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

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SUMMARY

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.

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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, Sa 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 (Sha er 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 (AmØlineau 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 (Sha er et al. 2006, GonzÆlez-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 Wake eld 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°