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INTRODUCTION: REVIEW

Effects of wind on the movement, behavior, energetics, and life history of seabirds

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ABSTRACT: For decades, studies have highlighted links between wind patterns and the behavior, ecology, distribution, energetics and life history of seabirds. However, only relatively recently have advancements in tracking technologies and improvements in the resolution of globally-available wind data allowed wind impacts on seabirds to be quantified across multiple spatiotemporal scales. Here, we review and synthesize current knowledge of the effects of wind on seabirds. We first describe global patterns of wind circulation and relevant atmospheric processes and discuss the relationship between seabird morphology, flight performance and behavior relative to wind. We then develop a conceptual model linking seabird movement strategies to wind, morphology, flight capabilities and central-place constraint. Finally, we examine how wind influences seabird populations via effects on flight efficiency and energetics, and wind impacts associated with climate variability and severe weather. We conclude by highlighting research priorities for advancing our understanding of the effects of wind on seabird ecology and behavior; these include assessing how and to what extent seabirds use ocean waves for efficient flight, understanding how seabirds sense and anticipate wind patterns, and examining how wind has shaped seabird evolution. Future research should also focus on assessing how wind modulates habitat accessibility, and how this knowledge could be incorporated into theory of seabird habitat use. Moreover, approaches that focus on mechanistic links between climate, wind and demography are needed to assess population-level effects, and will be imperative to understanding how seabirds may be impacted by climate-driven changes to wind patterns.

KEY WORDS: Marine birds · Morphology · Flight · Speed · Waves · Climate · Reanalysis · Wind patterns · Review

1. INTRODUCTION

Wind is ubiquitous, affecting the movement, energetics and life-history of flying animals across the globe (Chapman et al. 2011, Safi et al. 2013, Cornioley et al. 2016). Seabirds are highly mobile, long-lived species that traverse the seas and oceans, where wind speeds are stronger on average than over land (Archer & Jacobson 2005, Böttcher et al. 2007, Laubrich 2009, Hedegaard & Meibom 2012, Watson 2019). Long before birds could be equipped with tracking devices, scientists made some impressive inferences from scant observations, including that many species make global-scale migrations following circuitous rather than direct routes that mirror prevailing wind patterns (Dixon 1932, Wynne-Edwards 1935, Serventy

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1953, Kuroda 1957, Storr 1958) and that albatrosses exploit the wind to fly with little energetic cost (Rayleigh 1883). More than 3 decades of seabird tracking have provided a wealth of data on seabird movement and behavior, corroborating and expanding on this pioneering work (Shaffer et al. 2006, Guilford et al. 2009, Hedd et al. 2012, Dias et al. 2012, Bonnet-Lebrun et al. 2021a). Technological refinement and miniaturization of biologging devices is ongoing, continually improving our ability to observe seabirds in flight (Yoda 2019, Korpela et al. 2020, Conners et al. 2021). Concurrently, remotely-sensed and modeled wind data are becoming ever more accessible and at higher resolutions, facilitating simultaneous analysis of seabird movement and wind conditions (Wakefield et al. 2009a, Adams & Flora 2010, Hersbach et al. 2020, Ventura et al. 2020). These developments are greatly advancing our understanding of how wind influences seabirds at scales not previously possible, making it timely to review progress to date.

The impacts of wind on seabirds vary markedly among taxa and scales. For example, while the morphology and behavior of many species are adapted to exploit wind for efficient flight (Cone 1964, Sachs 2005, Pennycuick 2008, Kempton et al. 2022), evolutionary tradeoffs mean that strong winds impede rather than facilitate the flight of others (Spear & Ainley 1997a,b, Elliott et al. 2014). At fine scales, wind influences the flight mode, speed and energetic performance of seabirds (Pennycuick 1978, Alerstam et al. 1993, Spear & Ainley 1997a,b), shaping time and energy costs associated with foraging, breeding and migration (Amélineau et al. 2014, Elliott et al. 2014). Further, wind varies at fine scales in ways that are often difficult to predict (Böttcher et al. 2007, Laubrich 2009, Hedegaard & Meibom 2012, Watson 2019), and thus seabirds must sense and respond to it continuously, unlike many other environmental variables. At broader scales, wind influences when and where seabirds fly, during both breeding and migration (Shaffer et al. 2006, González-Solís et al. 2009, McLaren et al. 2014). Over evolutionary timescales, wind exerts a selection pressure that has profoundly shaped seabird biogeography, morphology and life history (Spear & Ainley 1997a, 1998, Suryan et al. 2008, Sato et al. 2009, Davies et al. 2010, Weimerskirch et al. 2012).

Here, we aim to synthesize, in a manner accessible to a general ecological audience, the current understanding of the effects of wind on movement, energetics, population processes, adaptation and biogeography of seabirds. In doing so, we highlight the spatiotemporal scales of these effects. We define spatiotemporal scales of 10s to 100s of meters and minutes–hours as *fine scale*; 1–1000 km and hours–weeks as *mesoscale*; 1000–10 000 km and weeks–months as *synoptic scale*, and above this, *macroscale* (adapted from Wakefield et al. 2009a, Shamoun-Baranes et al. 2017). The review is structured as follows: Section 2 sets the context with a brief primer on the main atmospheric processes that give rise to wind phenomena influencing seabird movement and ecology. Section 3 covers wing morphology and flight modes relative to wind. Section 4 deals with movement strategies with respect to wind at the meso- to macroscale, framed around a simple conceptual model. Section 5 examines how wind influences seabird energetics. Section 6 reviews wind-mediated effects of climate and severe weather on seabird populations. Section 7 concludes with twelve research questions that our review suggests should now be priorities to address. Throughout the text, we italicized key terms where they are first defined.

2. METEOROLOGICAL OVERVIEW OF WIND PHENOMENA THAT AFFECT SEABIRDS

In this section, we describe atmospheric processes that influence wind patterns of relevance to seabirds at different spatiotemporal scales and discuss sources of wind data available to seabird researchers. We include discussion of wind-driven waves due to their potential effects on seabird flight.

2.1. Macro- to mesoscale atmospheric processes and wind patterns

At the synoptic scale, seabird migratory routes mirror prevailing wind patterns (see Section 4.10). Wind patterns at this scale, such as the trade winds, doldrums, mid-latitude westerlies (directions of winds refer to the cardinal point from which they originate), and the locations and strength of both tropical and extratropical cyclones are driven by spatial variations in temperature and pressure and the rotation of the Earth (i.e. the Coriolis force; Randall 2015).

Within the tropics, low-altitude winds (i.e. those relevant to seabirds) are dominated by the *trade winds* — easterlies that drive moisture from approximately 25 to 30° latitude until their termination within a few degrees of the equator at the *intertropical convergence zone* (ITCZ). This region, also known as the *doldrums* (white areas near the equator in Fig. 1), is one of consistently weak horizontal wind speeds and warm, humid air which generates numerous intense convective storms (Klocke et al. 2017). These storms form the rising branch of the Hadley cell in which this air subsequently moves poleward and sinks between approx. 15 and 30° latitude, transporting energy aloft to the mid-latitudes (James 2003).

Mid-latitude westerlies are regions of persistent westerly winds between approx. 30 and 60° latitude. These regions are generally bounded on the equatorial side by the descending branch of the Hadley cell which contributes to the persistent subtropical high-pressure *anticyclonic systems* (indicated by tight circular diverging streamlines in Fig. 1) that influence much of the large-scale circulation patterns in the mid-latitudes (North et al. 2014). High-pressure anticyclones result in expansive regions of relatively low wind speed that can impede the movements of some seabirds (see Section 4.9). The westerlies result

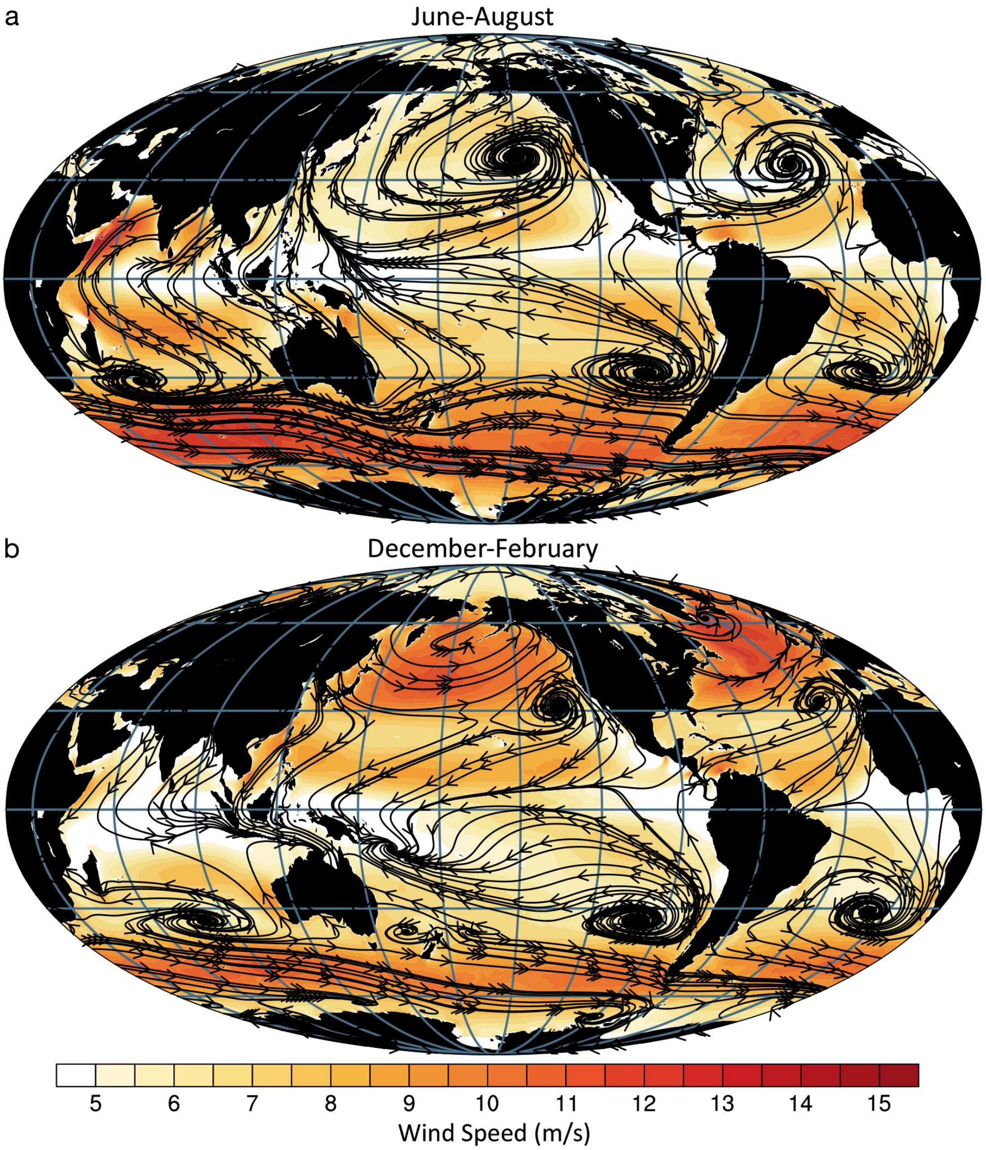


Fig. 1. Mean global wind direction (shown by streamlines/black arrows) and speed (shading) at 10 m above sea level from ERA5 reanalysis spanning 1959–2022. (a) Southern Hemisphere winter (June, July, August), (b) Northern Hemisphere winter (December, January, February). The doldrums are the equatorial areas in white, where monthly mean wind speed is <5 m s^{-1}. Storm tracks occupy red-shaded, high latitude areas. Mid-latitude westerlies are evident as regions of fast westerly winds in the North Pacific and North Atlantic during the Northern Hemisphere winter and in the Southern Ocean year-round. Streamlines provide a snapshot perspective of the wind field and are defined as curves which are tangent to the vector velocity field over the relevant time period for the data. Latitude and longitude grid lines are shown every 30°

from the Coriolis force acting on the wind that travels from these high-pressure regions towards the low-pressure region over the poles. Zonal migrations of seabirds often take advantage of positive wind support from mid-latitude westerlies (see Section 4.10; z*onal* and *meridional* refer to easterly–westerly and northerly–southerly movement or flow, respectively).

The wind and weather of the mid-latitudes are also affected on smaller scales (10s to 100s of kilometers) by the prevalence of *extratropical cyclones* (low pressure systems) that are formed through the interaction of warm and cold air masses (see regions of dark shading in Fig. 1). *Tropical cyclones* (regionally known as hurricanes or typhoons) tend to form between 5 and 15° latitude and then travel westward and poleward until they either dissipate or are entrained into the mid-latitude westerlies where they can transition into extratropical cyclones. Extratropical cyclones usually tend to form in the mid-latitudes, initially as instabilities at the frontal boundary between warm subtropical and cold subpolar air masses (Olaoluwa et al. 2022). The so-called *storm tracks* (mid- to high-latitude orange areas in Fig. 1) are the regions where mid-latitude cyclones most commonly form and propagate eastwards and where the mid-latitude transport of energy is the largest (Shaw et al. 2016). Most of the weather fronts and storms that seabirds experience outside the tropics are associated with these systems. Extratropical cyclones generally move eastwards with the prevailing westerlies. As the leading warm and trailing cold fronts associated with a typical extratropical cyclone pass, wind speed and direction shift in a stereotyped manner. Seabirds may be able to exploit these changes, such as rapid shifts in wind direction when a cold front passes, to improve their movement efficiency (see Section 4.9). In contrast with the comparatively weak surface winds of the tropical regions, the storm tracks of higher latitudes are regions of strong winds. Surface winds in the storm tracks of the North Pacific and North Atlantic are substantially more variable seasonally than in the Southern Ocean, where they are strong during all seasons (Fig. 1).

2.2. Meso- to fine-scale atmospheric processes affecting wind

At meso- to fine scales, seabirds are influenced by phenomena such as boundary layer turbulence, wind shear and thermals. The *atmospheric boundary layer* is the lowest part of the atmosphere which is strongly impacted by contact with the Earth's surface. It is usually <2–3 km deep, but over the oceans can be as shallow as a few hundred meters (Garratt 1994). Processes in this layer directly affect the flight speeds, altitudes and climb rates of birds (Treep et al. 2016; see our Sections 3.2.4, 3.3 & 4.6). Within the atmospheric boundary layer, vertical *wind shear*, the vertical gradient of wind velocity, is greatest close to the surface, where friction slows winds to zero. At altitudes of more than ~20–30 m above sea level, wind velocity is more uniform and shear lower (Wood 1973). Friction gives rise to turbulence in the boundary layer, which can influence seabird movement by modulating horizontal flow (Shamoun-Baranes et al. 2017).

Thermals, or columns of rising buoyant air that result from uneven heating near the Earth's surface, often occur within or alongside convective storms. Thermals at sea may be weaker than over land (Duriez et al. 2018), but occur commonly in the ITCZ, where frigatebirds *Fregatta* spp. exploit them to gain altitude, allowing low cost, long-distance horizonal gliding flight (see Section 3.2.4). Strong thermals often manifest as the ascending branches of deep convective towers in the tropics, causing the formation of cumulus clouds. However, weaker thermals also occur throughout the oceans in clear-sky conditions and within smaller cloud systems, such as those occurring around the edge of the doldrums.

2.3. Measurement and prediction of wind at sea

In situ measurements of wind at sea come mainly from ships and meteorological buoys. These data are important for calibrating other sources of marine wind data (Thomas & Swail 2011) and have also been used for colony-based seabird studies (Gilchrist et al. 1998, Shepard et al. 2019). However, they are costly and technically demanding to obtain. As a result, fewer direct observations are made at sea than on land. Moreover, disruption of the flow by ships and buoys themselves may bias wind speed and direction measurements (Taylor et al. 1999, Schlundt et al. 2020, Pizzo et al. 2021).

Marine surface-wind fields can also be derived from measurements made by cloud-penetrating, satellite-borne radar *scatterometers* (Atlas et al. 2001). Scatterometers provide global wind data at spatial scales as small as 25–50 km, and generally have twice-daily temporal resolution. These data can be used to assess how seabird movement and distribution are influenced by wind at broad spatial scales (e.g. Adams & Flora 2010). However, while scatterometers are an extremely useful tool to infer the low-level wind speed, measurements are biased by heavy rain and strong winds (Stiles & Yueh 2002). Further, approximately 7% of the ocean surface goes unobserved daily by scatterometers due to a lack of coverage between satellite swaths of the Polar Orbiting Environmental Satellites which house them (Rhome 2003). The first satellite scatterometers were deployed in the 1970s, but continuous ocean wind data from different scatterometers have only been available from the early 1990s onwards (Rhome 2003, Bentamy et al. 2017). Beginning in 1991, the European Space Agency (ESA) operated scatterometers on the ERS-1 (operational 1991–1995) and ERS-2 (1995–2001) satellites, while the National Aeronautics and Space Administration (NASA) operated the Seawinds scatterometer on the QuikSCAT (1999–2009) and the ADEOS-2 (2002–2003) satellites. Currently, the ESA operates the ASCAT-A (2006–present) and ASCAT-B (2013–present) scatterometers on METOP satellites (Rhome 2003, Bentamy et al. 2017).

Reanalysis products (e.g. MERRA-2, ERA-40 and ERA5) are produced by using global numerical models to assimilate myriad observations from ships, buoys, satellite scatterometers and other sources to produce continuous datasets with complete spatiotemporal coverage (Hersbach et al. 2020). These products are an invaluable resource for determining the climatology of global wind. The NASA Global Modeling and Assimilation Office produced the Modern-Era Retrospective analysis for Research and Applications, version 2 (MERRA-2), which replaced the initial MERRA product (Gelaro et al. 2017). ERA5 is the fifth-generation atmospheric reanalysis produced by the European Centre for Medium-Range Weather Forecasts and replaced previous ERA reanalyses, such as ERA-40 and ERA-Interim (Hersbach et al. 2020). At the global scale, ERA5 (used to produce Fig. 1; available at https://cds.climate.copernicus.eu/) has the highest spatial resolution (0.25°), and hourly temporal resolution, from 1950 onwards, at altitudes of 10 or 100 m (Hersbach et al. 2020). Its surface-wind predictions compare well to ground observations and are better than similar reanalyses, such as MERRA-2 (Olauson 2018, Graham et al. 2019, Tetzner et al. 2019). Confidence in ERA5 increases as additional observations become available and are assimilated, such as after 1979, when observations from satellites started to become available. Reanalysis products have been used to assess seabird movement across pelagic habitats (e.g. Frankish et al. 2022, Lempidakis et al. 2022b), and could be used to assess wind variability in seabird habitats over multiple decades.

Attempts to model, and therefore predict, wind at fine scales are hampered by (1) limited observations at sea at this scale; (2) the mathematical complexity of turbulence, which is prevalent at this scale; and (3) in the case of predicting over a global scale domain, computational limitations. High resolution atmospheric models (grid-spacing on the order of 0.1 to 10s of kilometers) are tractable over more limited regional domains. However, interactions between steady and persistent atmospheric features, such as the trade winds or the mid-latitude westerlies, and more transient features, such as weather fronts, extratropical cyclones, and tropical cyclones, also complicate efforts to model fine scale wind. As an alternative, statistical downscaling can translate the results of global climate models to finer resolutions. In general, more observations of ocean wind are needed to improve forecasts and estimates of wind speed and direction.

Seabird movements themselves, specifically changes in flight speed and direction, have been used to derive fine-scale wind speed and direction (Yonehara et al. 2016). However, bird movement often underestimates wind speed, and relationships have only been derived for 3 species of seabird that rely on wind for efficient flight and may be more complex for species that show variable flight behavior relative to wind. With further refinement, tagged seabirds may provide a means of measuring surface winds to help fill in spatial and temporal gaps in wind data from conventional observation methods (Yonehara et al. 2016).

2.4. Relationship between surface winds and ocean waves

Ocean surface waves can affect fine-scale seabird movements (see Section 3.2.3) and are primarily wind-driven (Semedo et al. 2011, Pizzo et al. 2021). *Wind waves* are generated by the atmospheric boundary layer wind, with their size being largely determined by the wind speed and the time and distance over which wind acts. When wind waves propagate beyond the spatiotemporal region of generation, they are known as *swell* or *ground swell*, and are typified by longer, less variable periods. The largest waves are generated at high latitudes where winds are stronger (Fig. 1), and swell can propagate across entire ocean basins (Young 1999).

Measuring and predicting surface winds is essential to characterizing patterns of wind-driven waves

(Young 1999, Semedo et al. 2011). Data on wave parameters such as height, direction and period are available globally from reanalysis products such as ERA5 at similar spatiotemporal scales to wind data. In contrast, statistical wind models, high-resolution regional models, and direct high-resolution observations of low-level wind and surface waves can provide information at smaller spatiotemporal scales. Wave height can also be estimated from the fine-scale motions of seabirds tagged with high resolution sensors as they move passively with ocean waves while sitting on the water (Uesaka et al. 2022).

Variability in wave data at fine scales is difficult to model; indeed, modeling the mobile interface between air and sea is a problem that has resisted solution for centuries. The challenge stems from the complexity of 2 interacting fluids of greatly differing densities, both of which are turbulent, as well as the broad range of relevant scales (from milometers to 100s of meters) over which wind acts to generate and drive waves (Sullivan & McWilliams 2010, Pizzo et al. 2021).

2.5. Mismatches in the resolutions of seabird, wind, and wave data

There is currently a mismatch between the scale at which seabird movement and both wind and waves can be observed. Advances in tagging technologies have greatly improved our ability to study fine-scale seabird behavior and to quantify metrics of energetic expenditure, relative to wind (see Sections 3.2 & 5.1). Devices such as tri-axial accelerometers and magnetometers typically record up to ~50 Hz and can be used to infer fine-scale movements and behavior (e.g. Elliott et al. 2014, Conners et al. 2021). However, wind measurement at sea over the large geographic areas used by most seabird species currently remains unfeasible at this resolution.

3. FLIGHT MORPHOLOGY, MODES AND PERFORMANCE OF SEABIRDS

In this section, we review links between wind, seabird morphology, flight modes (i.e. different means of locomotion), flight performance (e.g. speed, energetic efficiency), and biogeography. While at any given moment, morphology, flight mode and wind dictate flight performance, morphology and behavior are themselves products of adaptation to (among other things) wind. We note that the terms gliding and soaring are often used interchangeably in the seabird literature. Here, we define *gliding* simply as flight sustained via the use of potential energy, rather than by performing mechanical work using the flight muscles (Pennycuick 2008, Norberg 1985). We use the term *soaring* to refer to a specialized form of gliding flight sustained by the use of atmospheric energy, such as wind shear or uplift.

3.1. Seabird flight morphology and implications for flight relative to wind

3.1.1. The effects of wing shape and body mass on flight performance

Interpretation of seabird flight responses to wind requires an understanding of the influence of morphology. A detailed account of the underlying mechanics of bird flight is provided by Pennycuick (2008). Many structural traits influence flight, but here we focus on 3 of the most important: body mass (m; in g), wingspan (B; in m), and wing area (S; in m^2) (Pennycuick 1989). *Wingspan* is the distance between wing tips with elbow and wrist joints fully extended and is often estimated by measuring and doubling the *semi-span*, the distance from the body center line (i.e. spine) to the tip of the outermost primary. *Wing area* is often calculated by measuring and doubling the partial wing area, the area of one wing from wing tip to the body, and adding the area between the wings (root chord, which is the wing width at the body × shoulder width). The *wing loading* (Q; in N m^{-2})

$$Q = \frac{mg}{S} \tag{1}$$

is the weight per unit wing area, and g is the acceleration due to gravity. Aerodynamic theory predicts that characteristic *airspeeds* (speeds relative to the surrounding air) of birds in gliding (i.e. fixed-wing) flight scale with $\sqrt{Q}$ (see Section 3.3). Those in flapping flight, when a bird's wings must provide not only lift but also thrust, are predicted to be inversely proportional to $\sqrt{B}$ (Pennycuick 2008). Observation has shown that airspeeds of migrating birds in flapping flight also scale with Q, albeit to the power ~0.3 (Alerstam et al. 2007). Theoretically, stall speeds, and therefore minimum take-off speeds, scale with the square-root of wing loading, so wing loading may be adaptive to wind (Shaffer et al. 2001; see our Sections 3.1.3 & 3.4). It may also place an upper limit on overall body size because birds much larger than great albatrosses *Diomedea* spp. (which have the largest wingspans of extant birds) may not be able to flap fast enough to stay aloft under variable or unfavorable wind conditions (Sato et al. 2009). Wing loading also affects turn radius: frigatebirds, and other species that use thermal soaring flight, have relatively low wing loadings, allowing them to circle tightly, thereby remaining within narrow parcels of rising air (Pennycuick 1983). The *aspect ratio*,

$$R = \frac{B^2}{S} \tag{2}$$

is a dimensionless index of wing shape which provides a measure of aerodynamic efficiency in gliding flight (Norberg 2002). Long, narrow wings have high aspect ratios, producing less drag for a given speed than shorter, wider wings of the same wing loading (Pennycuick 1987b).

3.1.2. Differences in flight morphology among seabird taxa and implications for the use of wind

Seabird morphologies result not only from adaptation to flight and wind conditions but also to other functions, for example aquatic and terrestrial locomotion, resulting in a diversity of wing forms (Fig. 2) (Pennycuick 1982, Elliott et al. 2013). Birds are often categorized by the extent to which they use flapping

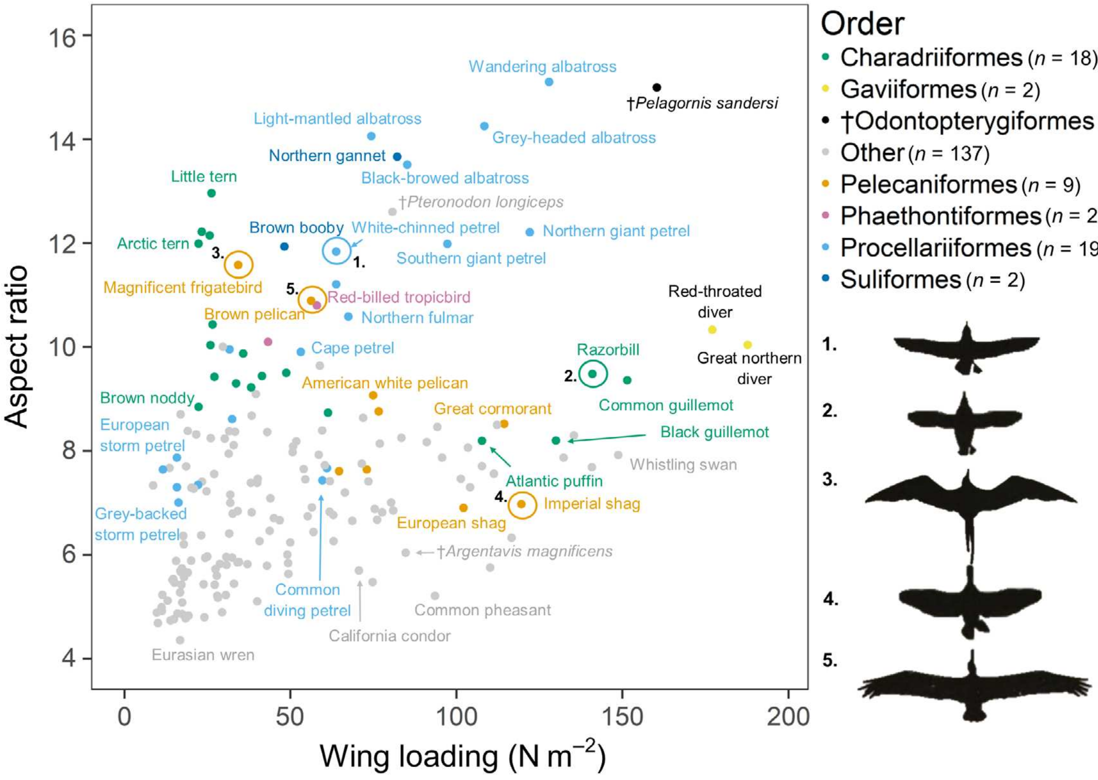


Fig. 2. The relationship between wing loading (N m^{-2}) and aspect ratio (dimensionless) for flying birds. Data for extant species were extracted from the Wings database within the Flight v.1.25 software (Pennycuick 2008, 2011) (n = 186 species, including 48 seabirds). Data for 3 extinct volant species and California condors *Gymnogyps californianus* were taken from Goto et al. (2022) and Ksepka (2014) to represent evolutionary extremes: *Pelagornis sandersi* (a dynamic soarer thought to have the largest wingspan of any animal), *Pteronodon longiceps* (a pterosaur thought to conduct dynamic and thermal soaring) and *Argentavis magnificens* (a terrestrial thermal soarer thought to be among the heaviest flying birds). Extinct taxa are indicated by †. For *Pelagornis sandersi*, we present the largest morphological values proposed by Ksepka (2014). Non-seabirds are shown in light grey, including *Pteronodon longiceps* (a marine reptile). Extant seabirds encompass species with the greatest wing loadings (divers, auks; diving specialists) and the greatest aspect ratios (albatrosses; soaring specialists) (Pennycuick 1982, Elliott et al. 2013). Seabirds with very high wing loadings (not illustrated), are flightless or nearly so (e.g. penguins, steamer ducks *Tachyeres* spp., great auks *Pinguinus impennis*). No seabirds have the combination of low wing loadings and low aspect ratios expressed by some terrestrial birds, perhaps due to seabirds' need to make progress against stronger winds or for a body size sufficient to thermoregulate in the marine environment. Example extant seabird silhouettes are taken from Pennycuick (1987b): (1) white-chinned petrel *Procellaria aequinoctialis*, representing the 'standard seabird'; (2) razorbill *Alca torda* with substantially shorter wings; (3) magnificent frigatebird *Fregata magnificens*, longer wings but a similar aspect ratio; (4) imperial shag *Leucocarbo atriceps*, wings shorter but area similar; and (5) brown pelican *Pelecanus occidentalis*, wing area larger but span only slightly increased

flight, which impacts flight costs and energy expenditure with respect to wind (see Sections 3.2.1 & 5): *soarers* rely primarily on atmospheric energy for efficient horizontal or vertical movement, *flappers* primarily use flapping flight, and *flap-gliders* use flapping flight interspersed with periods of gliding (Pennycuick 1987b). In addition, what we refer to as *flap-soarers* primarily use soaring flight, regularly supplemented by flapping when atmospheric conditions make soaring impractical. In order to interpret the large variation in wing morphology exhibited by seabirds, Pennycuick (1987b) introduced the concept of the 'standard seabird' model, based on a medium-sized petrel. While simplistic, the model demonstrates that slightly different wing shapes favor different flight modes and tradeoffs between flight performance, including with respect to wind, and foraging adaptations (Pennycuick 1975) (see Fig. 2 for details). Taxa at the ends of the soaring-flapping spectrum have little or no flexibility to vary their means of propulsion (Pennycuick 1987b). At one extreme, albatrosses have high aspect ratios, adapted to harvesting wind energy via dynamic soaring, which they can only do in moderate to strong winds (Pennycuick 2008, Kempton et al. 2022). They are poorly adapted to flapping flight, curtailing their flight performance in very light winds. At the other extreme, auks (Alcidae) have shorter, broader wings adapted for wing-propelled diving as well as flight, making them obligate flappers (Pennycuick 2008). Flying in strong headwinds is energetically costly for these species (Spear & Ainley 1998, Elliott et al. 2014). Most medium-sized seabirds, such as shearwaters and sulids (Sulidae), are intermediate, capable to a greater or lesser extent of both sustained flapping and, if wind speed is sufficient, of dynamic soaring (Weimerskirch et al. 2005b, Ropert-Coudert et al. 2006, Ainley et al. 2015, Gibb et al. 2017, Kempton et al. 2022). Frigatebirds are adapted to thermal soaring but are also capable of flapping flight (Pennycuick 1983, Weimerskirch et al. 2016). There is a consistent scaling relationship (Fig. 2) between wing loading and aspect ratio in some orders of seabirds (e.g. Procellariiformes; Warham 1977) but not others (e.g. Charadriiformes and Pelecaniformes; Brewer & Hertel 2007), possibly due to morphological tradeoffs between flight and other functions.

The preceding discussion of relationships between structure and function treats body mass and wing shape as phenotypically fixed, but seabird morphology is not fixed. It can be adjusted in response to wind conditions and behavioral goals, and over longer time scales, varies with food intake and energetic expenditure. At scales of seconds and more, seabirds can wing morph through movements of shoulder, elbow and wrist joints (Hedenström et al. 2002, Taylor et al. 2012). Flight generalists, such as gulls, can vary wing shape, effectively shifting their position on the wing loading-aspect ratio plot (Fig. 2), for example, reducing wing area in strong and gusty winds to improve stability (Harvey et al. 2019, Harvey & Inman 2022). In contrast, flight specialists, such as albatrosses, likely occupy a much smaller area on this plot. Changes in body mass resulting from e.g. prey capture, defecation, tissue growth and loss, alter wing loading and presumably, therefore, flight performance at scales of hours–weeks (Wendeln & Becker 1996, Weimerskirch et al. 2003a). For example, reductions in thick-billed murre *Uria lomvia* masses of approx. 3 to 6% from incubation to brooding are considered to be adaptive and increase flight efficiency (Croll et al. 1991, Elliott et al. 2008). However, while theoretical predictions have been made for how seabirds should use winds in response to changes in mass over the course of a foraging trip (Alerstam et al. 2019a), few studies have directly quantified links between changes in mass, wind use and flight performance (except see Clay et al. 2023). Flight feather molt also alters wing shape (Hedenström & Sunada 1999), likely affecting flight behavior and performance relative to wind. Theoretical evidence that aerodynamic costs of gaps in feathers due to molt increase with increasing aspect ratio (Hedenström & Sunada 1999) may explain why large birds such as albatrosses have a complex molt strategy that may take several years to complete (Weimerskirch 1991, Prince et al. 1993).

In addition to wing morphology and mass, tail position and the configuration and structure of tail and wing feathers can have substantial aerodynamic implications (Hedenström et al. 2002, Wang & Clarke 2015). Large Procellariiform seabirds require low drag and therefore have short tails, with albatrosses having some of the shortest relative to their aspect ratios (Thomas & Balmford 1995). In contrast, the long outer tail feathers of frigatebirds, which can be extended laterally to produce lift and increase maneuverability, are thought to be adaptations to facilitate aerial and kleptoparasitic feeding (Norberg 1995, Buchanan & Evans 2000, Brewer & Hertel 2007).

3.1.3. Within-species differences in morphology and flight performance relative to wind

Many seabird species exhibit sexual size dimorphism. Differences in body mass and wing shape between males and females likely influence flight performance but it remains unclear whether this is due to within-sex adaptation to different wind regimes or whether other factors lead to between-sex differences in space use and therefore wind regime (Shaffer et al. 2001, Phillips et al. 2004, Wakefield et al. 2009a). For example, male wandering albatrosses *Diomedea exulans* forage further south in regions with consistently faster wind speeds and have a greater mass and higher wing loading than females (Weimerskirch et al. 1993, Shaffer et al. 2001). Given that males therefore require stronger winds to take off from the sea surface, variation in flight performance may be the proximate mechanism mediating sex differences in foraging distributions (Shaffer et al. 2001, Clay et al. 2020, Orgeret et al. 2021). Female European shags *Phalacrocorax aristotelis*, which are lighter than males, forage for longer during strong onshore winds, possibly because they fly less efficiently in turbulent conditions (Lewis et al. 2015).

Juvenile and immature seabirds often have different flight capabilities than adults, but it can be difficult to disentangle whether this is due to behavioral or morphological ontogeny (Phillips et al. 2017, Ruaux et al. 2020). Tracking of Procellariiformes, northern gannets *Morus bassanus* and great frigatebirds *Fregata minor* has shown that within a few hours−weeks of departing their natal breeding colonies, juveniles traveled at speeds similar to those of adults, while juvenile wandering albatrosses were also able to orient with winds similarly to adults, suggesting that the ability to conduct complex flight behaviors is largely innate (Riotte-Lambert & Weimerskirch 2013, de Grissac et al. 2017, Corbeau et al. 2020, Frankish et al. 2020, Lane et al. 2021). Juvenile wandering albatrosses have longer wings and lower wing loading than adults, which is considered to be an adaptation to subtropical waters where winds are generally weaker (Weimerskirch et al. 2000a, Shaffer et al. 2001). In contrast, juvenile northern gannets were heavier and had shorter and narrower wings on departure than adults, but after a few days at sea are presumed to have similar flight performance (Wanless & Okill 1994). However, although immatures aged approx. 2–3 yr did not differ in wingspan or mass from adults, they had wider wings, resulting in slower theoretical minimum sink speeds (by 0.5 m s^{-1}; Wakefield et al. 2019).

3.2. Flight modes with respect to wind

Pioneering studies of seabird flight in relation to wind were based on direct observation of birds from land or ships (Pennycuick 1982, Spear & Ainley 1997a, Alerstam et al. 2007). Increasingly, bird-borne devices including GPS, accelerometers, magnetometers, gyroscopes, heart rate loggers, altimeters, and cameras are making it possible to assess flight behavior directly at high resolution, allowing different flight behaviors to be discriminated and quantified (Sakamoto et al. 2013, Spivey et al. 2014, Shamoun-Baranes et al. 2016, Bousquet et al. 2017, Gibb et al. 2017, S. Schoombie et al. 2023 in this Theme Section). Pairing these observations with wind data (see Section 2.3) can elucidate mechanistic links between seabird movement and wind. In the following sections, we focus on studies of flapping flight, and dynamic, wave-slope, thermal and orographic uplift soaring, as these flight modes have been particularly well-studied relative to wind. However, although we discuss these separately, in practice seabirds switch between and combine flight modes as wind conditions and goals dictate.

3.2.1. Flapping, flap-gliding and flap-soaring flight

Although many seabird taxa are adapted to specialize in particular flight modes (Mohamed et al. 2022), all volant seabirds use flapping flight to some extent. Wind conditions, in part, dictate when flapping flight is necessary and its efficiency. For example, birds may increase their wingbeat frequency or amplitude in order to increase their airspeed in response to headwinds (see Section 3.3) or to maintain stability (Elliott et al. 2014, Kogure et al. 2016, Yamamoto et al. 2017). The *ground speed* of a bird (speed of the bird relative to the ground) results from the vector sum of its airspeed and the wind speed. *Wind support* is the vectorial component of wind in the bird's preferred direction of movement (Fig. 3). Seabirds that primarily use flapping flight can reduce negative wind support (from headwinds) by flying close to the sea surface, where drag reduces wind speed (Krüger & Garthe 2001, McLaren et al. 2016, Tarroux et al. 2016).

Albatrosses predominantly fly by dynamic soaring when the wind is sufficient (Sachs 2005, Richardson 2011, Sachs et al. 2013), but often remain at rest on the water during periods of weak winds and limited waves (Pennycuick 1982, Jouventin & Weimerskirch 1990, Alerstam et al. 1993). Although they are thought to flap infrequently other than in light winds, it remains unclear exactly how they adapt to prevailing wind conditions by combining flapping and dynamic soaring. This has received even less atten-

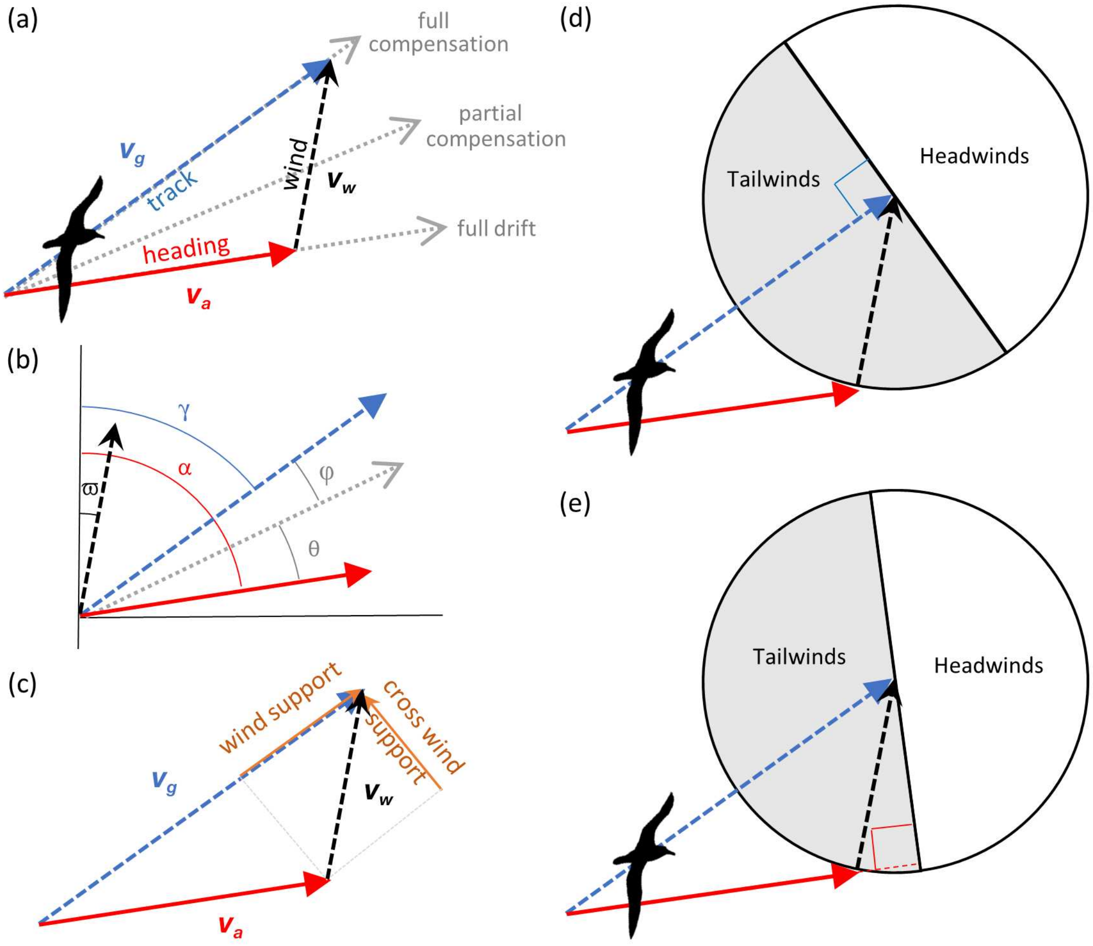


Fig. 3. Terms used to describe orientation and movement with respect to wind. (a) The triangle of velocities shows that ground speed ($\boldsymbol{v}_g$) is the vector sum of wind speed ($\boldsymbol{v}_w$) and airspeed ($\boldsymbol{v}_a$). The grey arrows indicate the bird's preferred direction of movement towards a goal at the beginning of a journey, illustrating 3 different drift compensation strategies: Under 'full compensation', the bird adjusts its heading sufficiently to compensate for advection by the wind; under 'partial drift' (or 'partial compensation') it adjusts its heading but not enough to compensate fully for drift; under 'full drift', it ignores advection by the wind, simply continuing on the initial bearing to the goal. Note that without further action, only the first strategy would result in the bird reaching its goal. For more drift compensation strategies, see Table 1. (b) The relationship between the corresponding angles using the partial drift strategy as an example. The bird travels through the air at $\boldsymbol{v}_a$, on heading α. Due to advection by the wind with speed $\boldsymbol{v}_w$ and direction ω, it moves over the ground along the track line in direction γ at speed $\boldsymbol{v}_g$. Drift, φ, is the angle between the bird's track and its goal. Compensation, θ, is the angle between its heading and its goal. In the text, we follow the convention that wind direction is that from which the wind blows but for analysis, ω is that towards which it blows. (c) Wind support, illustrated using the full compensation example, can be defined as the vector component of wind in the bird's preferred direction of movement. Under full compensation, this is the wind component in the bird's track direction (Safi et al. 2013) but under other drift compensation scenarios, support is less straightforward to calculate (Kemp et al. 2012). (d) In the seabird literature, it is common to define the terms 'tailwind' and 'headwind' relative to a bird's track direction (the convention we use in the text), but they could equally be defined relative to a bird's heading or (e) preferred direction of movement, if these were known. Based on Green & Alerstam (2002), Shamoun-Baranes et al. (2007), Chapman et al. (2011), and Safi et al. (2013)

tion in mid-sized Procellariiformes that use both soaring and flap-gliding flight (Kempton et al. 2022). Some species have been observed to use flapping flight less often as wind speed increases (Gibb et al. 2017, Keys et al. 2023 in this Theme Section). However, others have been observed to increase wingbeat frequency as headwinds increase (Spivey et al. 2014).

Studies to date have differed in the methods used to identify flapping behavior in seabirds. Accelerometers are increasingly being used to do so and to quantify flapping frequencies since flaps result in acceleration on the heave (dorso-ventrally oriented) axis (Ropert-Coudert et al. 2006, Sakamoto et al. 2013, Rattenborg et al. 2016). In some studies, individual flaps are identified by visual examination of the heave axis (Ropert-Coudert et al. 2006, Amélineau et al. 2014, Rattenborg et al. 2016, Shamoun-Baranes et al. 2016) or by automating the process of isolating spikes in the heave axis (S. Schoombie et al. 2023). Other methods include classifying behaviors from accelerometer characteristics to identify flapping frequencies (Sato et al. 2009) or to distinguish periods of flapping from time spent soaring, at the surface or underwater (Sakamoto et al. 2009, 2013, Conners et al. 2021). Spivey et al. (2014) use a combined time and frequency domain technique to identify the wingbeat frequency and flapping duty cycle. Flapping behavior has also been identified using video cameras deployed on seabirds (Keys et al. 2023, S. Schoombie et al. 2023). While different methods will be appropriate depending on the particular objective, those that automate the detection of flapping behavior should be prioritized to improve reproducibility and efficiency of analyses and to allow comparisons across studies.

3.2.2. Dynamic soaring

In *dynamic soaring*, sometimes referred to as wind-shear soaring, flight is sustained by energy gained by crossing wind shear gradients (Cone 1964). Dynamic soaring directly links seabird movement and energetics to wind, allowing flight at low energetic cost and therefore the exploitation of prey which are patchily distributed across vast expanses of ocean. The use of dynamic soaring for efficient flight has long been recognized, with early descriptions by Lord Rayleigh in 1883 and possibly even Leonardo da Vinci (ca. 1513–1515) (Richardson 2018). In its idealized conceptualization, seabirds, through dynamic soaring over the ocean, extract energy from the wind by following an S-shaped trajectory through the vertical wind shear layer (Fig. 4a) (Pennycuick 1982, 2002, Sachs 2005, 2016, Richardson 2011, Sachs et al. 2013, Richardson et al. 2018). *Gust soaring* is a proposed modification of this theory which recognizes that waves modulate airflow above the sea. It envisages that birds increase the efficiency of dynamic soaring by crossing the strong wind shear between the lee of large waves and the uninterrupted flow above, encountering a 'gust' as they do so (Pennycuick 2002, Richardson 2011).

Many studies have used mathematical modeling to assess the flight paths of albatrosses in dynamic soaring cycles (Rayleigh 1883, Idrac 1925, Sachs 2005, Richardson 2011), and, more recently, by combining modeling approaches with GPS data from tracked birds (Sachs et al. 2013, Sachs 2016, Bousquet et al. 2017). Maneuvers characteristic of the dynamic soaring cycle occur over tens to hundreds of meters (Sachs et al. 2013, Sachs 2016). Provided the wind speed is sufficiently high, the energy gained from crossing the wind-shear layer is sufficient to compensate for drag, sustaining flight for long periods without continuous flapping (Lissaman 2005, Sachs 2005, Richardson 2015, Bousquet et al. 2017). Theoretically, dynamic soaring is most efficient in crosswind flight and albatrosses largely avoid headwind flight (Spear & Ainley 1997a, Weimerskirch et al. 2000b, Wakefield et al. 2009a). Dynamic soaring albatrosses can make progress upwind by tacking like sailboats, alternating sequences of dynamic soaring cycles oriented to the left and to the right (Richardson 2015, Sachs 2016). However, in very strong winds, progress in the upwind direction is retarded by downwind advection (Richardson et al. 2018) as more tacking movements are needed to make forward movement relative to wind, causing tracks to be more meandering than in tailwind or crosswind flight (Sachs 2016) (see Section 4.10). Tagging studies have demonstrated that albatrosses increase their ground speeds with wind speed in tailwinds or crosswinds, and in headwinds, they show the fastest ground speeds when wind speeds are slower (Sachs 2016, Richardson et al. 2018). Albatrosses resort to upwind flight when maneuvering at fine scales to locate prey via olfaction (Nevitt et al. 2008), and particularly during breeding when birds need to return periodically to the colony (Suryan et al. 2008, Wakefield et al. 2009a, Thorne et al. 2016).

While best studied in albatrosses, dynamic soaring is also used frequently by other medium to large Procellariiform seabirds (Pennycuick 1982, Furness & Bryant 1996, Paiva et al. 2010, Ventura et al. 2020, Kempton et al. 2022) and these species also use cross- and tailwind flight more frequently than upwind flight (Paiva et al. 2010, Gibb et al. 2017, Richardson et al. 2018, Ventura et al. 2020, 2022), though gadfly petrels *Pterodroma* spp. use dynamic soaring primarily with quartering tailwinds (Spear & Ainley 1997a, Adams & Flora 2010, Campioni et al. 2023 in this Theme Section, Clay et al. 2023).

Kempton et al. (2022) note the challenge of proving empirically that birds gain energy from wind shear via dynamic soaring, because cyclical variation in mechanical energy — which is straightforward to demonstrate using high-resolution GPS data — can occur without extracting energy from wind. They showed that the phasing of undulations and horizontal turns of Manx shearwaters *Puffinus puffinus*, assessed using bird-borne cameras, were consistent with that expected during dynamic soaring, providing an objective technique for detecting dynamic soaring in other species.

3.2.3. Wave-slope soaring

Although it is suspected that seabirds use energy from ocean waves to facilitate efficient flight (Richardson 2011), very few studies have assessed this in detail. Wave-slope soaring birds are thought to reduce energetic expenditure by using updrafts associated with waves and their interaction with the wind (Wilson 1975, Pennycuick 1982, Blomqvist & Peterz 1984, Richardson 2011, Stokes & Lucas 2021). In its simplest conceptualization, this involves flying just ahead of a wave crest, gaining lift from the updraft caused by the rising water beneath (Fig. 4c) (Wilson 1975, Richardson 2011). Complexity is introduced when wind interacts with waves, with regions of uplift depending on wind speed and direction, wave size and period (Richardson 2011). Birds may be able to maximize the energy gained during wave-slope soaring by flying very close to the surface of the water, where the updraft is greatest (Richardson 2011). By soaring along the wave crest, birds can travel obliquely to the direction of wave propagation in this manner (Wilson 1975). Indeed, it is thought that brown pelicans *Pelecanus occidentalis* can travel long distances along coastlines (i.e. at right angles to the direction of wave propagation) by periodically crossing to the following wave using flapping flight (Stokes & Lucas 2021).

Wave-slope soaring could in theory be used in tandem with dynamic soaring (Withers 1979, Pennycuick 1982, Alerstam et al. 1993, Richardson 2011, Spivey et al. 2014). Indeed, species capable of wave-slope soaring may be adapted to particular wave as well as wind conditions (Suryan et al. 2008, Stokes & Lucas 2021). However, in typ-

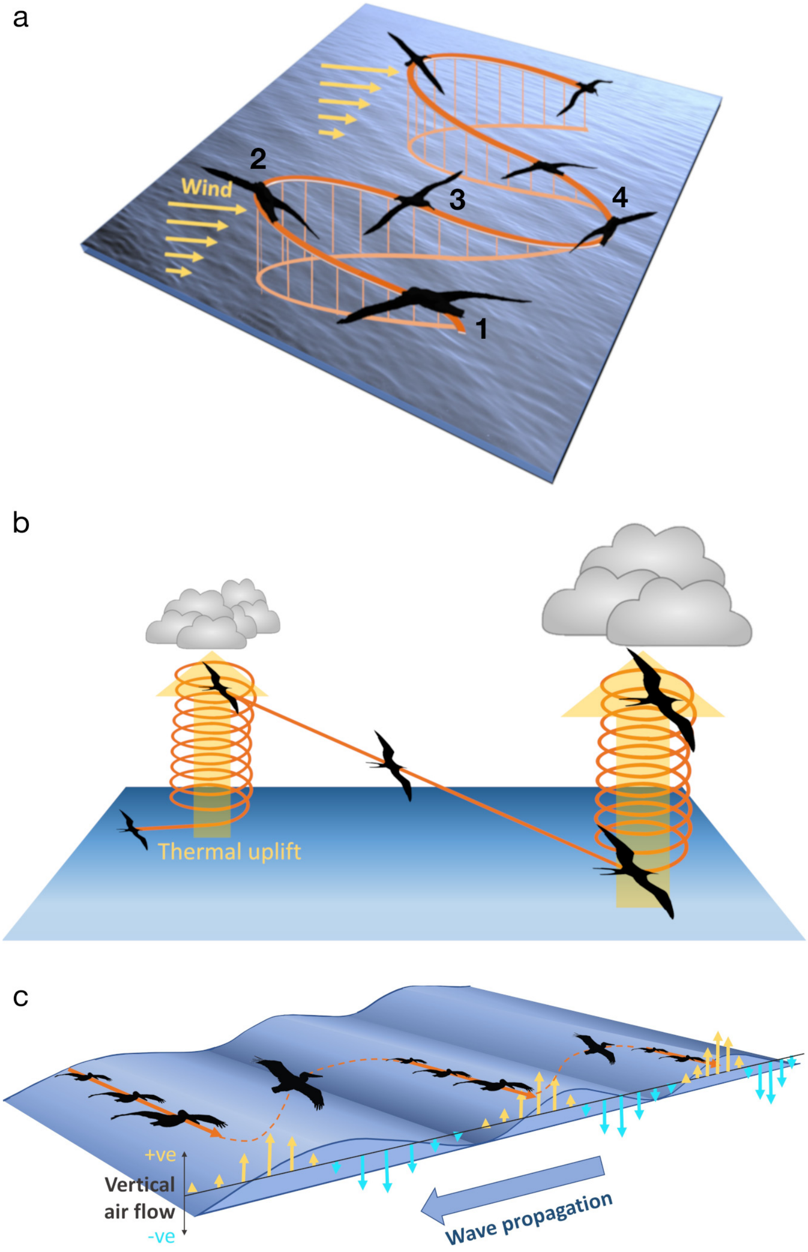


Fig. 4. Mechanisms by which seabirds use wind or rising air to sustain soaring flight. (a) The S-shaped flight trajectory of dynamic soaring relative to wind shear. At the lowest point of the dynamic soaring cycle, (1) birds turn into the wind, gaining airspeed, lift and potential energy. They continue to do so by rising though the shear layer. (2) They then execute a banked turn back downwind, before descending, converting potential to kinetic energy, but (3) also gaining additional airspeed by sinking through the shear layer. (4) They then turn back into the wind to repeat the cycle. (b) In thermal soaring, seabirds gain altitude by circling in warm rising air, often followed by sustained glides between thermals. In this example, a frigatebird uses thermals associated with convection under cumulus clouds. (c) In simple wave-slope soaring, seabirds fly alongside the leading edge of a wave, soaring on the updraft generated by the ascending wave crest. To make progress perpendicular to the direction of wave propagation (e.g. along a coastline), birds periodically cross onto the following wave. Wind interacting with waves (not illustrated) can give rise to complex patterns of wave-slope soaring (Richardson 2011)

ical conditions in the Southern Ocean, where most albatross species occur, dynamic soaring is estimated to provide 4–8 times more energy than wave-slope soaring (Richardson 2011). Theoretically, wave-slope soaring could be used by albatrosses in regions with large swell waves but no wind, and dynamic soaring in regions with high winds but small waves (e.g. in confined waters) (Richardson 2011).

The extent to which seabirds use wave-slope soaring during long foraging trips is unclear as studying fine-scale movements relative to waves remains challenging. Most descriptions of wave-slope soaring to date use direct observations (Pennycuick 1982, Richardson 2011, Stokes & Lucas 2021) rather than analyses of tag data. General wave characteristics can be assessed using reanalysis products (see Section 2.3), but individual waves or detailed characteristics of waves cannot be measured remotely across broad spatial scales, making it difficult to connect wide-ranging movement patterns of seabirds with waves, rather than wind.

3.2.4. Thermal and orographic soaring

Seabirds can take advantage of thermals to travel long distances without flapping (Hedenström 1993, Sage et al. 2022). When using *thermal soaring*, seabirds gain altitude from thermal uplift using distinctive circling flight, often alternating periods of altitude gain with sustained periods of gliding flight while losing altitude (Fig. 4b) (Pennycuick 1983, Hedenström 1993, Goto et al. 2022, Sage et al. 2022). This provides an energetically efficient, but slow, means of travel (Pennycuick 1987b). Uplift is greatest at the center of a thermal, and thus both a low sinking speed, which can be achieved with a low wing loading, and a small turn radius are ideal for thermal soaring (Pennycuick 1983, 2008, Goto et al. 2022). Frigatebirds can stay aloft for months at a time (Pennycuick 1983, Weimerskirch et al. 2016), alternating climbing within thermals to altitudes as high as 4000 m and gliding horizontally between them (Pennycuick 1983, Weimerskirch et al. 2003b, 2016). Large gulls *Larus* spp. and red-tailed tropicbirds *Phaethon rubricauda* also use thermals in this manner (Woodcock 1975, Shamoun-Baranes et al. 2016, Sage et al. 2022, Garde et al. 2023 in this Theme Section, van Erp et al. 2023 in this Theme Section). Convective conditions supportive of thermal soaring, including a thicker boundary, greater solar radiation (e.g. proximity to midday) and a greater temperature difference between the sea surface and the air, increase the probability of soaring (Shamoun-Baranes et al. 2016, Garde et al. 2023, van Erp et al. 2023). Red-tailed tropicbirds were also more likely to soar when flying with tailwinds, suggesting that the efficiency of thermal soaring is also influenced by wind (Garde et al. 2023).

Seabirds can also soar on *orographic uplift*—air rising as wind is deflected upwards over steep increases in topography (Pennycuick 1960, 1987b, Mehlum et al. 1988, Ainley et al. 2015, Sage et al. 2019, Mohamed et al. 2022), resulting in considerable energy savings (Sage et al. 2019, 2022). In coastal regions, artificial features such as buildings, raised roads and dikes can create sufficient orographic uplift to sustain soaring by gulls, potentially resulting in uplift corridors connecting habitat patches (Sage et al. 2019, 2022).

3.2.5. Sea-anchor soaring

Some Hydrobatidae storm petrels feed by *sea-anchor soaring*, also referred to as hovering or pattering. To do so, they face the wind, keeping their feet in contact with the water, soaring with outstretched wings, which is presumably less energetically expensive than hovering by flapping (Obst et al. 1987). Withers (1979) described this behavior as being analogous to a kite, where the feet dragging on the water counterbalance the aerodynamic drag produced by the bird facing into the wind. Use of this foraging behavior varies among species; those with low wing and low foot loading sea-anchor soar more frequently (Sausner et al. 2016). While theoretical studies have modeled the feasibility of this behavior relative to wind velocity and mechanisms of generating lift from the wings (Withers 1979, Sugimoto 1998), we are not aware of field studies that have verified how and under what wind conditions this behavior is used at sea.

3.3. Flight speeds with respect to wind

How seabirds vary their airspeed relative to wind is a fundamental component of flight behavior that is central to foraging, migration, and energetics (Shamoun-Baranes et al. 2007). Wind support may regularly match or exceed that of self-propulsion in seabirds (Liechti 2006, McLaren et al. 2014): mean wind speeds over the oceans are around 6 m s^{-1} overall, but 10 m s^{-1} in the windiest areas (Kållberg et al. 2005), where sustained speeds >20 m s^{-1} regularly occur (Yuan 2004), while airspeeds of seabirds range from approx. 7 to 20 m s^{-1} (Alerstam et al. 1993, 2007, Pennycuick 1997, Hedenström & Åkesson 2016, Howard et al. 2021). However, by varying their airspeed, seabirds can, to a certain extent, buffer the effects of wind, improving the efficiency of their movement (Shamoun-Baranes et al. 2007).

Optimal flight speeds of birds are likely influenced by a range of factors including motivation (e.g. whether searching for prey, commuting, migrating), central place constraint, and whether time, energy or both are limiting (Norberg 1981, Alerstam et al. 1993, Hedenström & Alerstam 1995, Spear & Ainley 1997b, Elliott & Gaston 2005, Wakefield et al. 2009a). Crucially, air and ground speeds also depend on wind speed and direction as well as on the flight mode of seabirds (Spear & Ainley 1997b, Richardson 2018). Broadly, seabirds have faster ground speeds in tailwinds, and ground speeds decrease when birds fly into headwinds (Spear & Ainley 1997b, Catry et al. 2004, Weimerskirch et al. 2005b, Dehnhard et al. 2021, Keys et al. 2023 in this Theme Section). Theoretical predictions show that the *maximum range speed*, the airspeed which maximizes energetic cost per unit distance, is higher in headwinds and lower in tailwinds (Pennycuick 1978). Accordingly, many studies have demonstrated that, regardless of flight mode, seabirds fly at higher airspeeds when flying into headwinds compared to tailwinds (Alerstam & Lindström 1990, Alerstam et al. 1993, Spear & Ainley 1997b). Recent studies have shown that flapping seabirds actively increase their airspeed in headwinds by increasing the strength of their wingbeats (Elliott et al. 2014, Kogure et al. 2016, McLaren et al. 2016), but this remains to be tested for soaring birds. This increase in airspeed can incur increased energetic costs for flapping birds (Elliott et al. 2014, Kogure et al. 2016). Species using flapping flight are thought to increase airspeeds to a lesser extent with increasing headwinds than those using soaring flight, since the energetic cost of flapping is high while the energetic expenditure of dynamic soaring is thought to be independent of airspeed (Pennycuick 1978, Alerstam et al. 1993). In contrast, flapping birds generally decrease airspeeds with stronger tailwinds (Pennycuick 1982, Hedenström et al. 2002; but see Mateos-Rodríguez & Bruderer 2012), whereas soaring species show no or minimal changes in airspeeds in response to stronger or weaker tailwinds (Spear & Ainley 1997b).

We note important considerations when comparing airspeeds of seabirds to wind speed. Firstly, wind and seabirds cannot simultaneously be observed at high spatiotemporal resolutions over long time periods, which limits our ability to understand how seabirds vary their airspeed in response to wind. By using *in situ* observations of wind speed and direction, early studies that estimated seabirds' airspeed from direct observations over short periods (e.g. Pennycuick 1982, 1987a, Spear & Ainley 1997b) may have provided more accurate estimates of wind at the time of the seabird observation. However, these observations provide only a brief snapshot of bird behavior in time. Tracking studies afford the opportunity to examine seabird airspeed relative to wind over long time periods, but rely on remotely sensed wind data which are limited in spatiotemporal resolution. Since airspeed is often calculated by subtracting the wind speed vector from the ground speed vector (Kogure et al. 2016, Collins et al. 2020), the resolution of wind data impacts both wind speed values and resulting airspeed estimates.

3.4. Biogeography

The global windscape is likely an important driver of seabird biogeography. Flight morphologies of seabird species are adapted to wind conditions in the regions they inhabit (Spear & Ainley 1998, Nourani et al. 2023), and wind patterns may limit the breeding ranges of some species (Suryan et al. 2008). Wind patterns vary considerably with latitude (Fig. 1) and are determinants of seabird distributions and community structure (Weimerskirch et al. 2000b, Smith & Hyrenbach D 2003, Davies et al. 2010). For example, Procellariiform seabirds are highly evolved to exploit strong winds, and most albatross species breed in regions that experience some of the greatest wind speeds and wave heights globally (Suryan et al. 2008). Available wind energy is likely an important determinant of species richness, although the mechanisms underlying this are unclear (Davies et al. 2010). It has been suggested that morphological specialization, particularly wing loading, is adaptive to particular wind and wave regimes and therefore geographical areas (Hertel & Ballance 1999, Suryan et al. 2008, Wakefield et al. 2009a, Clay et al. 2020, Nourani et al. 2023). Seabirds may use wind speed to gain lift when taking off (Kogure et al. 2016), and airspeeds and minimum take off speeds theoretically scale with wing loading (see Section 3.1.1). Thus, stronger winds may facilitate the high airspeeds and lift required for takeoff or sustained flight in birds with a higher wing loading, while birds with a lower wing loading would require less wind to take off or stay aloft (Shaffer et al. 2001, Suryan et al. 2008). Thus, species inhabiting windier regions, such as the Southern Ocean, should have higher wing loadings than those inhabiting the less windy tropical or subtropical oceans (Hertel & Ballance 1999, Shaffer et al. 2001, Suryan et al. 2008, Clay et al. 2020). Indeed, wing loading of 18 seabird species was positively associated with median wind speed in the vicinity of the colonies by Nourani et al. (2023). This study posited that higher airspeeds may also be advantageous in windier regions by allowing birds to counter wind drift. Spear & Ainley (1998) found that, in addition to having lower wing loading, tropical Procellariiformes also have larger tails than polar species, which may aid flight in light winds.

There is evidence that seabird distributions have shifted in recent decades concurrent with changes in wind speed and oceanographic conditions (Péron et al. 2010, Weimerskirch et al. 2012). Further research is required to assess links between wind regimes, morphological adaptation, and seabird distribution, and thereby understand how global wind patterns, both past and future, may influence seabird biogeography.

4. LINKING SEABIRD MORPHOLOGY, FLIGHT SPEED AND ROUTE OPTIMIZATION

In this section, we consider how movements at the mesoscale and larger, particularly of *pelagic seabirds* (i.e. those that inhabit the open ocean), are affected by and refined with respect to wind, comparing observations to theoretical predictions. In doing so, we develop a simple conceptual model of seabird movement with respect to wind. This serves as much to order disparate material and align it with existing theory as to generate testable predictions, and is not intended as an alternative to more advanced theory (Hedenström 2008, Alerstam 2011, Alerstam et al. 2019a). We concentrate on 2 types of movement: central-place foraging trips and migration. We define *central place foraging* as trips that repeatedly begin and end at a colony or roost (Orians & Pearson 1979). While *migration* also begins and ends at the colony, we distinguish it from central-place foraging here due to its greater spatiotemporal scale and seasonal synchrony. We use the term *route optimization* to include not only the choice of direction, but also when, how, how fast and sometimes how high to fly in response to wind and other constraints (Shamoun-Baranes et al. 2017).

While there has been extensive theoretical and empirical study of route optimization by *terrestrial birds* (i.e. non-seabirds), especially apropos of migration (Richardson 1990b, Berthold 2001, Liechti 2006, Nourani & Yamaguchi 2017, Shamoun-Baranes et al. 2017), seabirds have received less attention in this respect. Most literature on route optimization by seabirds is descriptive and due to technological limitations, biased towards large species during the breeding season, plus medium to large species during the non-breeding seasons (see brief reviews by Schneider 1991, Nourani & Yamaguchi 2017). Relatively little is known about smaller species and immatures (Rodríguez et al. 2019). We review existing theory and knowledge, as well as caveats in applying theory developed on terrestrial birds to seabirds, and describe the conceptual model.

4.1. Relevance of existing theory to seabirds

Although existing theory mainly concerns terrestrial bird migration (Alerstam et al. 2019a), much of it may also be applicable to seabirds, during both migration and central-place foraging, because (1) movement of seabirds during these periods is at a similar scale to that of many terrestrial bird migrations (1000s to 10 000s km) and therefore affected by the same meteorological phenomena, and (2) central-place foraging trips entail elements common to migration: a route, a goal, a period of time, and energy consumption (Alerstam & Lindström 1990, Liechti 2006, Schmaljohann et al. 2022). However, central-place foraging provisioning trips additionally involve transporting food, which affects flight performance and potentially, therefore, route choice (Houston 2006, Olsson & Bolin 2014, Alerstam et al. 2019a), and birds are more constrained during central-place foraging than migration (see Section 4.2). Moreover, seabirds differ from terrestrial birds in several key respects: (1) their prey are more widely dispersed (Schreiber & Burger 2002); (2) unless breeding, most avoid land and can alight at will, whereas many migrating terrestrial birds make extensive sea crossings during which they cannot alight (e.g. Gill et al. 2014). Seabirds are therefore less constrained in their stopover behavior, and *fly-and-forage* migration, involving frequent stops to feed (Strandberg & Alerstam 2007, Alerstam 2011), is much more common (Bonnet-Lebrun et al. 2021a); (3) dynamic soaring, virtually unknown among terrestrial birds (but see Richardson 2018), is highly efficient but restricts flight direction and performance relative to the wind direction (see

Section 4.3); (4) many terrestrial birds migrate at high altitudes to take advantage of favorable winds (Alerstam 1979, Shamoun-Baranes et al. 2017) whereas most seabirds remain within the *surface layer* (<100 m) while at sea (Krüger & Garthe 2001, Johnston et al. 2013, Cleasby et al. 2015, Ross-Smith et al. 2016); (5) seabirds live longer and have a lower fecundity than most terrestrial birds, meaning they should prioritize their own survival over that of their offspring and act more as energy- than time-minimizers (Weimerskirch 1992, Cornioley et al. 2016, Schmaljohann et al. 2022); (6) seabirds have a longer period of immaturity than most terrestrial birds, a trait which may allow them to learn more efficient movement strategies (Schreiber & Burger 2002); and (7) adult mortality is higher during migration among (migratory) land birds than seabirds (Sillett & Holmes 2002, Newton 2010, Klaassen et al. 2014).

4.2. Constraints and predictions

On departing a colony or roost, it can be assumed that a seabird's initial *goal* is one or more food patches (Olsson & Bolin 2014). For migrating birds, these comprise stopover or wintering areas (Schmaljohann et al. 2022b). Although the approximate location(s) of these patches may be informed by memory, public information, or genetic inheritance (Mettke-Hofmann & Gwinner 2003, Danchin et al. 2004, Liedvogel et al. 2011, Aikens et al. 2022), searching is usually required to locate them at fine scales (Weimerskirch 2007, Fauchald 2009). In contrast, it is generally assumed that the location of the ultimate goal of the trip, the colony, is well known (McLaren et al. 2016, Goto et al. 2017).

As a first approximation, it can be assumed that the degree of *constraint* on a seabird's movement (e.g. when, where, how, how far, or how fast to travel) is inverse to the time available to reach its goal while still maintaining fitness, including reproductive success (Olsson & Bolin 2014). All other things being equal, the maximum distance traveled from the colony during a central-place foraging or migration trip should be inversely proportional to this constraint (Matthiopoulos et al. 2022). Wind support (Fig. 3) may regularly match or exceed the bird's self-propulsion speed, in strong winds dramatically limiting possible routes (Liechti 2006, McLaren et al. 2014). Hence, slower birds should be more selective of the wind conditions under which they fly, following more circuitous routes and possibly be more selective of altitude, than faster birds (Fig. 5) (Alerstam 1978, Chapman et al. 2011). In most taxa, central-place constraint is greatest when birds are continuously brooding and/or guarding small chicks, and lower during other breeding stages (Shaffer et al. 2003). Constraint during migration is lower still, and inward migration is usually considered more time-constrained than outward migration due to competitive advantages of early arrival at breeding sites (Nilsson et al. 2013). Constraints on immature seabirds are poorly studied but are presumably lower still. Other route choice restrictions, such as con- and heterospecific attraction (Veit & Harrison 2017) or avoidance (Hipfner et al. 2012, Wakefield et al. 2013), are beyond the scope of this review but may be important.

Dynamic soaring imposes further constraints: firstly, birds using this mode of flight largely avoid headwinds (Spear & Ainley 1997a, Weimerskirch et al. 2000b, Wakefield et al. 2009b, Adams & Flora 2010, Ventura et al. 2022), except when very time-constrained or when undertaking fine-scale prey search or capture movements (Nevitt et al. 2008, Suryan et al. 2008, Wakefield et al. 2009b, Thorne et al. 2016). Dynamic soarers travelling to upwind goals, therefore, tend to follow circuitous routes (Gibb et al. 2017). Secondly, while flapping seabirds can reduce negative wind support by flying close to the surface (Krüger & Garthe 2001, McLaren et al. 2016), dynamic soaring necessitates repeatedly entering the upper wind shear layer, presumably resulting in downwind advection, which can be compensated for only at a cost to ground speed (Richardson et al. 2018). Hence, not only does wind modulate time and energy costs, making some locations more accessible than others, it does so differently for flapping and soaring seabirds (Fig. 5).

Our conceptual model posits that (1) flapping flight is adapted to shorter-ranging, time-minimizing strategies and flight in light or unpredictable winds; (2) dynamic and wave-slope soaring are adapted to longer-ranging, energy-minimizing strategies in stronger, supportive and more predictable winds; and (3) as time constraint increases or goal distance decreases, birds shift from energy- to time-minimization strategies. Flap-soarers have the morphological flexibility to use flapping or soaring flight, and therefore act in ways intermediate between these extremes.

Energy minimization strategies predicted by theory include taking more circuitous routes, with positive wind support (McLaren et al. 2014, Kranstauber et al. 2015) and more frequent feeding opportunities (Alerstam 2001); allowing, rather than compensating for, drift (Chapman et al. 2011); reducing airspeed in tail-

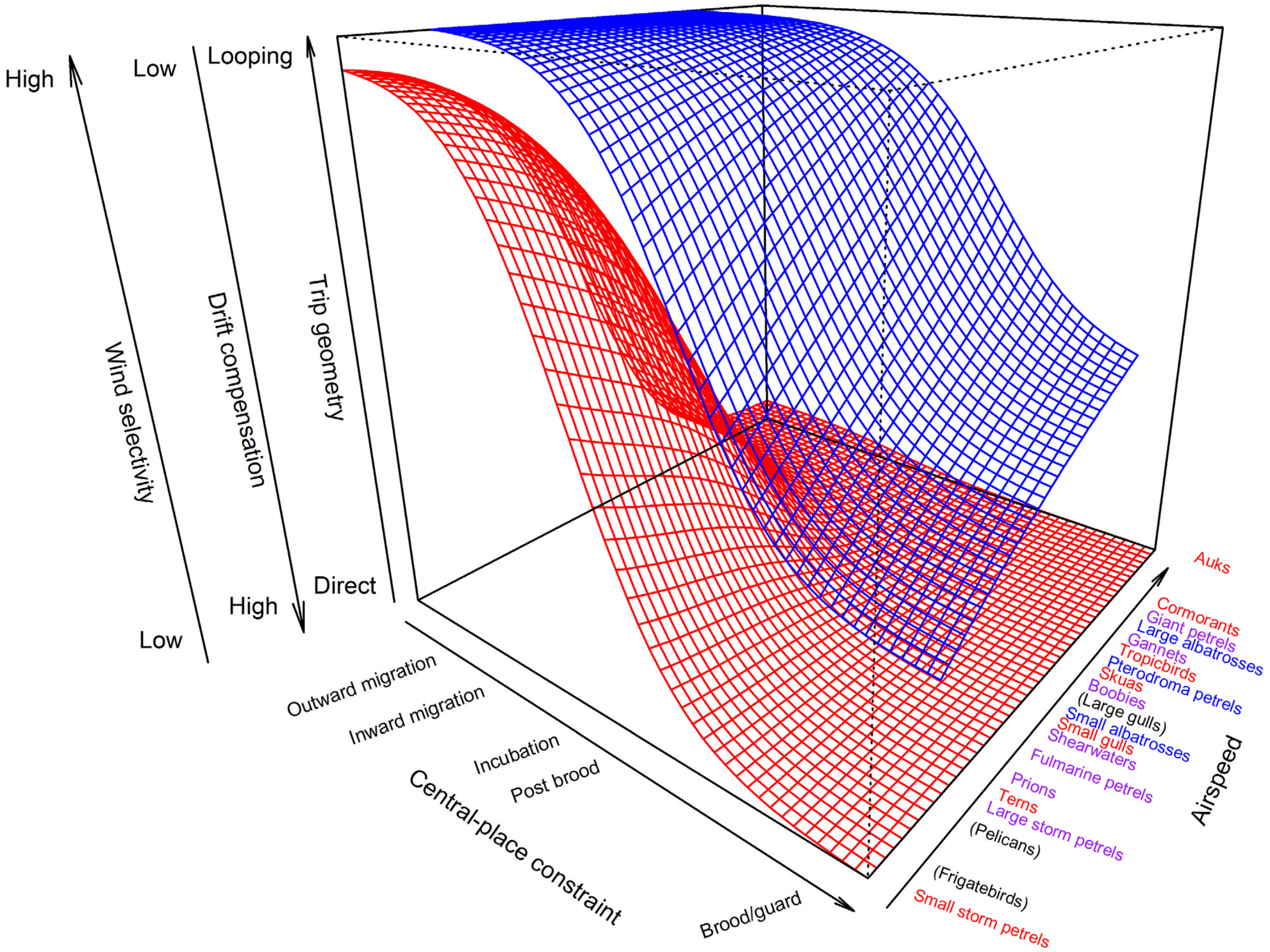


Fig. 5. Conceptual model of the relationship between seabird wind orientation optimization strategies (z-axis), flight mode, airspeed and central-place constraint. Trips beginning and ending at the colony, including migrations, range from direct, with high compensation for drift and low wind selectivity (time-minimizing) to looping, with high selection for wind conditions and less compensation for drift (energy-minimizing). The red and blue surfaces indicate hypothetical strategies expected in flapping and dynamic soaring flight, respectively. For most seabirds, central-place constraint (the inverse of the time available to make a round trip) is greatest during the brood/guard stage, and lowest during migration and other non-breeding periods. A bird's ability to counter negative wind support is limited by its airspeed, which is constrained by morphology. Morphology itself is adapted not only to wind conditions but also to foraging mode and other selective pressures, so although airspeed broadly scales with size, diving seabirds have proportionately shorter wings and therefore higher airspeeds than similarly-sized surface feeders (Pennycuick 1987b). Under most degrees of constraint, obligate flappers (taxa colored red) are expected to compensate for drift more, be less wind-selective, and follow more direct routes than dynamic soarers. When weakly constrained, it should also be energetically advantageous for flappers with low airspeeds to compensate for drift less and reduce negative wind support by taking more circuitous routes and being more wind-selective. Dynamic soaring is most energetically efficient in crosswind to tailwind flight, so dynamic soarers (blue) should follow a similar strategy under most degrees of constraint. When constraint is high, however, they may resort to flap-soaring along more direct routes. Flap-soarers (purple) employ strategies intermediate between the red and blue surfaces, depending on wind conditions, for example, flapping when winds are light or contrary. Frigatebirds and pelicans (black) use thermal- and wave-slope soaring, respectively, so are likely to behave more like dynamic soarers than flappers. Large gulls use a wide variety of soaring and flapping techniques so their response to wind is more flexible (Shamoun-Baranes et al. 2016). Relative positions of taxa on the airspeed-axis are based on observed, rather than theoretical, airspeeds (Alerstam et al. 1993, 2007, Pennycuick 1997, Spear & Ainley 1997b, Hedenström & Åkesson 2016, Howard et al. 2021), assuming the same (nominal) wind speed across taxa. Note that increasing or decreasing the wind speed would shift taxa to the left or right on this axis. For a biomechanical explanation of why soaring seabirds have a narrower range of airspeeds than flapping seabirds, see Pennycuick (1987b)

winds (Alerstam & Lindström 1990); and being more selective of when and in which direction to fly with respect to wind (Liechti 1995, McCabe et al. 2018). Time-minimization entails the opposite traits (Anderson et al. 2020). In the following sections, we review if and how seabirds conform to these expectations.

4.3. Goal selection with respect to wind

Before considering how wind affects route choice, we consider whether it affects goal choice. Most fundamentally, breeding sites that afford easier access to food, contingent on prevailing wind conditions, may be preferred (Pennycuick 1989). This hypothesis has not been tested (but see Lempidakis et al. 2022a), and any effect of wind would have to be large to outweigh the effects of prey distribution. At the level of central-place foraging trips, some shearwaters select further foraging locations when wind support is positive (De Pascalis et al. 2020, Afán et al. 2021) but this is not so for breeding fulmarine petrels in Antarctica (Dehnhard et al. 2021). It has also been hypothesized that due to mass gain while central-place foraging, upwind or crosswind destinations are less costly to access than downwind locations, with this effect increasing with wind speed (Pennycuick et al. 1984, Pennycuick 1989, Alerstam et al. 2019a). Although frequently alluded to, this hypothesis has not been tested robustly and anecdotal support is mixed: for example, among central-place foraging sulids (flappers/flap-soarers), different populations forage predominantly upwind (Grémillet et al. 2004, Weimerskirch et al. 2008), downwind (Young et al. 2010, Amélineau et al. 2014, Lane et al. 2019) or with no wind bias (Weimerskirch et al. 2005a, Kappes et al. 2011). In the case of birds in simple gliding flight, mass gain due to foraging would increase airspeed during the return leg but the effects of load carrying on dynamic soaring flight remain poorly understood, so it is unclear how this hypothesis pertains in this scenario (Alerstam et al. 2019a). Moreover, there are examples of breeding dynamic soarers predominantly foraging either upwind (Wakefield et al. 2009b, Dehnhard et al. 2021) or downwind (Navarro & González-Solís 2009, Raymond et al. 2010) of their colonies. There is some evidence that on outward central-place foraging flights, dynamic soaring shearwaters preferentially fly crosswind, but it is unclear if this affects goal selection (Gibb et al. 2017, Kempton et al. 2022). Most migratory seabirds exhibit little individual variation in their wintering locations (Phillips et al. 2005, van Bemmelen et al. 2017, Franklin et al. 2022b) but there is circumstantial evidence that albatross and large petrels select wintering areas most accessible from their colonies (Revell & Somveille 2017, Frankish et al. 2020, Somveille et al. 2020). A few species, such as Cory's shearwaters *Calonectris borealis*, regularly switch wintering locations between years (Dias et al. 2011), but this is not thought to be due to variation in wind conditions (Dell'Ariccia et al. 2018).

4.4. Selecting when to fly in response to wind conditions

Having selected a goal, birds can reduce energetic costs by selecting to fly during periods with more favorable wind support (Åkesson & Hedenström 2000, Alerstam 2011). However, waiting costs time, so it is efficient to be selective only if the onset of favorable winds is predictable and likely to occur within a tolerable period (McCabe et al. 2018). Seabirds do not conform well to the typical terrestrial bird migration paradigm due to their ability to alight at will on the sea and forage more frequently (Bonnet-Lebrun et al. 2021a).

Migratory schedules of seabirds are usually highly consistent both within and among individuals, but departure timing is more variable post-breeding than post-wintering (Franklin et al. 2022a), so seabirds may have more flexibility to synchronize post-breeding migrations with favorable winds. Indeed, most reports of pelagic seabirds selecting when to fly in response to wind conditions are from post-breeders. For example, Cory's shearwaters have been found to time movements with periods of favorable wind support (Felicísimo et al. 2008), whereas Manx shearwaters tend to pause migration when they encounter transient negative wind support, likely also to allow self-provisioning (Guilford et al. 2009). Non-breeding northern fulmars *Fulmarus glacialis* are more likely to remain at the colony when winds are light and flight costs are higher (Furness & Bryant 1996), and newly fledged wandering albatrosses wait for favorable winds before beginning their first long-distance flight to the subtropical convergence (Weimerskirch et al. 2006). Having departed, migrating albatrosses (and presumably other soaring seabirds) select when to halt or continue flight in response to wind conditions encountered en route (see Section 4.3).

The hypothesis that central-place foraging (i.e. more time-constrained) seabirds should be less selective in timing movements than migrants has not, to our knowledge, been tested. There are examples of central-place foraging seabirds selecting when to fly in response to wind: Antarctic-breeding fulmarine petrels time colony return trips to avoid contrary offshore katabatic winds (Dehnhard et al. 2021) and breeding wandering albatrosses remain on the water in very light winds (Jouventin & Weimerskirch 1990, Clay et al. 2020). In contrast, breeding black-legged kittiwakes *Rissa tridactyla* are not selective about the wind conditions they fly in (Collins et al. 2020).

4.5. Drift and compensation

The rate at which a seabird makes progress towards its goal results from the sum of wind support and the component of its airspeed along a beeline to that goal (Fig. 3). In particular, airspeed relative to local wind speed is limiting. If the wind is aligned other than towards the bird's goal, the bird will *drift* to the left or right of a beeline to that goal unless it *compensates* by altering its heading or speed or altitude (Alerstam 1979). The responses of migrating terrestrial birds to drift have been studied extensively (Liechti 1995, Alerstam 2011, McLaren et al. 2014). They range from *full drift* (i.e. no compensation), through *partial*, to *full compensation* (Table 1) (Chapman et al. 2011).

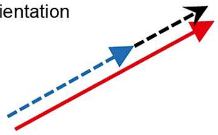
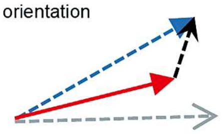
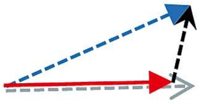
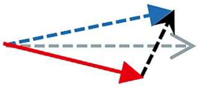
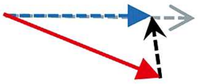
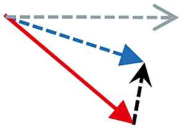
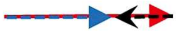
Wind conditions and a bird's flight, sensory and cognitive capabilities limit which strategies can be employed in particular circumstances (Nathan et al. 2008, Alerstam 2011, McLaren et al. 2014, Shamoun-Baranes et al. 2017). In particular, airspeed relative to local wind speed is limiting. If wind speed exceeds airspeed, the range of directions in which a bird can make headway and the extent to which it can counter drift is severely curtailed, even to the extent that goal arrival via full compensation or goal orientation becomes impossible (Alerstam 1978, Chapman et al. 2011, McLaren et al. 2014) unless airspeed can be increased (Liechti 1995, McLaren et al. 2016; see our Section 3.3). Dynamic soarers are more limited in their ability to modulate their airspeed relative to wind (Weimerskirch et al. 2000b, Sachs 2016). This is in part because the source of motive power is the wind itself, whereas in flapping birds it is independent of wind. However, observed maximum airspeeds of dynamic soaring albatrosses are considerably lower than those predicted by theory and achieved by equivalently sized model gliders (Richardson & Wakefield 2022). The reasons for this remain unclear, but it is hypothesized to be because the wings of albatrosses are not strong enough to sustain the forces associated with dynamic soaring at higher airspeeds (Richardson et al. 2018, Richardson & Wakefield 2022). Given these limitations, we anticipate that birds that rely largely on dynamic soaring are also limited in their ability to compensate directly for drift (Fig. 5). Flapping birds with low maximum airspeeds (relative to local wind speed) will also be limited in this respect, whereas fast flappers should have more flexibility to compensate for drift, allowing them to make more direct trips in strong or variable winds. However, while increasing airspeed reduces flight time, it also increases energetic expenditure (Pennycuick 2008), which may, in part, explain why larger flapping seabirds are shorter-ranging than smaller ones (Watanabe 2016).

The degree of compensation for drift should depend on time constraint and the nature of the goal — it should be greater when approaching the colony (a point location) than when goals are broader, such as with wintering areas or food patches (Alerstam 2011, Tarroux et al. 2016). There have been few studies of drift compensation by seabirds (Table 1), perhaps because assessing drift, and therefore inferring what strategy is being used, is difficult if the bird's goal and preferred direction of movement is unknown (Green & Alerstam 2002, Shamoun-Baranes et al. 2007). A simplifying assumption during return journeys is that the goal is the colony (McLaren et al. 2016, Goto et al. 2017). Consistent with theoretical predictions for migrants, studies showed that central-place foraging *Calonectris* shearwaters, lesser black-backed gulls *Larus fuscus* and Antarctic petrels *Thalassoica antarctica*, all compensated increasingly for drift as they approached their colonies on return legs (Navarro & González-Solís 2009, Tarroux et al. 2016, Goto et al. 2017). The latter were also thought to undergo drift on outward trips, although their goals were unclear (Tarroux et al. 2016).

Strategies that allow drift imply either the ability to remember drift and compensate for it later (Liechti 2006), or true navigation (the ability to return to a known goal from a place they have never visited before; Holland 2014). The mechanisms of avian navigation are still much under debate (Alerstam 2006, Holland 2014, Guilford & de Perera 2017) but it seems likely that adult Procellariiformes at least are capable of true navigation (Gagliardo et al. 2013, Goto et al. 2017, Padget et al. 2017, 2019). Compensation also requires the ability to orient and sense drift, directly or indirectly (Alerstam 2011, Chapman et al. 2011). For example, streaked shearwaters *C. leucomelas* were able to compensate for drift over the open ocean, possibly via a map sense or reference to wave patterns (Alerstam & Pettersson 1976), but compensation was complete only when birds were in sight of land (Goto et al. 2017). Similarly, Antarctic petrels drifted extensively when crossing featureless land, implying that visual cues are necessary to assess drift (Tarroux et al. 2016). Tracking of immature seabirds suggests that, as with land birds (Alerstam 2011), orientation is innate but compensation is learned early in life (Yoda et al. 2017, Wynn et al. 2020).

An alternative way of reaching distant goals for birds whose flight style or airspeed limits their ability

Table 1. Orientation strategies in response to wind drift recognized by Chapman et al. (2011) with examples in seabirds. In some cases, the goal of the bird was unknown, so it is unclear if these represent true strategies or proximate consequences of other behaviors. Vectors (redrawn from Chapman et al. 2011) represent the bird's heading and airspeed (red), the wind speed and direction (black), and the bird's track and ground speed (blue). Grey arrow indicates the direction of the bird's goal, not a vector

Strategy	Comments and seabird examples
1. Passive downstream transport 	Seabirds resting on the water, sea ice or floating detritus are advected downstream (e.g. Sánchez-Román et al. 2019). Frigatebirds soar in thermals, which are themselves advected downwind (Weimerskirch et al. 2016).
2. Active downstream orientation 	Incubating Cory's shearwaters from the Canaries in the NE trade winds fly downwind while foraging (Navarro & Gonzalez-Solis 2009). Northward migrating sooty shearwaters in the Pacific and Atlantic initially head eastwards downstream in order to gain positive support from the SE trade winds further along their route (Shaffer et al. 2006, Hedd et al. 2012).
3. Overdrift or compass-biased downstream orientation 	Could be used early in a journey to divert to areas of positive wind support or avoid areas of negative wind support further ahead (Vansteelant et al. 2017).
4. Full drift 	Some recently fledged seabirds undergo full drift (Yoda et al. 2017, Wynn et al. 2020). Adaptive drift involves using full or partial drift early in journeys, increasingly replacing this with full compensation as the goal is approached (Alerstam 2011). Full drift could also be used by seabirds not constrained to return to a central place if their aim is only to search for prey via olfaction, which is most efficient crossflow (Nevitt et al. 2008). If heading is constantly adjusted to match the goal direction, full drift results in *goal orientation* (McLaren et al. 2014).
5. Partial compensation/ partial drift 	Used by central-place foraging streaked shearwaters returning to their colony when out of sight of land (Goto et al. 2017).
6. Complete compensation 	Could be used late in trips, during *adaptive drift* (Alerstam 2011). Used by central-place foraging streaked shearwaters returning to their colony when within sight of land (Goto et al. 2017). Used by Arctic terns during coastal and possibly sometimes oceanic migration (Hedenström & Åkesson 2016, Redfern & Bevan 2022).
7. Overcompensation 	Could be used early in a journey to divert to areas of positive wind support or avoid areas of negative wind support further ahead (Vansteelant et al. 2017). Used by Arctic terns during coastal migration (Hedenström & Åkesson 2016).
Upstream orientation 	Used by seabirds when taking off (e.g. Clay et al. 2020), albatrosses searching by olfaction (Nevitt et al. 2008) and gannets and terns (Wakeling & Hodgson 1992, Lane et al. 2019) when foraging. Birds locating colonies or prey via olfaction may approach them upwind (Vickers 2000, Gagliardo et al. 2013, Reynolds et al. 2015).

to compensate for drift directly is to follow routes that are more circuitous but provide positive wind support (McLaren et al. 2014). Finding the most optimal of such routes is a complex task, analogous to 'Zermelo's problem', which was classically posed as that of what course a boat should follow to cross a shear flow in the least time (Zermelo 1931). Surprisingly, only the correct initial departure heading, which can be found via optimal control theory, is required to solve this problem (Techy 2011, Jardin & Bryson

2012). For example, a bird moving perpendicular to wind shearing from weak to strong flow (e.g. flying from the doldrums to the mid-latitude westerlies), should initially overcompensate for drift by turning upwind of a beeline to the goal, thus reducing compensation required when stronger winds are encountered further on the journey (McLaren et al. 2014). Optimal control theory has been used to study optimal orientation in birds and turtles (Hays et al. 2014, McLaren et al. 2014, Pinti et al. 2020) but not yet in pelagic seabirds. Its application to this group could be very informative because it can predict optimal routes through relatively complex wind fields (Techy 2011, McLaren et al. 2014). Rather, simple anisotropic (i.e. direction-dependent) cost functions have been used to estimate least cost paths for migratory and central-place foraging seabirds (Felicísimo et al. 2008, González-Solís et al. 2009, Raymond et al. 2010). *Least-cost paths* describe the most efficient route from one location to another, and incorporate landscape costs of movement as well as distance traveled (Etherington 2016). It is unclear whether these paths are truly optimal because cost is defined and calculated in a somewhat ad hoc manner, but the approach is relatively straightforward to implement and has proved informative. For example, paths followed by shearwaters (*Ardenna, Calonectris* and *Puffinus* spp.) during transequatorial migrations were very similar to putative least cost paths, despite being 25–50% longer than great circle (i.e. shortest) routes (Felicísimo et al. 2008, González-Solís et al. 2009). Another simple approach is to compare the observed travel time to that that it would take to travel along tracks randomized by inversion, rotation, reshuffling of segments, or varying departure date. Using this method, Ventura et al. (2020, 2022), showed that central-place foraging trips by Desertas petrels *Pterodroma deserta* and Bulwer's petrels *Bulweria bulwerii* are more time efficient than randomly perturbed trips.

4.6. Altitude selection

Although flying seabirds are confined mostly to the surface layer of the atmosphere, they tend to fly at higher altitudes with supporting winds and vice versa (Krüger et al. 2016, McLaren et al. 2016, Shamoun-Baranes et al. 2017, Kumagai et al. 2023 in this Theme Section). Additionally, dynamic soarers reach greater heights in windy conditions than flappers (Richardson 2011, Sachs et al. 2013, Ainley et al. 2015) and species that use the ground effect, wherein lift is increased and drag is reduced close to the ground (e.g. skimmers *Rynchops* spp. and probably many other taxa), fly very low in light winds (Withers & Timko 1977, Rosén & Hedenström 2001). In contrast, frigatebirds and large gulls regularly travel hundreds to thousands of meters above sea level when thermal soaring (McLaren et al. 2016, Weimerskirch et al. 2016, van Erp et al. 2023), and some otherwise low flying species travel at similar heights when crossing land on migration or en route to and from their breeding sites (Duffy et al. 2013, McLaren et al. 2016, Tarroux et al. 2016, Redfern & Bevan 2022). Great frigatebirds typically fly between 30 and 600–700 m above sea level, alternating between soaring within and gliding between thermals (Weimerskirch et al. 2016).

Wind speed and direction vary with altitude, so theory predicts that these higher-flying species should select altitudes with the most favorable wind support, if necessary tolerating drift at higher altitudes, and correcting it at lower ones as their goal is approached (Alerstam 1979). This hypothesis is well supported in terrestrial birds (Shamoun-Baranes et al. 2017) but has only been explored in 2 seabird species. Studies showed that the choice of altitude with respect to wind for breeding Antarctic petrels was complex, apparently involving a trade-off between wind support and drift (Tarroux et al. 2016). In stronger winds, they commuted at low altitude, resulting in appreciable drift. Otherwise, they selected higher altitudes, with more favorable support. Lesser black-backed gulls returning to their colony used a combination of soaring and high-altitude tailwinds, broadly conforming to the altitude selectivity hypothesis (McLaren et al. 2016). At a finer vertical scale, theory predicts that birds travelling in the wind shear layer should travel closer to the surface when their goal is upwind and vice versa (Alerstam et al. 2019a). Indeed, the ability to reduce negative wind support by flying close to the surface may be crucial in allowing small species, such as storm petrels, to inhabit windy areas like the Southern Ocean.

Given that many other seabirds increase height when approaching and leaving colonies (Pennycuick 1987b), altitude selectivity may play a wider role in seabird route optimization, especially during breeding, when time is limited (Alerstam et al. 2019a). Understanding these and other wind-related effects on flight height has gained a new imperative recently because flight height is a key determinant of the risk posed to seabirds of collision with offshore windfarms, which are proliferating (Dierschke et al. 2016, Best & Halpin 2019, Croll et al. 2022).

4.7. Topographic effects

Pelagic seabirds spend most of their time away from land, but many travel along coastlines and over land en route to and from their goals (Duffy et al. 2013, Tarroux et al. 2016, Gutowsky et al. 2021, Lane et al. 2021). During these periods, orographic effects may influence route optimization. Seabirds traveling parallel to coastlines move closer inshore when encountering headwinds and further out in tailwinds, presumably due to shear reducing wind speed in proximity to the coastline (Mateos & Arroyo 2011, Wakefield et al. 2019). When over or in proximity to land, some species soar on thermals or orographic uplift (Pennycuick 1987b, Shamoun-Baranes et al. 2016). These effects could modulate foraging or migration route choice, making coastal routes more or less efficient. However, seabirds may also follow coastlines as navigational cues (Goto et al. 2017) or simply because they act as barriers en route to a goal (Padget et al. 2019). Separating these effects from those of orographic wind effects on route choice is difficult (Alerstam 1978) and has not, to our knowledge, been attempted for pelagic seabirds.

4.8. Selecting how to fly: flapping vs. soaring

For the purposes of our conceptual model (Fig. 5), we assume that seabirds that are capable of flapping or soaring can improve orientation efficiency by using flapping flight in light or contrary winds or when very time-constrained. Conversely, they can switch to soaring flight in stronger, supportive winds, and during less constrained periods. Presumably, while flexibility in flight mode buffers against variability in wind conditions, it also imposes costs in scenarios where purely soaring or flapping flight would be more efficient. Since dynamic soarers can switch to wave-slope soaring in light winds (Suryan et al. 2008, Spivey et al. 2014; see our Section 3.2.3), wave conditions could also affect route choice.

4.9. Movement with respect to synoptic scale weather systems and storms

Winds associated with mid-latitude synoptic-scale pressure systems and fronts follow predictable patterns (see Section 2.1). Seabirds should therefore be able to reduce energetic, and potentially time, costs by routing appropriately around these systems (Blomqvist & Peterz 1984, Richardson 1990b, McLaren et al. 2014). This indeed seems to be the case, at least for large dynamic soarers and small migrating flappers. Albatrosses, shearwaters and *Pterodroma* spp. have all been observed adjusting their courses in response to changing wind conditions in order to maintain positive flow support (Weimerskirch et al. 1993, Reinke et al. 1998, Adams & Flora 2010). For example, in the southern hemisphere, high pressure anticyclones are slow moving with light, counterclockwise winds, while low pressure cyclones have more rapid clockwise flow (the situation is mirrored in the northern hemisphere). Wandering albatrosses migrating west across the Indian Ocean from Western Australia to Crozet, against the prevailing mid-latitude westerlies, exploit these patterns by diverting north to gain positive support from cyclones and south to do so from anticyclones (Murray et al. 2003a,b). Similarly, migrating Arctic terns *Sterna paradisaea* are thought to use the eastern limbs of cyclones to cross the Southern Ocean rapidly north to south (Alerstam et al. 2019b). However, light wind associated with the centers of anticyclones can also delay dynamic soarers, so albatrosses may try to avoid becoming trapped within these regions (Jouventin & Weimerskirch 1990, Spruzen & Woehler 2002). There is some evidence that central-place foraging albatrosses and shearwaters use similar strategies (Catry et al. 2004, Weimerskirch et al. 2012, Afán et al. 2021), but surprisingly little attention has been paid to the response of breeding seabirds to synoptic scale weather systems (Adams & Flora 2010). There is currently no evidence to assess the hypothesis that flappers are less selective than soarers with respect to synoptic scale weather patterns.

Very strong winds can cause mortality via physical injury or displacement inland (Hass et al. 2012, Weimerskirch & Prudor 2019, Thiebot et al. 2020). Response to storms varies among and within species (Nourani et al. 2023). For example, brown pelicans, juvenile great frigatebirds and red-footed boobies *Sula sula* avoided the strongest winds associated with tropical cyclones by remaining ashore (Weimerskirch & Prudor 2019, Wilkinson et al. 2019), whereas adult great frigatebirds and black-naped terns *Sterna sumatrana* did so by flying around the cyclone's edge (Weimerskirch & Prudor 2019, Thiebot et al. 2020). Nourani et al. (2023) observed that Atlantic yellow-nosed *Thalassarche chlororhynchos* and wandering albatrosses avoided high winds associated with intense mid-latitude cyclones by flying towards the systems' centers, but 16 other species in this study showed no avoidance of high winds. Breeding streaked shearwaters circumnavigated tropical cyclones when they could, but flew toward the eye of the storm when they were sandwiched between land and the storm (Lempidakis et al. 2022b). They also flew away from land as wind speed increased. The effect of storms on seabird route choice beyond episodic instances is unknown, but it is possible that certain areas or periods are avoided. However, storm avoidance costs time and energy, and may displace birds into areas with unfavorable foraging conditions (Clairbaux et al. 2021). Conceivably, the tradeoff between these costs and the advantages of storm avoidance might shift depending on other constraints. For example, seabirds could be less storm-avoidant during breeding, though since seabirds are strongly *K*-selected, they are unlikely to risk very dangerous conditions for the sake of their offspring.

4.10. Looping vs. direct trip geometry

We now consider the relationship between the overall geometry of trips, flight modes, and wind. We expect the strategies reviewed above to give rise to trips on a spectrum ranging from *direct* (following the same path out and back between the colony and the goal) to *looping* (following a circuitous and different path out and back; Fig. 6). Hereafter, we use the terms direct and looping to refer to trips lying towards one or other end (rather than the extremes) of this spectrum. Terrestrial bird migration theory generally assumes that looping trips result from either a reliance on positive wind support or from birds using different stopovers on the outward and return legs (Elkins 2004, Schmaljohann et al. 2022), with more evidence in support of the former (Shamoun-Baranes

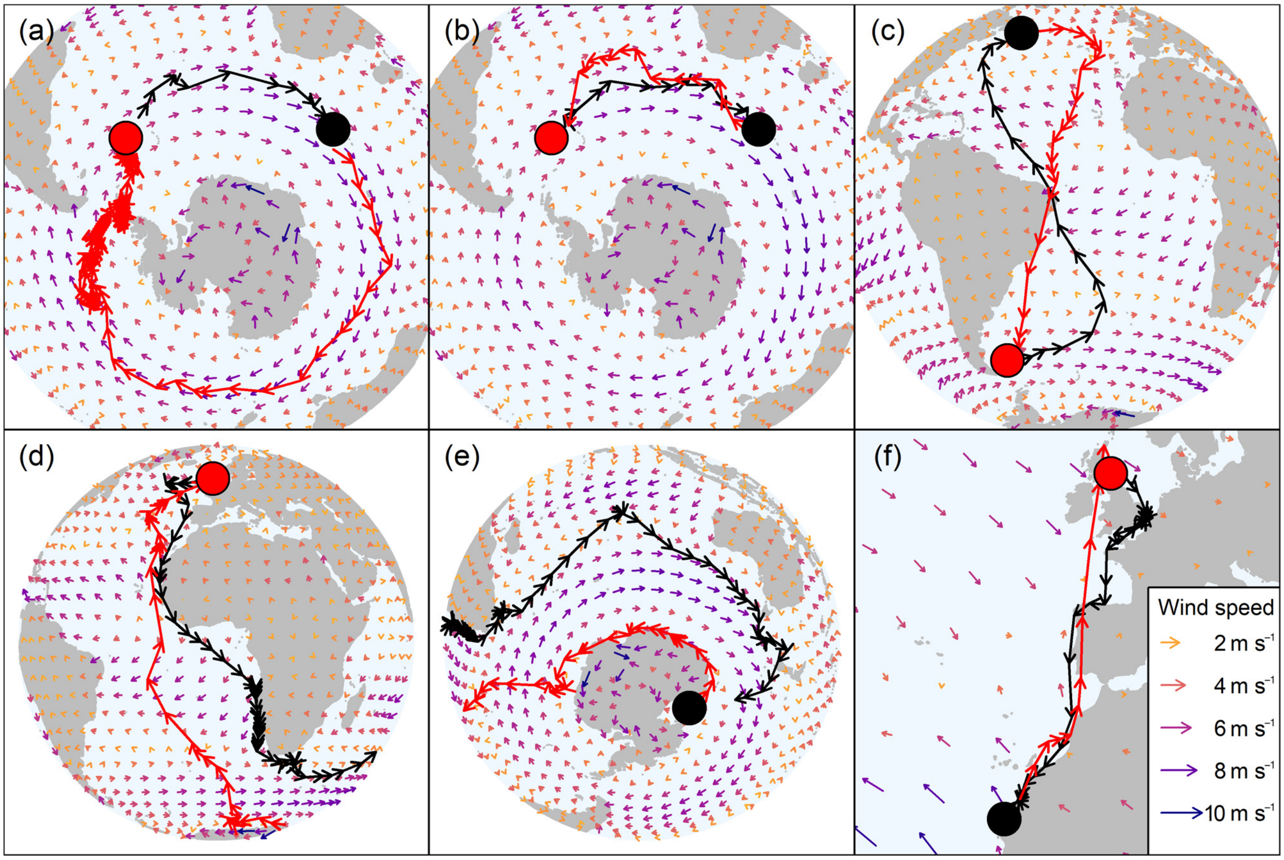


Fig. 6. Examples of migratory paths relative to wind followed individual seabirds: (a) long annular or (b) shorter, direct zonal migrations are undertaken by grey-headed albatrosses (fast dynamic soarers); (c) long looping meridional migrations by sooty shearwaters (fast flap-soarers); (d–e) looping meridional/zonal migrations by Arctic terns (slow flappers); and (f) shorter, direct meridional migrations by northern gannets (fast flappers). Black and red arrows: daily post-breeding and return migratory movement, respectively; red and black dots: breeding and wintering locations; gridded arrows: estimates of wind speed at 10 m above the surface averaged across each individual's period of movement (ERA5 data in Hersbach et al. 2020; downloaded from the Copernicus Climate Change Service [C3S] Climate Data Store). Outward northern gannet migration was GPS-tracked (J. W. E. Jeglinski unpubl. data). All other bird stages were tracked via light-based geolocation (Croxall et al. 2005, Grecian et al. 2019, Redfern & Bevan 2022, E. D. Wakefield unpubl. data)

et al. 2017). In the case of seabirds, wind has also largely been assumed to explain looping migration (e.g. Kuroda 1957, Shaffer et al. 2006, Felicísimo et al. 2008) but for central-place foraging trips, the hypothesis that trip geometry is dependent on resource distribution has received more attention: Weimerskirch (2007) argued that direct and looping trips are adapted to predictable and unpredictable prey distributions, respectively. Here, we assume that trip geometry is adapted to both food distribution *and* wind conditions (Pennycuick 1987b, Nathan et al. 2008). In short, direct and looping trips should arise when time and energy are optimized, respectively (Fig. 5).

First, we consider trips made by soaring seabirds. In strong and persistent mid-latitude westerlies of the Southern Ocean (Fig. 1), movements of dynamic soaring albatross are most obviously affected by wind, with migrations primarily being in the zonal direction. For example, both wandering and grey-headed albatrosses *Thalassarche chrysostoma* undertake zonal migrations, moving eastwards with positive wind support and eventually returning to the colony by circumnavigating the globe (Dixon 1932) or returning westward along more-or-less the reverse track (Fig. 6a,b) (Nicholls et al. 1995, Croxall et al. 2005, Phillips et al. 2005, Landers et al. 2011, Weimerskirch et al. 2015). As described in the previous subsection, positive support can be maintained during the return leg through the selective use of synoptic scale pressure systems (Murray et al. 2003a,b). Albatrosses also generally take looping trips during relatively unconstrained central-place foraging stages (Weimerskirch 2007, Suryan et al. 2008), traveling clockwise or counterclockwise, depending on the destination, to follow prevailing wind patterns (Weimerskirch et al. 2000b). When very time-constrained, or when foraging close to their colonies, most albatrosses make more direct trips, sometimes with negative wind support (Wakefield et al. 2009a, Thorne et al. 2016). *Pterodroma* petrels also proceed predominantly via dynamic soaring (Spear & Ainley 1997b) and mainly undertake looping trips with positive wind support, both during migration and central-place foraging (Adams & Flora 2010, Pinet et al. 2011, Clay et al. 2019, 2023, Ventura et al. 2020, Campioni et al. 2023). Frigatebirds rely on thermal soaring. Sometimes, especially during chick-rearing, they make short (<72 h), relatively direct trips from the colony (Weimerskirch et al. 2004). However, during incubation and non-breeding, when they are less constrained, they make looping trips, which during non-breeding can have diameters of approx. 2000–5000 km (Weimerskirch et al. 2004, 2016).

Next, we consider flap-soarers, which includes most medium-sized Procellariiformes (Spear & Ainley 1997b). During the non-breeding period, many shearwaters (*Ardenna*, *Calonectris* and *Puffinus* spp.) use positive support from prevailing winds to make looping or 'figure of eight' migrations around and between ocean basins (Fig. 6c) (Shaffer et al. 2006, Felicísimo et al. 2008, Guilford et al. 2009, Hedd et al. 2012). These paths may be adapted to food distribution as well as wind. Consistent with predictions for optimal orientation in complex flows (Riley et al. 1999, Techy 2011, McLaren et al. 2014), departure and goal directions often differ widely, suggesting initial diversion from the preferred direction of movement in order to gain positive support further ahead. For example, post-breeding, sooty shearwaters from colonies in the South Pacific and South Atlantic migrating to the North Pacific and North Atlantic (i.e. northwards) initially fly thousands of kilometers east in the mid-latitude westerlies before turning northwest and making more rapid progress towards their goal due to positive and predictable support from the southeast and northeast trade winds (Fig. 6c). While breeding, this group usually make looping (Navarro & González-Solís 2009, Raymond et al. 2010, Schoombie et al. 2018) but also sometimes more direct central-place foraging trips (Meier et al. 2015, Wischnewski et al. 2019), possibly facilitated by their ability to switch between flapping and dynamic soaring (Ainley et al. 2015, Gibb et al. 2017, Kempton et al. 2022). In some instances, looping trips are highly stereotyped, presumably due to optimization with respect to persistent wind patterns (Navarro & González-Solís 2009).

Most flapping seabirds with medium to low airspeeds that undertake trans-equatorial migrations also follow looping routes (Kopp et al. 2011, Gilg et al. 2013, Weimerskirch et al. 2015, van Bemmelen et al. 2017). However, their trajectories differ subtly from those of flap-soaring petrels, presumably due to their greater ability to counter drift and traverse areas of light wind. For example, migratory routes of Arctic terns suggest that this species sometimes chooses routes that offer positive wind support but also follows routes that minimize distance when negative wind support is not strong (Fig. 6d,e) (Egevang et al. 2010, Stenhouse et al. 2012, Fijn et al. 2013, Hensz 2015, Alerstam et al. 2019b, Hromádkova et al. 2020, Wong et al. 2021, Redfern & Bevan 2022). Black-legged kittiwakes *Rissa tridactyla* from some, but not all, populations also follow looping routes during the non-breeding period, but it is not clear if this is a consequence of wind optimization or food distribution (Bogdanova et al. 2011, Orben et al. 2015, Amélineau et al. 2021). Less is known about the migration routes of storm petrels, the smallest and slowest pelagic seabirds to proceed primarily by flapping flight (Spear & Ainley 1997b), but Pollet et al. (2014) observed that Leach's storm petrels *Hydrobates leucorhous* tracked from the Northwest Atlantic migrated clockwise around the North Atlantic following the prevailing winds.

Faster flapping seabirds that undertake long migrations generally do so more directly, following similar outward and return routes, presumably due to their great ability to counter drift and/or a lack of reliance on positive wind support. For example, Sabine's gulls *Xema sabini* migrate across the equator from Arctic breeding areas to the Benguela and Humboldt upwellings, following the coast where this is aligned in the preferred direction of movement and crossing the ocean directly otherwise (Stenhouse et al. 2012, Gutowsky et al. 2021). Northern gannets migrating between mid-latitude breeding colonies and low latitude wintering areas in the North Atlantic also do so directly, following similar outward and return routes along the coast (Fig. 6f) (Montevecchi et al. 2012, Lane et al. 2021). Auks have the highest airspeeds of any flapping seabirds (Pennycuick 1997) and while some follow overall looping routes, most migrate relatively directly or without clear overall patterns, with route choice probably being influenced more by food distribution, and possibly advection by surface currents, than wind (Amélineau et al. 2021).

When central-place foraging, predominantly flapping seabirds make both looping and direct trips. This is true of smaller taxa, such as *Hydrobates* spp. (Bolton 2020, Collins et al. 2022), which have relatively low airspeeds, and larger ones, such as sulids (Weimerskirch 2007, Wakefield et al. 2015). Subjectively, it appears that faster flapping seabirds may make more direct trips, though it is difficult to disentangle the effects of prey availability or predictability and wind patterns. For example, auks (obligate flappers) rarely undertake looping trips (Evans et al. 2013, Owen et al. 2019, Bonnet-Lebrun et al. 2021b). Northern gannets make direct trips when returning to individually preferred foraging locations (Wakefield et al. 2015), and do not alter course markedly to achieve favorable wind support (Amélineau et al. 2014), presumably because they can compensate for adverse drift (Lane et al. 2019). Similarly, central-place foraging black-legged kittiwakes and Phalacrocoracidae spp. do not alter flight destination in response to wind but instead compensate by increasing wing beat strength and thereby airspeed in headwinds (Yoda et al. 2012, Kogure et al. 2016, Collins et al. 2020).

4.11. Summary of conceptual model

We have attempted to align the findings of seabird studies, most of which are empirical, with existing theory, via a simple conceptual model which contrasts traits of flapping and soaring seabirds (Fig. 5). Our review suggests that the general patterns described by the model are valid: soaring flight is energetically efficient but constrains heading with respect to the wind, necessitating more circuitous routes and greater wind selectivity. Conversely, flapping flight allows more flexibility to buffer against wind conditions, favoring fast, time-minimizing flight along more direct routes. However, this is energetically costly, resulting in shorter ranges. Slow flapping birds behave similarly to soaring birds due to a similar inability to counter drift. Many species are intermediate between flappers and soarers and shift towards time minimizing movement as central-place constraint increases. However, we note that these conclusions are tentative and remain to be tested properly.

4.12. The omniscience paradox: How do seabirds know which routes are more efficient?

It is clear that dynamic soaring and flap-soaring seabirds seek to optimize their routes relative to meso- to macroscale wind patterns. How they achieve this is paradoxical because to correctly calculate optimal routes requires omniscience of wind conditions over all potential routes, which encompass areas beyond individual's immediate perception (McLaren et al. 2014). The first potential explanation is that seabirds use indirect cues to anticipate wind conditions (Richardson 1990a, Berthold 2001). Synoptic scale wind patterns at sea often evolve predictably over periods of hours to days (see Section 2.1). For example, the westward passage of a mid-latitude cyclone is accompanied by stereotyped changes in atmospheric pressure, wind direction, temperature, cloud type and cover, and precipitation (Burch 2018), all of which seabirds can probably perceive (Chapman et al. 2011, O'Neill 2013, Martin 2017). These cues, combined with simple rules of thumb, similar to those used by mariners prior to the advent of modern forecasting (Burch 2018), could be sufficient to allow birds to optimize their headings and departure times (Blomqvist & Peterz 1984, Murray et al. 2003b, Adams & Flora 2010). Macroscale wind patterns are seasonally predictable, but even at this scale, it is advantageous to fine-tune migration departure times (Felicísimo et al. 2008). Possibly, this is achieved by seabirds sensing local changes in atmospheric pressure teleconnected to wind conditions thousands of kilometers further along their intended route (Gill et al. 2014).

The second potential explanation is that routes are optimized based on information sampled by many individuals. This could be integrated via genetic adaptation, public information exchange and cultural transmission (Guttal & Couzin 2010, Liedvogel et al. 2011, Mueller et al. 2013, Németh & Moore 2014, Kranstauber et al. 2015, Aikens et al. 2022), refined by individual and possibly social learning during seabirds' unusually long period of maturation (Riotte-Lambert & Weimerskirch 2013, Mendez et al. 2017, Collet et al. 2020, Yoda et al. 2021). Among land birds, there is evidence that relatively simple programs, such as departure vectors, are genetically inherited and but refined in life (Mellone et al. 2013, Sergio et al. 2014, Vansteelant et al. 2017, Shamoun-Baranes et al. 2017). There may also be this case in seabirds: for example, migration routes of shearwaters are more efficient in established than nascent shearwater populations (Fayet et al. 2020) and improve as birds mature (Campioni et al. 2020, Wynn et al. 2022). Moreover, some seabirds routinely travel in flocks, which may facilitate public information exchange and collective responses to wind (Wakefield et al. 2019).

Notwithstanding the impressive abilities of seabirds to respond to wind conditions by adopting routes and behaviors that increase travel efficiency, it is worth recalling that these behaviors are often suboptimal (González-Solís et al. 2009, McLaren et al. 2016), sometimes catastrophically so (Hass et al. 2012, Clairbaux et al. 2021, Shepard 2021). Understanding the causes of seabird wrecks could inform our understanding of the mechanisms they use to respond to wind successfully most of the time.

5. SEABIRD ENERGETICS RELATIVE TO WIND

Energetic expenditure influences biological processes across spatiotemporal scales and, thus, provides a mechanistic link between individual and population-level processes. For animals that fly or swim, the flow of air or water relative to their direction of movement has important consequences for their energetic cost of travel (Chapman et al. 2011). Moreover, balancing costs of transport with energy acquisition is paramount for central-place foragers and can directly influence fitness and reproductive success (Sæther et al. 1993, Chastel et al. 1995, Navarro & González-Solís 2007). In the following sections, we focus on studies that have estimated energetic expenditure during flight relative to wind conditions, and approaches that allow the direct implications for individuals and populations to be assessed.

5.1. Energetic cost of travel relative to wind

Quantifying energy expenditure in relation to wind is challenging due to the long and remote nature of seabird foraging trips in a highly dynamic airspace. Early studies focused on the metabolic energy needed for flight (power input; Norberg 1996). The doubly labeled water (DLW) technique traces the movement of water and carbon dioxide through the body using stable isotopes to estimate mean oxygen consumption over entire foraging trips (Butler et al. 2004). The DLW technique can thus provide estimates of *field metabolic rate*, which includes basal metabolism and describes the total energy that a free-ranging animal metabolizes over a specific period of time (Dunn et al. 2018), and has been used since the early 1980s to study seabird energetics (Shaffer 2011). This method can provide information on seabird energetics integrated over entire foraging trips, but cannot resolve the energetic costs of particular behaviors within those trips (Shaffer 2011). Heart-rate loggers were first deployed on foraging seabirds in the early 1990s and can be used as a proxy for energy expenditure over both short and long time scales (Butler & Woakes 1984, Bevan et al. 1994, 1995, Weimerskirch et al. 2000b, Green et al. 2001). However, directly linking heart rate with energy expenditure requires calibration using gas respirometry under controlled conditions, which is challenging at remote field sites (Bevan et al. 1994). Recent advances in biologging have improved our ability to resolve relationships between seabirds and wind in real time by allowing locations to be measured simultaneously with metrics of instantaneous energy costs. Rather than measuring the metabolic energy needed for flight, these studies focus on the power output, or the mechanical power required to fly. Tri-axial accelerometry can be used to estimate wingbeat frequency (Spivey et al. 2014, Collins et al.

2020) and overall dynamic body acceleration (ODBA), which can be used as a proxy for energy expenditure in flight when calibrated (Wilson et al. 2006, Gleiss et al. 2011, Halsey et al. 2011, Amélineau et al. 2014, Elliott et al. 2014). However, ODBA assumes that energy expenditure is due to self-propulsion and therefore may not perform well when variability in energy expenditure is independent of movement, such as when thermoregulatory costs dominate (Ste-Marie et al. 2022) or when animals are subject to environmental acceleration (Wilson et al. 2020). During dynamic soaring, for example, centrifugal forces may be large but may not be directly related to an animal's energy expenditure.

Together, these approaches have highlighted the varying costs of flight relative to wind for different behaviors and species. Field metabolic rates associate with wind speed, though relationships vary greatly between species with differing morphologies and flight modes (Gabrielsen et al. 1987, 1991, Furness & Bryant 1996, Mullers et al. 2009, Kroeger et al. 2020). Flapping flight is energetically expensive (Butler 1991, Hedenström 1993), with energy expenditure being proportional to the number of flaps or the extent to which flapping flight is used (Weimersbkirch et al. 2000b, Ropert-Coudert et al. 2006, Sakamoto et al. 2013). Birds also modulate wingbeat amplitude, and may do so more than wingbeat frequency during energy-demanding activities such as climbing or taking off (Krishnan et al. 2022). Broadly, soaring seabirds have lower energy expenditure at sea than those relying primarily on flapping (Adams et al. 1986, 1991, Ballance 1995, Bevan et al. 1995, Mullers et al. 2009). Within flap-gliding seabirds, the mechanical cost of flight is greater for those that flap more often (Birt-Friesen et al. 1989, Ballance 1995, Ropert-Coudert et al. 2006).

Direct measurements have shown that flapping activity varies with wind conditions (see Section 3.2.1), with increased wingbeats and/or energy expenditure in headwinds, across species relying on different flight types (Amélineau et al. 2014, Elliott et al. 2014, Kroeger et al. 2020). Since dynamic soaring relies on strong winds for efficient flight, species relying on dynamic soaring have higher energy expenditure when wind speed is low (Furness & Bryant 1996, Kroeger et al. 2020). However, the resolution of available wind data limits our ability to understand fine-scale relationships between flight energetics and wind.

Relationships between seabird airspeed and commonly-used metrics of the mechanical costs of flight such as wingbeat frequency are weak, while relationships between airspeed and wind speed are strong (see Section 3.3) (Elliott et al. 2014, Collins et al. 2020). Simply put, while seabirds modify their airspeed based on wind (e.g. increasing airspeed in headwinds), the energetic costs of doing so are not well understood. Wind tunnel studies measuring both metabolic costs and mechanical power have demonstrated that metabolic costs do not vary linearly with mechanical power and that flight muscle efficiency, which influences energetic costs, varies with flight speed and between individuals (Ward et al. 2001, Morris et al. 2010). Further, *postural costs* of flight, energetic costs of non-muscular physiological systems and muscles other than the pectoralis muscles, may be central to understanding flight energetics in birds (Morris et al. 2010). Postural costs are not reflected by metrics of wingbeats, may not be well represented by ODBA (Williams et al. 2015, Wilson et al. 2020), and may vary with flight speed (Morris et al. 2010). To better understand wind impacts on seabird flight energetics, further studies conducted in wind tunnels or using concurrent heart rate and accelerometer tags are needed to calibrate metrics of the mechanical costs of flight relative to energetic expenditure.

5.2. Wind impacts on central-place foraging energetics and implications for life history

During breeding, when seabirds must return to the colony regularly to provision chicks or relieve their partner, accessibility of foraging areas is central to foraging energetics and can influence breeding success (Chivers et al. 2012, Paredes et al. 2012, Ponchon et al. 2014, Fayet et al. 2021). By influencing the cost of travel, wind can modulate the inverse relationship between accessibility and distance from the colony (see Section 4) . For example, in wandering albatrosses and Juan Fernández petrels *Pterodroma externa*, stronger wind speeds or increased tail winds increase ground speeds, allowing them to reach foraging grounds more quickly and decrease foraging trip durations (Weimerskirch et al. 2012, Cornioley et al. 2016, Clay et al. 2023). Favorable winds can also allow seabirds to forage in more distant foraging grounds. For example, breeding Scopoli's shearwaters *Calonectris diomedea* travel further from the colony during stronger winds without increasing trip duration (De Pascalis et al. 2020).

Wind can also impact foraging energetics during central-place foraging, providing a potential mechanistic link between wind and demography. Energetic expenditure while foraging can influence chick provisioning rates, adult body condition, and reproductive success (Weimerskirch et al. 2003a, Regular et al. 2014, Evans et al. 2020). By influencing flight costs and energy budgets, changes in wind strength and direction may also have repercussions for colony attendance, self-maintenance, chick provisioning, chick growth, phenology, breeding propensity, hatching and breeding success, all of which can have implications for seabird life history and population dynamics. For example, in flapping seabirds, strong winds can increase energy expenditure and decrease provisioning rates and survival of chicks (Gabrielsen et al. 1987, Konarzewski & Taylor 1989, Christensen-Dalsgaard et al. 2018). However, in some circumstances, adult seabirds can buffer negative impacts of unfavorable winds on their chicks by switching prey species, or by increasing provisioning rates on days with more favorable winds (Elliott et al. 2014). For dynamic-soaring seabirds, strong winds have been associated with positive impacts on demographic rates through effects on foraging energetics. Wandering albatrosses have increased ground speeds and reduced trip durations as a result of increases in wind speed over a 40 yr period, leading to increased adult mass and reproductive success (Weimerskirch et al. 2012, Cornioley et al. 2016). Wind can also affect the quality of nesting sites. For example, among cliff-nesting alcids, the probability of a successful landing at the nest decrease (Shepard et al. 2019) and predation rates by gulls increase (Gilchrist et al. 1998) with wind speed.

5.3. Energy landscapes

Elucidating relationships between wind and the cost of travel in seabirds is key to understanding how the effects of wind on habitat accessibility at the individual level scale up to influence population dynamics. Technological developments which allow energy expenditure to be assessed in the field in real-time present the opportunity to assess fine-scale relationships between the environment, movement and energetics (Amélineau et al. 2014, Louzao et al. 2014). This in turn enables the development of *energy landscapes*, which relate animal location in space and time to the cost of transport through a heterogeneous environment (Wilson et al. 2012, Shepard et al. 2013). Energy landscapes can provide a powerful tool for assessing how and why animals behave in response to variability in wind and wave conditions (Wilson et al. 2012). Using this approach, flight costs can be modeled relative to variable wind conditions and flight trajectories (Afán et al. 2021) and changes in costs can be assessed by time period, or between individuals or populations (Louzao et al. 2014).

6. EFFECTS OF CLIMATE VARIABILITY AND SEVERE WEATHER ON SEABIRDS

Climate change and severe weather are listed as a threat to nearly 40 species of seabirds, of which around half are threatened by storms and flooding (Dias et al. 2019). The literature on seabirds published in recent decades includes many studies of the effects of wind, or climate variability or change in general, on individuals and populations. As these studies are mostly correlational, multiple causal mechanisms could underly relationships between climate and demographic rates. Here, we consider what these mechanisms might be, distinguishing between those with *direct effects*, e.g. that change the cost of transport or inflict mortality directly, and those with *indirect effects*, e.g. by altering prey abundance.

6.1. Changes in wind patterns associated with climate metrics

Various indices describe large-scale climate patterns of climatic variability on scales from weeks to decades that drive wind variability. We focus here on examples related to the El Niño-Southern Oscillation (ENSO) and the Southern Annular Mode (SAM), which reflect major shifts in global wind patterns. The ENSO cycle is a periodic, low-frequency phenomenon, occurring every 3 to 7 yr, characterized by shifts in low-level wind fields in the Tropical Pacific. During the El Niño phase, easterly trade winds in the central Pacific decrease or reverse in direction, while during the La Niña phase, easterly trade winds increase in intensity (Barber et al. 1996, Schwing et al. 2002, Collins et al. 2010). The Southern Oscillation Index (SOI) quantifies the development and intensity of ENSO events. El Niño events are associated with extended periods of negative SOI, while prolonged periods of positive SOI are typical of La Niña events. The SAM describes north-south shifts in position and intensity of strong mid-latitude westerly winds in the Southern Ocean occurring over decades to centuries. Under a positive SAM, the Southern Ocean westerlies intensify and contract southward and vice versa (Fogt & Marshall 2020).

6.2. Direct effects of climate-driven wind variability on seabirds

Although many studies have described putative impacts of climate variability on seabirds (see Section 6.3), few have explicitly assessed the direct effects of wind variability on seabirds during these climate cycles. Poleward shifts and increased intensity of westerly winds in the Southern Ocean associated with positive SAM were correlated with faster travel speeds and improvements in wandering albatross foraging success and life-history traits at Crozet Islands over a 40 yr period. However, a continued shift southward, as predicted under climate change scenarios, is anticipated to create unfavorable foraging conditions (Weimerskirch et al. 2012). Over a 15 yr period, the survival of northern giant petrels *Macronectes halli* was correlated with stronger meridional winds linked with ENSO (Gianuca et al. 2019). Incubating Laysan albatrosses *Phoebastria immutabilis* showed increased travel speeds and mass gain in stronger winds during El Niño conditions, while the costs of traveling in headwinds during brooding trips might play a role in lower reproductive success observed during La Niña conditions (Thorne et al. 2016). Understanding the impacts of wind-mediated cost of travel in the context of climate variability would improve our ability to predict the impacts of climate-driven changes in wind patterns on seabirds (see Section 6.5).

6.3. Indirect effects of wind-driven variability on seabirds

Wind can influence seabirds indirectly through effects on oceanography and prey distributions, and macroscale impacts of climate variability on resource availability have been the subject of previous review papers (Durant et al. 2004, Grémillet & Boulinier 2009, Chambers et al. 2011, Sydeman et al. 2012, 2015, Jenouvrier 2013). Here, we focus on key mechanisms through which wind influence prey distributions, with a focus on ENSO and SAM, upwelling and sea ice.

During El Niño events, decreased primary production in the eastern tropical Pacific has repercussions throughout the food chain, including for seabirds, which face starvation as resources dwindle (Schreiber & Schreiber 1984). The effects of ENSO on seabirds depend on the spatial location. Although El Niño impacts seabirds negatively in the eastern Pacific (Hodder & Graybill 1985, Anderson 1989, Wilson 1991), in the central North Pacific, El Niño events were associated with better foraging conditions, habitat accessibility and reproductive success for albatrosses (Thorne et al. 2015). The SOI, closely associated with ENSO, has been linked in Scopoli's shearwater to the survival of adults and return rates of first-time breeders, the latter considered to indicate higher costs of first reproduction if conditions were poor in the previous winter (Genovart et al. 2013).

Among Antarctic or sub-Antarctic seabirds, higher survival or breeding success is generally associated with positive SAM (Pardo et al. 2017, Cleeland et al. 2021). In emperor penguins *Aptenodytes forsteri*, the survival of adults and juveniles as well as breeding success has also been linked to this index (Massom et al. 2009, Abadi et al. 2017). This is thought to be because wind patterns associated with the SAM influence sea-ice extent and duration, and, in turn, the distance from breeding colonies to open water. Strong westerly winds in the Southern Ocean also increase Ekman transport and hence upwelling, promoting primary production and aggregating key prey, such as Antarctic krill *Euphausia superba*, close to shore (Bernard et al. 2017).

Coastal upwelling is enhanced by strong offshore winds, in turn increasing primary production and, directly or indirectly, the abundance and distribution of mid-trophic-level consumers, including zooplankton, fish, and squid, ultimately benefitting seabirds (Ainley & Hyrenbach 2010, Goschen et al. 2012, Dehnhard et al. 2013). Indeed, upwelling causes the high productivity of eastern boundary current ecosystems worldwide, including the California, Humboldt, Canary and Benguela systems, which are global seabird hotspots (García-Reyes et al. 2013). In other systems, very strong winds increase the mixed layer depth, suppressing primary production and dispersing prey vertically, resulting in longer trip durations, lower prey encounter rates and reduced foraging efficiency for seabirds even after storms have passed, suggesting a prolonged effect on the horizontal or vertical distribution of prey (Barreau et al. 2021). Conversely, seabirds may benefit from a shoaling of the thermocline during light winds because prey aggregate around this feature (Saraux et al. 2015). Similarly, the lower breeding success of diving seabirds in the North Pacific in windier conditions is thought to be a consequence of reduced stratification leading to lower fish recruitment up to 2 yr later (Zador et al. 2013).

Wind also influences sea-ice dynamics, driving the timing and extent of the spring breakup and associated phytoplankton bloom, and hence abundance, several months later, of key species such as euphausiids. Indeed, the influence of wind will often be lagged where the physical effects take time to propagate through the food web. In the northern Bering Sea, strong southerly (warm) winds during winter 2017/2018 delayed the formation and reduced the extent of sea ice, likely limiting ice algae and delaying the phytoplankton bloom that usually fuels both pelagic and benthic food webs; this led to unprecedented adult mortality, breeding deferral, late breeding and widespread failure of seabirds (Siddon et al. 2020). Similarly, in the Okhotsk Sea, variation in wind direction and associated water circulation patterns from 1987–1994 influenced the timing of breakup of sea ice and water temperature, and resulted in contrasting trends in reproductive success of piscivorous and planktivorous alcids (Kitaysky & Golubova 2000). Winds can also drive the formation of polynyas, which are important for a range of pagophilic species (Dehnhard et al. 2020). Normally, strong katabatic winds help push sea ice away from the coast and allow access to open water (usually polynyas), but in 2013, winds from the east forced penguins to walk across large areas of sea ice, greatly reducing provisioning rates and causing widespread breeding failure (Ropert-Coudert et al. 2015, Labrousse et al. 2021). Delayed hatching and poor fledging success in snow petrels *Pagodroma nivea* in years of higher sea-ice concentrations was attributed to various other mechanisms, namely reduced mixing of the water column and a delayed spring bloom, obstructed access to prey, and more days with high winds, presumably increasing flight costs (Sauser et al. 2021).

Lastly, through impacts on atmospheric and ocean circulation and finer-scale wind and weather patterns (especially precipitation), large-scale climate indices affect the distribution of marine plastics (Welden & Lusher 2017). Similarly, climate indices can influence the long-range transportation of other pollutants, particularly Persistent Organic Pollutants (POPs) and mercury, which are correlated with contaminant levels in seabirds (Bustnes et al. 2010, Foster et al. 2019).

6.4. Effects of storms and changes in wind patterns at breeding sites

Severe storms can cause high losses of seabird eggs or chicks, including through high winds or storm surges which can sweep away adults and nest contents, or incessant sea spray causing chilling and subsequent mortality (Wolfaardt et al. 2012, Newell et al. 2015). The impact of a storm is likely to depend on timing, with small chicks potentially the most vulnerable to chilling. In combination with sea-level rise, storm surges and tidal inundation associated with high winds are a major risk to low-lying seabird colonies, including on low atoll islands in the Pacific Ocean (Reynolds et al. 2015). In warmer years, wind speeds and directions that increase evaporation and water stress can kill Magellanic penguin *Spheniscus magellanicus* chicks, particularly at exposed nests (Boersma & Rebstock 2014). High winds can destroy nests in trees, and falling trees or branches cause breeding failure, which can compound negative effects of wind on foraging efficiency of adults at sea (Monticelli et al. 2014, Weimerskirch & Prudor 2019). Strong gradients in wind speed and direction at breeding colonies have also been associated with land-based crash-landing mortalities in albatrosses (J. Schoombie et al. 2023 in this Theme Section). Effects of wind on breeding success may be apparent only at exposed colonies and not those in sheltered bays (Johnson & Colombelli-Négrel 2021). Landslides or falling trees caused by major storms can also destroy breeding habitat of burrowing petrels (Waugh et al. 2020). Changes to wind patterns can also impact heat stress in seabirds; for example, heat stress associated with low winds and high air temperatures can result in chick mortality (Sherley et al. 2012).

Seabird wrecks associated with large storms can affect large numbers of seabirds; in some years, tens of thousands of birds are known to be killed, and many more are likely to be affected in remote and stormier regions where there is little coastal monitoring (Shepard 2021). Hurricanes can also displace birds far inland (Hass et al. 2012). Some seabird populations can experience multiple cyclones per month (Clairbaux et al. 2021). Thermodynamic modelling by Fort et al. (2009) suggested that wrecks may be caused by the direct effect of high wind speeds on foraging costs. In contrast, a study by Clairbaux et al. (2021) concluded that energy expenditure during cyclones was not particularly high in surface-feeding or diving seabirds; instead, birds were likely unable to feed because a change in prey distribution or behavior in response to e.g. currents, wave action, increased turbidity, and/ or reduced light, reducing prey availability or detectability. The vulnerability of different seabird species to cyclones depends on fasting capability, which is lower in smaller birds (Clairbaux et al. 2021), and also on behavior, as some pelagic species are less vulnerable because they fly at greater altitude or move out of the path of cyclones (Weimerskirch & Prudor 2019, Thiebot et al. 2020).

Wind and weather influences when snow clears from frozen ground, determining its availability for nesting and hence seabird arrival and laying dates, and also where snow accumulates during the breeding season, affecting hatching or fledging success (Lynch et al. 2012). Indeed, on Ardley Island, on the west Antarctic Peninsula, abandonment of nesting or molting sites by penguins over a period of hundreds of years was likely driven by a change in wind patterns associated with a positive SAM causing more snow to accumulate (Yang et al. 2019). Late wind-driven snow can also block nest sites, resulting in partial or complete breeding failure (Descamps et al. 2023) even in years with ostensibly favorable foraging conditions (Büßer et al. 2004).

6.5. Wind patterns under climate change

Climate change is having widespread effects on global patterns of wind and ocean currents (Yin 2005, Toggweiler & Russell 2008, Sallée et al. 2008). Understanding the consequences of these changes for seabird populations is a major challenge. While the mean thermodynamic global response to increased concentrations of greenhouse gasses has been modeled with a high confidence, the regional response is driven by local dynamics and is much harder to predict (Shepherd 2014). As a result, predicting detailed future wind patterns is difficult and may need to rely heavily on probabilistic approaches (Shepherd 2014). Interpreting surface climate change observed in the Southern Hemisphere over the last 50 yr is particularly difficult because much of the trend in the SAM is due to changes in ozone, not greenhouse gasses (Thompson & Solomon 2002, Thompson et al. 2011). However, climate models predicted some changes to global-scale circulation robustly, including a poleward shift of the mid-latitude westerlies and storm tracks (Toggweiler 2009, Chang et al. 2012, Voigt et al. 2021). The latter, plus a poleward shift of warm sea-surface temperatures, will result in both tropical- and mid-latitude cyclones extending to higher latitudes in the future. In addition, the storm track in the Southern Ocean is expected to strengthen (Barnes & Polvani 2013). It is possible to use the current dominant modes of variability as a template with which to consider the impact of changing wind patterns. For example, developing a broader understanding of links between SAM, wind patterns and seabird movement and life history would allow us to assess the consequences of SAM shifting into a more consistently positive or negative phase in the future.

7. CONCLUSIONS AND FUTURE RESEARCH PRIORITIES

Our review highlights how wind shapes seabird ecology across ecological and spatiotemporal scales. At fine scales, wind speed and direction, together with morphology, influence flight speeds, behavior, and the energetic cost of different flight modes. At meso- and synoptic scales, wind can strongly affect when, where, and how seabirds fly during both central-place foraging and migration. At macroscales, climate-driven wind variability has been correlated with changes in seabird demographic rates, and over evolutionary time scales, wind may influence seabird biogeography.

In synthesizing current understanding of the effects of wind on seabirds, we encountered many unanswered questions. We conclude by highlighting what we consider to be the twelve most important questions for future research in this area to address:

7.1. What is the relative importance of different flight modes?

Understanding which flight modes are used, how they relate to wind conditions across spatiotemporal scales, and their energetic implications will enhance our ability to predict the impacts of wind on seabird populations. In particular, relationships between wind and wingbeat frequency and amplitude, and the use of auxiliary flapping by predominantly soaring seabirds (and vice versa), remain poorly understood.

7.2. What are the quantitative relationships between wind and flight costs?

Despite ample evidence that wind affects seabird flight, the explanatory power of models relating flight costs to wind conditions remains relatively poor. Notwithstanding variation due to measurement error, this suggests that our understanding of the mechanisms of seabird flight are incomplete and possibly that seabirds are adept at buffering the effects of variation in wind. Future studies should quantify variation in energetic cost (measured by bird-borne loggers or other means) due to mechanistic components, such as muscle properties, wing morphing, or wing loading, with the ultimate aim of accurately predicting energetic costs under different movement scenarios.

7.3. How and why do seabird flight heights vary with wind conditions?

While many studies of seabird flight behavior have focused on horizontal movement, few have explored the vertical dimension. Quantifying variability in altitude is necessary for better distinguishing seabird flight modes, accurately describing the wind fields experienced, and understanding route optimization strategies. Moreover, it will greatly improve our ability to anticipate and mitigate the risk of collision with offshore wind farms, which are proliferating.

7.4. How do ocean waves influence seabird movements and energetics?

Understanding how seabirds use ocean waves to fly is fundamental to obtaining a full theory of seabird flight but interactions between waves and wind make this a complex task. Nonetheless, the availability of bird tracking and reanalysis wave data mean initial analyses are now feasible.

7.5. What are the impacts of light winds on seabirds?

Most research assessing the effects of wind on seabirds has focused on regions with strong mean wind speeds. The extent to which light winds caused by episodic (e.g. transitory high anticyclones) or climatic (e.g. the doldrums) phenomena impact seabird movements, energetics and fitness is therefore less well understood. This is particularly important given that forecasts suggest that light winds will become more common in some areas under climate change.

7.6. To what extent does wind modulate habitat accessibility and how can this be integrated into habitat selection theory and models?

It is evident that wind affects seabird distributions, from the community level downwards, but the extent to which this is due to its effects on movement rather than indirect effects (e.g. on ocean productivity) is unclear. Moreover, while there is some evidence that wind affects goal choice, the practicalities of incorporating wind-mediated variation in accessibility into habitat selection and demographic models remains unresolved.

7.7. How applicable is existing theory on the effects of wind and the movements of terrestrial birds to those of seabirds and how can it be refined for the latter?

While there is a considerable body of theory on the effects of wind on bird migration, it focusses on terrestrial birds rather than seabirds. Adapting and refining this theory for seabirds, including their relatively long-distance foraging movements, remains a major challenge, but one that should lead to a more complete overall theory of bird migration.

7.8. How do seabirds sense and anticipate wind conditions?

Despite only being able to directly perceive local wind conditions, seabirds are able to follow routes and react to changing wind conditions en route in ways that increase the efficiency of movement towards their goal. This suggests an ability to use local environmental cues to anticipate wind conditions elsewhere in space and time. Determining how they do this, and why seabirds sometimes fail to avoid adverse wind conditions, is challenging, necessitating advances in our understanding of sensory and navigational systems, cognition, ontogeny, genetics and social interactions.

7.9. What are the relative roles of genetics, social effects and individual learning on movement responses to wind?

There remains considerable uncertainty about the extent to which the reaction norms and migratory programs that allow seabirds to respond efficiently to wind are inherited vs. learned; how plastic the behavioral norms are and how variable they are among individuals and taxa; and the extent to which they are inherited (genetically or culturally) or learned (individually or socially).

7.10. How can understanding broader-scale wind patterns and flyways improve seabird conservation?

It is clear that because wind support imposes the same broad constraints across taxa, many seabirds follow similar migration routes. This likely gives rise to global seabird flyways, equivalent to those now well-mapped for terrestrial birds. Such flyways have long been recognized as priority conservation features. Failure to map seabird flyways hampers conservation as these may be where man-made barriers, such as wind farms, plus interactions with fisheries, could have the greatest impacts. Future work should prioritize mapping seabird flyways, and consider whether their management would be most effective using static or dynamic measures, for example targeting vulnerable stages of the annual cycle.

7.11. To what extent have historical wind patterns driven seabird evolution?

Given the many effects of wind on seabirds identified by our review, it is likely that wind has exercised a strong selective pressure on seabirds. For example, within the Procellariiformes, albatrosses were basal, suggesting that dynamic soaring may have been key to the radiation of this group, possibly because it made the pelagic realm accessible from land at a cost not hitherto achievable by purely flapping seabirds. If so, changes in wind patterns that allowed long-distance, down or crosswind flight, for example due to continental realignment and the opening or closing of isthmuses, may have played a key role in seabird diversification.

7.12. How can seabird studies better predict population-level impacts of wind under climate change?

Climate-driven changes in wind patterns have the potential to strongly impact seabirds, from the individual to the population level. Further research is needed to clarify mechanistic links in the chain of causality between climate, wind and demography. Mechanistically-informed models, particularly those incorporating energetic costs and gains, will improve our understanding of wind impacts and ability to predict how these will change in a warming world.

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