support to the importance of olfactory information to navigation capacity. Collet *et al.* (2015) investigated the influence of visual cues on albatross movement decisions in relation to fishing vessel activity. The results indicated that birds detect fishing vessels from up to 30 km away, at the limit of what was considered their theoretical maximum visual range. At the WSC2, seabird navigation was the focus of a presentation session. One topic of discussion was the "exploration-refinement hypothesis" (originally proposed by Guilford *et al.* 2011), which suggests that some seabirds rely on large-scale exploratory movements during their immature years, rather than strict genetic or cultural control, which become refined over time through learning and memory into an individual movement strategy. Ultimately, understanding navigation capacity will require combining biologging research with field and lab-based behavioural experiments, and exploring internal mechanisms determining sensory perception. With cross-disciplinary collaboration, there is hope that the black box of albatross navigation will continue to open.

It should also be noted that some factors remain impossible to realistically measure, such as an individual's unique history of experiences that influence both its motivations to move and its decisions concerning when and where to move. Regardless of our inability to quantify an individual's experiences, such experiences should still be recognized as a potentially significant contributor to both intra- and inter-individual variation in movement paths. Building a custom conceptual ME framework is thus a valuable exercise in identifying all factors likely to influence an individual's movements, whether or not those factors are typically measured or discussed in the biologging literature.

CONCLUSIONS

This review identifies general trends and shortcomings in the albatross-biologging movement research. As the number of studies published in a given year and the number of individuals composing each dataset continue to grow, so too will the breadth and complexity of questions asked about the drivers of albatross movement. Future work should look to overcome the heavy species bias toward Wandering Albatross in the published literature, as well as to move away from tendencies to record relatively easily quantified or qualified intrinsic factors and external elements. We should explore more thoroughly the interactions within and among components in driving individual movements. This will require attempting to quantify, for each unique biologger-equipped individual, multiple factors within the multidimensional vector of interacting intrinsic factors, rather than assuming all individuals are ecologically equivalent. The work to date has laid the groundwork for exploring and describing

albatross movements and has suggested probable drivers of the observed patterns, mainly at the group level. As cross-disciplinary technological and analytical tools are developed, in-depth investigations of movement in terms of unique individual internal states, navigation capacity, and motion capacity will inevitably become more common. Biologging research has an important role to play in effective conservation and management strategies for all threatened species, including the albatrosses (Table 1; Cooke 2008, Burger & Shaffer 2008, IUCN 2015), as well as in gaining a more comprehensive understanding of the complex movement ecology of these magnificent animals.

REFERENCES

ABLE, K.P. & ABLE, M.A. 1996. The flexible migratory orientation system of the Savannah Sparrow (*Passerculus sandwichensis*). *Journal of Experimental Biology* 8: 3-8.

ÅKESSON, S. & ALERSTAM, T. 1998. Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses? *Journal of Avian Biology* 29: 618-625.

ÅKESSON, S. & HEDENSTRÖM, A. 2007. How migrants get there: migratory performance and orientation. *Bioscience* 57: 123.

ÅKESSON, S., LUSCHI, P., BRODERICK. A.C., GLEN, F., GODLEY, B.J., PAPI, F. & HAYS, G.C. 2001. Oceanic long-distance navigation: do experienced migrants use the earth's magnetic field? *Journal of Navigation* 54: 419-427.

ÅKESSON, S. & WEIMERSKIRCH, H. 2005. Albatross long-distance navigation: comparing adults and juveniles. *Journal of Navigation* 58: 365-373.

ÅKESSON, S. & WEIMERSKIRCH, H. 2014. Evidence for sex-segregated ocean distributions of first-winter wandering albatrosses at Crozet Islands. *PLoS One* 9: 1-10.

ALDERMAN, R., GALES, R., HOBDAY, A.J. & CANDY, S.G. 2010. Post-fledging survival and dispersal of shy albatross from three breeding colonies in Tasmania. *Marine Ecology Progress Series* 405: 271-285.

ANGELIER, F., SHAFFER, S.A., WEIMERSKIRCH, H. & CHASTEL, O. 2006. Effect of age, breeding experience and senescence on corticosterone and prolactin levels in a long-lived seabird: the wandering albatross. *General and Comparative Endocrinology* 149: 1-9.

ANGELIER, F., SHAFFER, S.A., WEIMERSKIRCH, H., TROUVÉ, C. & CHASTEL, O. 2011. Corticosterone and foraging behavior in a pelagic seabird. *Physiological and Biochemical Zoology* 80: 283-292.

ANGELIER, F., WEIMERSKIRCH, H., DANO, S. & CHASTEL, O. 2007. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behavioural Ecology and Sociobiology* 61: 611-621.

ARNOULD, J.P., BRIGGS, D.R., CROXALL, J.P., PRINCE, P.A. & WOOD, A.G. 1996. The foraging behaviour and energetics of wandering albatrosses brooding chicks. *Antarctic Science* 8: 229-236.

ASHMOLE, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103: 458-473.

BANG, B.G. 1966. The olfactory apparatus of tube-nosed birds (Procillariiformes). *Acta Anatomica (Basel)* 65: 393-415.

BANG, B.G. 1971. Functional anatomy of the olfactory system in 23 orders of birds. *Acta Anatomica (Basel)* 79: 1-76.

BENSON, S.R., EGUCHI, T., FOLEY, D.G., et al. 2011. Large-scale movements and high-use areas of western Pacific leatherback turtles, Dermochelys coriacea. *Ecosphere* 2: 1-27.

BONADONNA, F., BAJZAK, C., BENHAMOU, S., IGLOI, K., JOUVENTIN, P., LIPP, H.P. & DELL'OMO, G. 2005. Orientation in the wandering albatross: interfering with magnetic perception does not affect orientation performance. *Proceedings of the Royal Society Biological Sciences* 272: 489-495.

BONADONNA, F., BENHAMOU, S. & JOUVENTIN, P. 2003. Orientation in "featureless" environments: the extreme case of pelagic birds. In: BERTHOLD, P. & GWINNER, E. (Eds.) *Bird Migration*. Heidelberg, Germany: Springer-Verlag.

BONADONNA, F., CHAMAILLE-JAMMES, S., PINAUD, D. & WEIMERSKIRCH, H. 2003. Magnetic cues: are they important in Black-browed Albatross *Diomedea melanophris* orientation? *Ibis (London 1859)* 145: 152-155.

BRIDGE, E. 2006. Influences of morphology and behavior on wing-molt strategies in seabirds. *Marine Ornithology* 19: 7-19.

BURGER, A.E. & SHAFFER, S.A. 2008. Application of tracking and data-logging technology in research and conservation of seabirds. *Auk* 125: 253-264.

CAIRNS, D.K. 1989. The regulation of seabird colony size: a hinterland model. *American Naturalist* 134: 141-146.

CATRY, P., PHILLIPS, R.A. & CROXALL, J.P. 2004. Sustained fast travel by a gray-headed albatross (*Thalassarche chrysostoma*) riding an Antarctic storm. *Auk* 121: 1208-1213.

CATRY, P., PHILLIPS, R.A., PHALAN, B. & CROXALL, J.P. 2006. Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysostoma*. *Proceedings of the Royal Society Biological Sciences* 273: 1625-1630.

CATRY, P., PHILLIPS, R.A., PHALAN, B., SILK, J. & CROXALL, J. 2004. Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Marine Ecology Progress Series* 280: 261-273.

COLLET, J., PATRICK, S.C. & WEIMERSKIRCH, H. 2015. Albatrosses redirect flight towards vessels at the limit of their visual range. *Marine Ecology Progress Series* 526: 199-205.

CONNERS, M.G., HAZEN, E.L., COSTA, D.P. & SHAFFER, S.A. 2015. Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. *Movement Ecology* 3: 1-20.

COOKE, S. 2008. Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research* 4: 165-185.

COOKE, S.J., HINCH, S.G., WIKELSKI, M., ANDREWS, R.D., KUCHEL, L.J., WOLCOTT, T.G. & BUTLER, P.J. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution* 19: 334-343.

CROSSIN, G.T., PHILLIPS, R.A., TRATHAN, P.N., FOX, D.S., DAWSON, A., WYNNE-EDWARDS, K.E. & WILLIAMS, T.D. 2012. Migratory carryover effects and endocrinological correlates of reproductive decisions and reproductive success in female albatrosses. *General and Comparative Endocrinology* 176: 151-157.

CROSSIN, G.T., PHILLIPS, R.A., WYNNE-EDWARDS, K.E. & WILLIAMS, T.D. 2013. Postmigratory body condition and ovarian steroid production predict breeding decisions by female gray-headed albatrosses. *Physiological and Biochemical Zoology* 86: 761-768.

EDWARDS, A.E. 2008. Large-scale variation in flight feather molt as a mechanism enabling biennial breeding in albatrosses. *Journal of Avian Biology* 39: 144-151.

FERNÁNDEZ, P. & ANDERSON, D.J. 2000. Nocturnal and diurnal foraging activity of Hawaiian albatrosses detected with a new immersion monitor. *Condor* 102: 577-584.

FISHER, H.I. 1971A. The Laysan albatross: its incubation, hatching, and associated behaviours. *Living Bird* 10: 19-78.

FISHER, H.I. 1971B. Experiments on homing on Laysan Albatrosses, *Diomedea immutabilis*. *Condor* 73: 389-400.

FRINGS, B.H. & FRINGS, M. 1961. Some biometric studies on the albatrosses of Midway Atoll. *Condor* 63: 304-312.

FROY, H., LEWIS, S., CATRY, P., ET AL. 2015. Age-related variation in foraging behaviour in the Wandering Albatross at South Georgia: no evidence for senescence. *PLoS One* 10: e0116415.

GOULD, J.L. 1998. Sensory bases of navigation. *Current Biology* 8: 731-738.

GRANADEIRO, J.P., PHILLIPS, R.A., BRICKLE, P. & CATRY, P. 2011. Albatrosses following fishing vessels: how badly hooked are they on an easy meal? *PLoS One* 6: 1-7.

GUILFORD, T., FREEMAN, R., BOYLE, D., DEAN, B., KIRK, H., PHILLIPS, R.A. & PERRINS, C. 2011. A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. *PLoS One* 6: e21336.

GUTOWSKY, S.E., GUTOWSKY, L.F.G., JONSEN, I.D., LEONARD, M.L., NAUGHTON, M.B., ROMANO, M.D. & SHAFFER, S.A. 2014. Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. *Movement Ecology* 2: 1-14.

GUTOWSKY, S.E., TREMBLAY, Y., KAPPES, M.A., ET AL. 2014. Divergent post-breeding distribution and habitat associations of fledgling and adult Black-footed Albatrosses *Phoebastria nigripes* in the North Pacific. *Ibis* 156: 60-72.

GUTOWSKY, S.E., LEONARD, M., CONNERS, M., SHAFFER, S. & JONSEN, I.D. 2015. Individual-level variation and higher-level interpretations of space use in wide-ranging species: an albatross case study of sampling effects. *Frontiers in Marine Science* 2: 1-17.

HAGEN, M., WIKELSKI, M. & KISSLING, W.D. 2011. Space use of bumblebees (*Bombus* spp.) revealed by radio-tracking. *PLoS One* 6: e19997.

HEDD, A. & GALES, R. 2005. Breeding and overwintering ecology of shy albatrosses in southern Australia: year-round patterns of colony attendance and foraging-trip durations. *Condor* 107: 375-387.

HEDD, A., GALES, R., BROTHERS, N. & ROBERTSON, G. 1997. Diving behaviour of the Shy Albatross *Diomedea cawta* in Tasmania: initial findings and dive recorder assessment. *Ibis* 139: 452-460.

HUIN, N. & PRINCE, P.A. 1997. Diving behaviour of the grey-headed albatross. *Antarctic Science* 9: 243-249.

IUCN. 2015. The IUCN Red List of Threatened Species. [Available online at: http://www.iucnredlist.org. Accessed 15 January 2016].

JOUVENTIN, P. & DOBSON, F.S. 2002. Why breed every other year? The case of albatrosses. *Proceedings of the Royal Society Biological Sciences* 269: 1955-1961.

JOUVENTIN, P. & WEIMERSKIRCH, H. 1990. Satellite tracking of Wandering albatrosses. *Nature* 343: 746-748.

KABAT, A.P., PHILLIPS, R.A., CROXALL, J.P. & BUTLER, P.J. 2007. Differences in metabolic costs of terrestrial mobility in two closely related species of albatross. *Journal of Experimental Biology* 210: 2851-2858.

KAPPES, M.A., SHAFFER, S.A., TREMBLAY, Y., ET AL. 2010. Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Progress in Oceanography* 86: 246-260.

KENYON, K. & RICE, D. 1958. Homing of Laysan Albatrosses. *Condor* 60: 3–6.

LABOCHA, M.K. & HAYES, J.P. 2012. Morphometric indices of body condition in birds: a review. *Journal of Ornithology* 153: 1-22.

LANGSTON, N. & HILLGARTH, N. 1995. Moult varies with parasites in Laysan Albatrosses. *Proceedings of the Royal Society Biological Sciences* 261: 239-243.

LANGSTON, N.E. & ROHWER, S. 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. *Oikos* 76: 498-510.

LECOMTE, V.J., SORCI, G., CORNET, S., ET AL. 2010. Patterns of aging in the long-lived wandering albatross. *Proceedings of the National Academy of Sciences of the United States of America* 107: 6370-6375.

MACKLEY, E., PHILLIPS, R., SILK, J., WAKEFIELD, E., AFANASYEV, V., FOX, J. & FURNESS, R. 2010. Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Marine Ecology Progress Series* 406: 291-303.

MARDON, J., NESTEROVA, A.P., TRAUGOTT, J., SAUNDERS, S.M. & BONADONNA, F. 2010. Insight of scent: experimental evidence of olfactory capabilities in the wandering albatross (*Diomedea exulans*). *Journal of Experimental Biology* 213: 558-563.

MARTIN, G.R. 1998. Eye structure and amphibious foraging in albatrosses. *Proceedings of the Royal Society B: Biological Sciences* 265: 665-671.

MEYERS, R.A. & STAKEBAKE, E.F. 2005. Anatomy and histochemistry of spread-wing posture in birds. 3. Immunohistochemistry of flight muscles and the "shoulder lock" in albatrosses. *Journal of Morphology* 263: 12-29.

MOURITSEN, H., HUYVAERT, K.P., FROST, B.J. & ANDERSON, D.J. 2003. Waved albatrosses can navigate with strong magnets attached to their head. *Journal of Experimental Biology* 206: 4155-4166.

MUHEIM, R., PHILLIPS, J.B., ÅKESSON, S., MUHEIM, R., PHITTIPS, B. & AKESSON, S. 2006. Polarized light cues underlie compass calibration in songbirds. *Science* 313: 837-839.

MURRAY, M.D., NICHOLLS, D.G., BUTCHER, E. & MOORS, P.J. 2003. How Wandering Albatrosses use weather systems to fly long distances. 2. The contributions of Antarctic LOWs to travel westwards across the Indian Ocean. *Emu* 103: 59-65.

NATHAN, R., GETZ, W.M., REVILLA, E., HOLYOAK, M., KADMON, R., SALTZ, D. & SMOUSE, P.E. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* 105: 19052-19059.

NATHAN, R. & GIUGGIOLI, L. 2013. A milestone for movement ecology research. *Movement Ecology* 1: 1-3.

NEVITT, G.A. 2008. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *Journal of Experimental Biology* 211: 1706-1713.

NEVITT, G.A. & BONADONNA, F. 2005. Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biology Letters* 1: 303-305.

NEVITT, G.A., LOSEKOOT, M. & WEIMERSKIRCH, H. 2008. Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proceedings of the National Academy of Sciences of the United States of America* 105: 4576-4581.

NEVITT, G.A., VELT, R.R. & KAREIVA, P. 1995. Dimethyl sulfide as a foraging cue for Antarctic Procellariiform seabirds. *Nature* 376: 680-682.

O'CONNOR, C., NORRIS, D.R., CROSSIN, G.T. & COOKE, S.J. 2014. Biological carryover effects : linking common concepts and mechanisms in ecology and evolution. *Ecosphere* 5: 1-11.

O'NEILL, P. 2013. Magnetoreception and baroreception in birds. *Development, Growth, and Differentiation* 55: 188-197.

ORIANS, G.H. & PEARSON, N.E. 1979. On the theory of central place foraging. In: Horn, D.J., Mitchell, R.D. & Stairs, G.R. (Eds.) *Analysis of Ecological Systems*. Columbus, OH: Ohio State University Press.

PARDO, D., BARBRAUD, C. & WEIMERSKIRCH, H. 2013. Females better face senescence in the wandering albatross. *Oecologia* 173: 1283-1294.

PATRICK, S.C., CHARMANTIER, A. & WEIMERSKIRCH, H. 2013. Differences in boldness are repeatable and heritable in a long-lived marine predator. *Ecology and Evolution* 3: 4291-4299.

PATRICK, S.C. & WEIMERSKIRCH, H. 2014. Personality, foraging and fitness consequences in a long lived seabird. *PLoS One* 9: e87269.

PENNYCUICK, C.J. 1982. The flight of petrels and albatrosses observed in South Georgia and its vicinity. *Philosophical Transactions of the Royal Society B: Biological Scieneces* 300: 75-106.

PENNYCUICK, C.J. 2002. Gust soaring as a basis for the flight of petrels and albatrosses (Procellariiformes). *Avian Science* 2: 1-12.

PHILLIPS, R.A., McGILL, R.A., DAWSON, D.A. & BEARHOP, S. 2011. Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Marine Biology* 158: 2199-2208.

PHILLIPS, R.A., SILK, J.R.D., CROXALL, J.P., AFANASYEV, V. & BENNETT, V.J. 2005. Summer distribution and migration of nonbreeding albatrosses: Individual consistencies and implications for conservation. *Ecology* 86: 2386-2396.

PHILLIPS, R.A., SILK, J.R.D., PHALAN, B., CATRY, P. & CROXALL, J.P. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society B: Biological Sciences* 271: 1283-1291.

PICKERING, S.P.C. 1989. Attendance patterns and behaviour in relation to experience and pair-bond formation in the wandering albatross *Diomedea exulans* at South Georgia. *Ibis* 131: 183-195.

PICKERING, S.P.C. & BERROW, S.D. 2001. Courtship behaviour of the Wandering Albatross *Diomedea exulans* at Bird Island, South Georgia. *Marine Ornithology* 29: 29-37.

PINAUD, D., CHEREL, Y. & WEIMERSKIRCH, H. 2005. Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Marine Ecology Progress Series* 298: 295-304.

PRINCE, P.A., HUIN, N. & WEIMERSKIRCH, H. 1994. Diving depths of albatrosses. *Antarctic Science* 6: 353-354.

RICHARDSON, P.L. 2011. How do albatrosses fly around the world without flapping their wings? *Progress in Oceanography* 88: 46-58.

RIOTTE-LAMBERT, L. & WEIMERSKIRCH, H. 2013. Do naive juvenile seabirds forage differently from adults? *Proceedings of the Royal Society B: Biological Sciences* 280: 1-9.

RODHOUSE, P.G. & BOYLE, P.R. 2010. Large aggregations of pelagic squid near the ocean surface at the Antarctic Polar Front, and their capture by grey-headed albatrosses. *ICES Journal of Marine Science* 67: 1432-1435.

ROHWER, S., VIGGIANO, A. & MARZLUFF, J.M. 2011. Reciprocal tradeoffs between molt and breeding in albatrosses. *Condor* 113: 61-71.

SAKAMOTO, K.Q., TAKAHASHI, A., IWATA, T. & TRATHAN, P.N. 2009. From the eye of the albatrosses: a bird-borne camera shows an association between albatrosses and a killer whale in the Southern Ocean. *PLoS One* 4: e7322.

SAKAMOTO, K.Q., TAKAHASHI, A., IWATA, T., YAMAMOTO, T., YAMAMOTO, M. & TRATHAN, P.N. 2013. Heart rate and estimated energy expenditure of flapping and gliding in black-browed albatrosses. *Journal of Experimental Biology* 216: 3175-3182.

SALAMOLARD, M. & WEIMERSKIRCH, H. 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the Wandering Albatross. *Functional Ecology* 7: 643-652.

SHAFFER, S.A., COSTA, D.P. & WEIMERSKIRCH, H. 2001. Behavioural factors affecting foraging effort of breeding wandering albatrosses. *Journal of Animal Ecology* 70: 864-874.

SHAFFER, S., COSTA, D.P. & WEIMERSKIRCH, H. 2003. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology* 17: 66-74.

SHAFFER, S.A., WEIMERSKIRCH, H. & COSTA, D.P. 2001. Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*. *Functional Ecology* 15: 203-210.

SILVERMAN, E., VEIT, R. & NEVITT, G. 2004. Nearest neighbors as foraging cues: information transfer in a patchy environment. *Marine Ecology Progress Series* 277: 25-36.

SUGISHITA, J., TORRES, L.G. & SEDDON, P.J. 2015. A new approach to study of seabird-fishery overlap: connecting chick feeding with parental foraging and overlap with fishing vessels. *Global Ecology and Conservation* 4: 632-644.

SURYAN, R.M., ANDERSON, D.J., SHAFFER, S.A., ET AL. 2008. Wind, waves, and wing loading: morphological specialization may limit range expansion of endangered albatrosses. *PLoS One* 3: e4016.

SURYAN, R.M. & FISCHER, K.N. 2010. Stable isotope analysis and satellite tracking reveal interspecific resource partitioning of nonbreeding albatrosses off Alaska. *Canadian Journal of Zoology* 88: 299-305.

TAYLOR, F., TERAUDS, A. & NICHOLLS, D. 2004. Tracking ocean wanderers — the global distribution of albatrosses and petrels. *Results from the Global Procellariiform Tracking Workshop,* 1–5 September, 2003, Gordon's Bay, South Africa. Cambridge, UK.

TICKELL, W.L.N. 2000. *Albatrosses*. Sussex, UK: Pica Press.

TORRES, L., SAGAR, P., THOMPSON, D. & PHILLIPS, R.A. 2013. Scaling down the analysis of seabird-fishery interactions. *Marine Ecology Progress Series* 473: 275-289.

TORRES, L., THOMPSON, D., BEARHOP, S., VOTIER, S., TAYLOR, G., SAGAR, P. & ROBERTSON, B. 2011. White-capped albatrosses alter fine-scale foraging behavior patterns when associated with fishing vessels. *Marine Ecology Progress Series* 428: 289-301.

TREMBLAY, Y., BERTRAND, S., HENRY, R., KAPPES, M., COSTA, D. & SHAFFER, S.A. 2009. Analytical approaches to investigating seabird–environment interactions: a review. *Marine Ecology Progress Series* 391: 153-163.

VEIT, R.R. & PRINCE, P.A. 1997. Individual and population level dispersal of Black-browed Albatrosses *Diomedea melanophris* and Grey-headed Albatrosses *D. chrysostoma* in response to Antarctic krill. *Ardea* 85: 129-134.

WAKEFIELD, E., PHILLIPS, R.A. & MATTHIOPOULOS, J. 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series* 391: 165-182.

WAKEFIELD, E.D., PHILLIPS, R.A., MATTHIOPOULOS, J., FUKUDA, A., HIGUCHI, H., MARSHALL, G.J. & TRATHAN, P.N. 2009. Wind field and sex constrain the flight speeds of central-place foraging albatrosses. *Ecological Monographs* 79: 663-679.

WAKEFIELD, E.D., PHILLIPS, R.A., TRATHAN, P.N., ET AL. 2011. Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs* 81: 141-167.

WARHAM, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. London, UK: Academic Press.

WARHAM, J. 1996. *The Behaviour, Population Biology and Physiology of the Petrels.* San Diego, CA: Academic Press.

WEIMERSKIRCH, H. 1995. Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* 102: 37-43.

WEIMERSKIRCH, H., BARBRAUD, C. & LYS, P. 2000. Sex differences in parental investment and chick growth in Wandering Albatrosses: fitness consequences. *Ecology* 81: 309-318.

WEIMERSKIRCH, H., CHEREL, Y., CUENOT-CHAILLET, F. & RIDOUX, V. 1997. Alternative foraging strategies and resource allocation by male and female wandering albatross. *Ecology* 78: 2051-2063.

WEIMERSKIRCH, H., CHEREL, Y., DELORD, K., JAEGER, A., PATRICK, S.C. & RIOTTE-LAMBERT, L. 2014. Lifetime foraging patterns of the wandering albatross: Life on the move! *Journal of Experimental Marine Biology and Ecology* 450: 68-78.

WEIMERSKIRCH, H. & GUIONNET, T. 2002. Comparative activity pattern during foraging of four albatross species. *Ibis* 144: 40-50.

WEIMERSKIRCH, H., GUIONNET, T., MARTIN, J., SHAFFER, S.A. & COSTA, D.P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society B: Biological Sciences* 267: 1869-1874.

WEIMERSKIRCH, H., PINAUD, D., PAWLOWSKI, F. & BOST, C-A. 2007. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *American Naturalist* 170: 734-743.

WEIMERSKIRCH, H., SHAFFER, S.A., MABILLE, G., MARTIN, J., BOUTARD, O. & ROUANET, J.L. 2002. Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation, and the effects of human disturbance. *Journal of Experimental Biology* 205: 475-483.

WEIMERSKIRCH, H., WILSON, R.P. & LYS, P. 1997. Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. *Marine Ecology Progress Series* 151: 245-251.

WIKELSKI, M., ARRIERO, E., GAGLIARDO, A., ET AL. 2015. True navigation in migrating gulls requires intact olfactory nerves. *Scientific Reports* 5: 17061.

WILTSCHKO, W. & WILTSCHKO, R. 1996. Magnetic orientation in birds. *Journal of Experimental Biology* 199: 29-38.

YOUNG, L.C., VANDERLIP, C., DUFFY, D.C., AFANASYEV, V. & SHAFFER, S.A. 2009. Bringing home the trash: do colony-based differences in foraging distribution lead to increased plastic ingestion in Laysan albatrosses? *PLoS One* 4: e7623.