The Pacific as the world's greatest theater of bird migration: Extreme flights spark questions about physiological capabilities, behavior, and the evolution of migratory pathways

Theunis Piersma,[1,2,*] Robert E. Gill Jr.,[3] Daniel R. Ruthrauff,[3] Christopher G. Guglielmo,[4] Jesse R. Conklin,[1] and Colleen M. Handel[3]

[1]Rudi Drent Chair in Global Flyway Ecology, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, the Netherlands
[2]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Texel, the Netherlands
[3]U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska, USA
[4]Department of Biology, Western University, London, Ontario, Canada
*Corresponding author: theunis.piersma@nioz.nl

ABSTRACT

The Pacific Basin, by virtue of its vastness and its complex aeroscape, provides unique opportunities to address questions about the behavioral and physiological capabilities and mechanisms through which birds can complete spectacular flights. No longer is the Pacific seen just as a formidable barrier between terrestrial habitats in the north and the south, but rather as a gateway for specialized species, such as shorebirds, to make a living on hemispherically distributed seasonal resources. This recent change in perspective is dramatic, and the research that underpins it has presented new opportunities to learn about phenomena that often challenge a sense of normal. Ancient Polynesians were aware of the seasonal passage of shorebirds and other landbirds over the Pacific Ocean, incorporating these observations into their navigational "tool kit" as they explored and colonized the Pacific. Some ten centuries later, systematic visual observations and tracking technology have revealed much about movement of these shorebirds, especially the enormity of their individual nonstop flights. This invites a broad suite of questions, often requiring comparative studies with bird migration across other ocean basins, or across continents. For example, how do birds manage many days of nonstop exercise apparently without sleep? What mechanisms explain birds acting as if they possess a Global Positioning System? How do such extreme migrations evolve? Through advances in both theory and tracking technology, biologists are poised to greatly expand the horizons of movement ecology as we know it. In this integrative review, we present a series of intriguing questions about trans-Pacific migrant shorebirds and summarize recent advances in knowledge about migratory behavior operating at temporal scales ranging from immediate decisions during a single flight, to adaptive learning throughout a lifetime, to evolutionary development of migratory pathways. Recent advances in this realm should stimulate future research across the globe and across a broad array of disciplines.

Keywords: atmosphere, climate change, comparative biology, cognition, conservation, evolution, phylogeography, shorebirds

---

LAY SUMMARY

- The Pacific Ocean was long considered a barrier too formidable for most terrestrial birds to cross, but this perspective has recently been upended by documentation of astonishing migratory feats.
- By virtue of the Pacific's immense size and climatic complexity, the study of 'extreme' migrants in this arena promotes a deeper understanding of basic migratory phenomena.
- We review the behavioral and physiological capabilities that support extreme trans-Pacific flights of migratory shorebirds.
- We examine integral research questions on current, developmental, and evolutionary aspects of migratory behavior, with the Pacific Basin as a backdrop.
- Extreme long-distance migrants in the Pacific region challenge underlying assumptions of bird physiology, orientation, and behavior, providing a rich study system for creative, comparative scientific inquiries.

Le Pacifique, plus grand théâtre de migration d'oiseaux au monde: des vols extrêmes suscitent des questions sur les capacités physiologiques, le comportement et l'évolution des voies migratoires

RÉSUMÉ

Le bassin du Pacifique, en raison de son immensité et de son paysage aérien complexe, offre des opportunités uniques d'aborder les questions relatives aux capacités et mécanismes comportementaux et physiologiques grâce auxquels les oiseaux peuvent effectuer des vols spectaculaires. Le Pacifique n'est plus considéré comme une formidable barrière entre les habitats terrestres du nord et du sud, mais plutôt comme une passerelle permettant à des espèces spécialisées, comme les limicoles, de vivre de ressources saisonnières réparties dans l'hémisphère. Ce récent changement de perspective est radical et la recherche qui le sous-tend a offert de nouvelles possibilités d'apprendre sur des phénomènes qui défient souvent le sens de la normalité. Les Polynésiens anciens connaissaient le passage saisonnier des limicoles et d'autres oiseaux terrestres au-dessus de l'océan Pacifique, et ils ont intégré ces observations dans leur « boîte à outils » de navigation lorsqu'ils ont exploré et colonisé le Pacifique. Quelque dix siècles plus tard, les observations visuelles systématiques et la technologie de suivi ont révélé beaucoup de choses sur les mouvements de ces limicoles, particulièrement l'énormité de leurs vols individuels sans escale. Cela soulève un large éventail de questions, qui nécessitent souvent des études comparatives impliquant la migration d'oiseaux vers d'autres bassins océaniques ou d'autres continents. Par exemple, comment les oiseaux gèrent-ils de nombreux jours d'exercice ininterrompu apparemment sans dormir? Quels mécanismes expliquent que les oiseaux agissent comme s'ils possédaient un système de positionnement global? Comment des migrations aussi extrêmes évoluent-elles? Grâce aux progrès de la théorie et des technologies de suivi, les biologistes sont sur le point d'élargir considérablement les horizons de l'écologie des déplacements telle que nous la connaissons. Dans cette revue intégrée, nous présentons une série de questions intrigantes sur les limicoles migrateurs transpacifiques et nous résumons les progrès récents des connaissances sur le comportement migratoire à des échelles temporelles allant des décisions immédiates pendant un seul vol à l'apprentissage adaptatif tout au long de la vie, en passant par le développement évolutif des voies migratoires. Les progrès récents dans ce domaine devraient stimuler les recherches futures dans le monde entier et dans un large éventail de disciplines.

Mots-clés: atmosphère, changements climatiques, biologie comparative, cognition, conservation, évolution, phylogéographie, limicoles
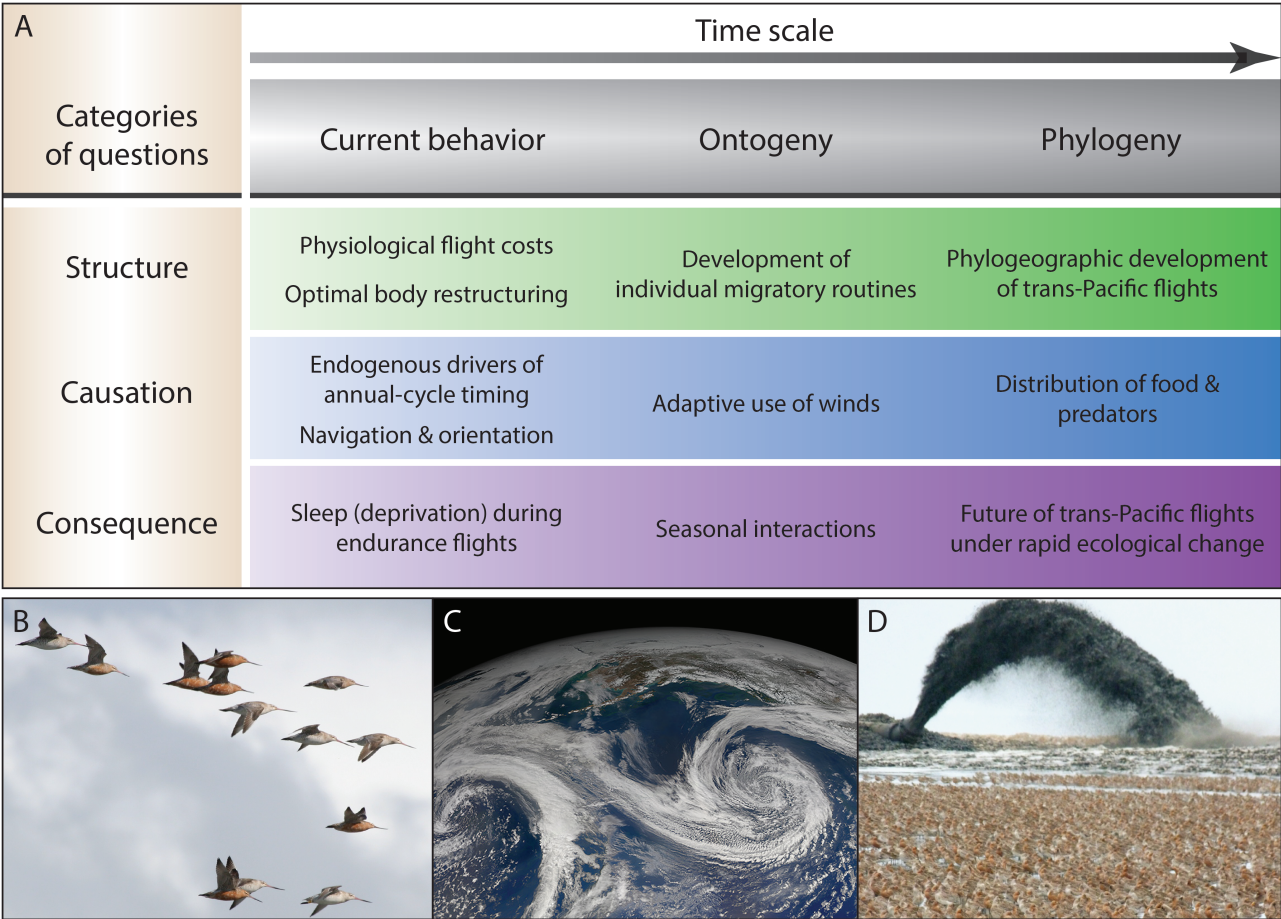
INTRODUCTION

Research over the past three decades has revealed the extraordinary physiological and cognitive capabilities of migratory birds. These findings have raised new questions about what stimulates birds to undertake such journeys (e.g., intrinsic state or proximate stimulus, behavioral reinforcement, genetic programming; see Hogan 2017) and what mechanisms enable them to do so. How might their behavioral decisions and actions affect their life history (e.g., reaching their destination, changing their course en route, or on the next journey)? Biological insights, whether behavioral, physiological, ecological, or evolutionary in nature, usually grow from clever comparisons among habitats, biological communities, species, or populations of a species living in areas with different characteristics. In such comparisons, having enough variation is crucial. In several different ways, the Pacific is an "ecological theater," and the birds living their lives in this area have upended previously supposed limits on fuel stores (Piersma and Gill 1998), flight range and endurance exercise (Gill et al. 2009, Piersma 2011b), wind and weather forecasting (Gill et al. 2014), and navigational achievements (Williams and Williams 1999). It is in this light that we review the seasonal migrations of a group of terrestrial birds, the shorebirds (waders, Charadrii), that move across and around the largest water body on Earth, the Pacific Ocean, and examine the unique features of the extreme migrations that occur there.

In this review, we focus on what we do *not* know and the potential for future scientific inquiry. We provide a brief overview of what makes the Pacific Basin an amazing theater of migration and offer background about the shorebirds that regularly cross its vast and complex aeroscape in spectacular flights. Using Hogan's (2017) formal behavioral framework, we then present some key findings from recent research in the Pacific Basin and the intriguing questions about migratory behavior that have resulted. We suggest several potentially productive avenues for future research on these amazing marathon migrants and for comparative studies in other geographic regions and with other groups of birds (cf. Burger and Shaffer 2008, LaSorte et al. 2016, Carneiro et al. 2020, Watts et al. 2021).

A BEHAVIORAL FRAMEWORK FOR RESEARCH QUESTIONS

In this prospective review, we address questions about trans-Pacific migrants couched in a framework integrating functional (e.g., structure, causation, consequence) and temporal (e.g., current behavior, ontogeny, phylogeny) considerations (Hogan 2017; Figure 1). This framework builds on the philosophical perspectives of key scientific predecessors, including Mayr (1961), Tinbergen (1963), Laland et al. (2011), and others. Whereas Mayr recognized the function of a behavior as related to mechanistic traits ("how" questions) and Tinbergen recognized function as related to purpose ("why" questions), Laland et al. (2011)

| A	Time scale		
Categories of questions	Current behavior	Ontogeny	Phylogeny
Structure	Physiological flight costs / Optimal body restructuring	Development of individual migratory routines	Phylogeographic development of trans-Pacific flights
Causation	Endogenous drivers of annual-cycle timing / Navigation & orientation	Adaptive use of winds	Distribution of food & predators
Consequence	Sleep (deprivation) during endurance flights	Seasonal interactions	Future of trans-Pacific flights under rapid ecological change

FIGURE 1. In this integrative review we formulate and address several intriguing questions about the behavior of trans-Pacific migrant shorebirds within a framework (A) organized by category of the question (structure, causation, or consequence of the behavior) and the time scale over which it is operating. Current behavior addresses questions relative to the immediate effects on behavior of an individual, ontogeny relates to developmental effects or changes within an individual's lifetime, and phylogeny pertains to evolutionary changes in behavior over generations. Additional questions could easily be formulated for many of these topics relative to different categories or time scales. The behavioral framework is based on Hogan (2017) and developed from Piersma (2018). Examples of questions that we address here include: (B) How do birds strategically optimize organ size, fuel storage, and selection of diet and foraging sites before a trans-Pacific flight? (C) How do individual migrants learn to use winds adaptively? (D) What does the future portend for trans-Pacific flights under rapid ecological change, including anthropogenic changes to critical stopover and staging areas? Photo credits: (B) Bartailed Godwits by J. R. Conklin; (C) NASA image of North Pacific storms by Norman Kuring, 9 May 2014; (D) reclamation of Yellow Sea intertidal by David S. Melville.

argued that the distinction between "how" and "why" actually inhibits progress in biology: the dichotomy fails to recognize the myriad feedbacks between traits, environments, and gene expression (e.g., Turner 2007, Piersma and van Gils 2011, Jablonka and Lamb 2014, Badyaev 2018). Hogan (1994, 2017) reconciled these distinctions by reforming the topics in the categories of structure, causation, and consequence across three scales related to time: current behavior, individual development, and evolutionary history. Applying Hogan's framework enables a more complete understanding of a particular behavior, such as the seemingly odd preference of House Martins (*Delichon urbicum*) for old, parasite-infested, mud nests (cf. Piersma 2018).

In this review, we apply Hogan's framework to examine 11 intriguing questions about trans-Pacific migrations of shorebirds to build scaffolding for future inquiries about avian migratory behavior (Figure 1). The time scale of these questions ranges from behavior of individual birds during a single flight (current migratory behavior), to development of migratory behavior across an individual's lifetime (ontogeny), to evolutionary changes in behavior over generations (phylogeny and ecological shaping factors). Our questions address the structure (mechanisms), causation (stimulus), and consequence (effects) of different aspects of migratory behavior. Inevitably, some topics are more fully explored than others. To inspire thoughts and
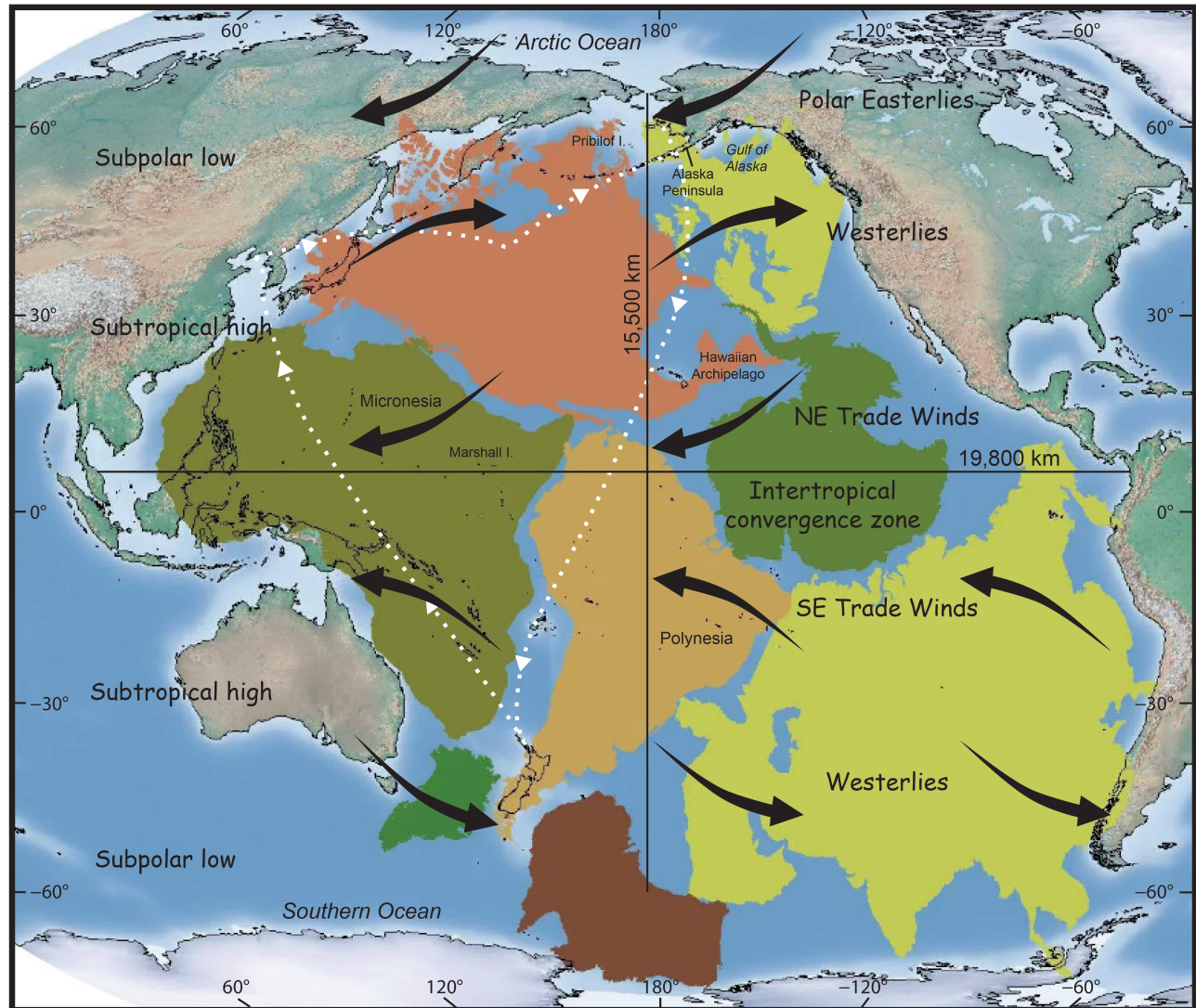
FIGURE 2. The vastness of the Pacific Basin as a theater for nonstop bird migration is illustrated relative to the size of the Earth's landmasses, which even together total 10% less than the areal extent of the Pacific Ocean (165,250,000 km²). The Pacific extends ~15,500 km from the Bering Strait south to the Southern Ocean (−60º) and 19,800 km from the Malay Peninsula east to the coast of Colombia. The Pacific Basin spans 4 major zones of global high and low atmospheric pressure (left) and 5 global wind belts (right). Arrows show broad-scale prevailing wind directions (after Gill et al. 2014). Three long, nonstop flights completed during the annual migration of satellite-tracked Bar-tailed Godwit E7 (dashed white lines) are shown to provide perspective on the dynamic aerosphere through which godwits regularly navigate (after Battley et al. 2012). Map credit: "The Continents and Greenland in the Pacific Ocean" by Chris Stephens; data source: NaturalEarthData.com (base map = Robinson projection; continents and Greenland = Fuller projection).

connections not currently envisioned, we have tried to cast our net widely.

THE PACIFIC BASIN AS *MAXIMUM THEATRUM*

The Pacific Basin annually hosts some of the most spectacular animal movements occurring in nature, including those of marine mammals, fishes, reptiles, and birds (Block et al. 2011). Many discoveries in this dynamic realm have expanded the limits of our understanding about how and why such movements occur and have evolved. The challenging physical attributes of the Pacific Basin itself (Figure 2) are key to unlocking the mysteries surrounding the physiological and behavioral capabilities of migrating organisms, particularly terrestrial birds.

By any measure, the Pacific Basin is huge, having a surface area of more than 165 million square kilometers, representing 30% of the Earth's surface, 10% more than the combined landmass of all the Earth's continents (NOAA 2020; Figure 2). At maximal extent, the Pacific measures ~19,800 km between the shores of Colombia and the Malay Peninsula, and ~15,500 km from the Southern

Ocean (60°S) to the Bering Sea (NOAA 2020). The Pacific contains more islands (~25,000) than the rest of the world's oceans combined, most occurring in the tropical central and western Pacific and seldom spaced more than a day's flying time apart for most birds. In contrast, the northern and eastern Pacific have far fewer and more widely dispersed islands (Nunn 2009), requiring nonstop flights of several days for terrestrial birds migrating south. However, many more islands occurred throughout the Pacific during the last glacial maximum (LGM; 26,500–19,000 years before present) when sea level was 125 m lower (Nunn 2009, Harris et al. 2014), and such significant geological changes could have influenced the evolution of extreme long-distance migration across the Pacific and other oceans.

While the Pacific now encompasses vast stretches of open ocean that may challenge migration of terrestrial birds, the Basin's patterns of atmospheric circulation and the strength and direction of associated winds are generally predictable over intra- and inter-seasonal, interannual, and interdecadal time scales (Ahrens 2016, Lee and Kim 2003), thus likely shaping and facilitating numerous migratory pathways across the Pacific. Investigations on how birds transit this complex, basin-wide windscape during multi-day flights have already provided unique insights on the limits and capabilities of birds relative to navigation, orientation, physiology, and behavior, but, as we shall see, leave many learning opportunities to come.

A CHRONOLOGY OF HUMAN AWARENESS OF LANDBIRDS AT SEA

Knowledge of bird movements across oceanic expanses is embedded in the traditional ecological knowledge of indigenous people who used seasonal observations of animals as aids to navigation when beyond view of land (Barr 2003, Cunliffe 2017, Crowe 2018, Feinberg 2020). Indeed, the folklore and mythology of Polynesian cultures are rich with stories of pelagic and terrestrial birds, but the prominence of a few migratory species in Polynesian folklore, including the Bar-tailed Godwit (*Limosa lapponica*; Māori *Kuaka*) and cuckoo species (*Eudynamys* and *Cuculus*), highlights awareness by indigenous people of seasonal directional movements by terrestrial birds and their use as navigational aids by seafarers (Woodley 2009, Barr 2003, Whaanga et al. 2018, Richter-Gravier 2019). It is from this traditional ecological knowledge and subsequent historical observations that we apply Western science's reductionist and mechanistic approach (Burkes, in Inglis 1993) to offer the "how's" and "why's" of the phenomenon of transoceanic flights by shorebirds.

Naturalists in the 17th and 18th centuries began to question the origins, destinations, and regularity of the occurrence of shorebirds and other landbirds seen over open ocean (Woodley 2009). By the 19th century it had become clear that the regular occurrence of northern-hemisphere species in New Zealand and Australia did not represent vagrants blown off course on their southward migrations, and by the mid-20th century the resident and migratory avifauna of the Pacific Basin was generally understood. Assessments of the seasonal occurrence and pathways used by these species, however, were just beginning. Early efforts speculated on the possibility of transoceanic migration by terrestrial birds spanning over 10,000 km, but observers believed that birds necessarily stopped along the way to refuel (Baker 1951, Mayr 1953, Lack 1959; see also Bull 1948, W. Oliver and R. Stidolph in Woodley 2009:184).

An appreciation for the lengths of nonstop flights first came from large-scale markings of Ruddy Turnstones (*Arenaria interpres*) and Bristle-thighed Curlews (*Numenius tahitiensis*) in Alaska, which offered empirical evidence of their regular migration into the central Pacific up to 3,000–4,000 km south of Hawaii (Thompson 1973, Sonsthagen et al. 2015, Pyle and Pyle 2017, Marks et al. 2020). Kinsky and Yaldwyn (1981) postulated that Pacific Golden-Plovers (*Pluvialis fulva*) could fly ~8,000 km nonstop from Alaska to Niue Island in the South Pacific, based on energetic calculations. The idea that Bar-tailed Godwits were flying nonstop between Alaska and New Zealand was first proposed by Dick Sibson in the mid-1980s (A. Riegen personal communication; Woodley 2009:138), but compelling evidence for such flights had actually begun to accumulate in the late 1970s. Flocks of thousands of godwits were observed on Alaskan estuaries in late autumn (Gill et al. 1981, Gill and McCaffery 1999) gaining large amounts of fat (Piersma and Gill 1998) and were observed to depart en masse in association with strong, favorable southerly winds (Gill and Jorgensen 1979). Shortly after these departures, large increases in numbers of godwits were documented in New Zealand (A. Riegen personal communication; Woodley 2009). This migratory feat was confirmed in 2007 when godwits were tracked via satellite telemetry on nonstop flights of 8,100–11,700 km from Alaska to New Zealand and eastern Australia (Gill et al. 2009). Advances in tracking technology have since revealed that several other shorebird species engage in similar epic flights across open oceans (e.g., Senner et al. 2014, Johnson et al. 2020, Kuang et al. 2020, Ruthrauff et al. 2021). Indeed, such long-distance flights may be common among these shorebirds for sound biological reasons (Conklin et al. 2017; see beyond).

CURRENT MIGRATORY BEHAVIOR

Any inquiry on animal behavior should begin with a description of that behavior. On this descriptive basis, we can, and will, ask all kinds of questions. Building on solid evidence for trans-Pacific migrations by shorebirds instrumented with satellite tags (Figure 3), or geolocators
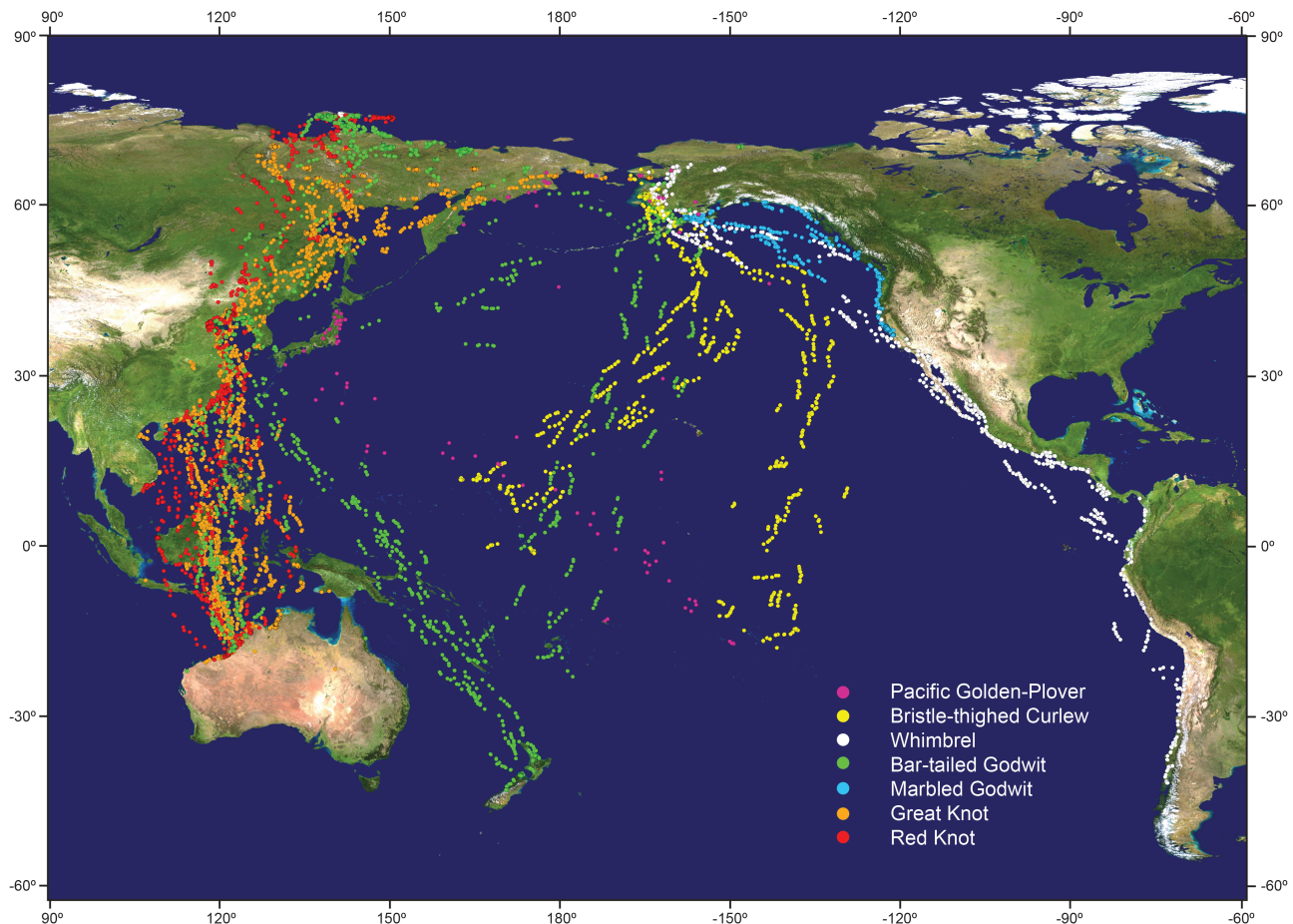
FIGURE 3. Locations of individual shorebirds of 7 species tracked throughout the Pacific Basin by the USGS Alaska Science Center (2019), Global Flyway Network (https://www.globalflywaynetwork.org), and international partners from 2005–2019. Data curated and map (Plate Carrée projection) compiled by T. Lee Tibbitts (USGS Alaska Science Center).

(e.g., Conklin et al. 2010, Johnson et al. 2012), we here discuss current behavior of individual birds in light of the following: (1) the energetics required for these amazingly long flights; (2) the reorganization of body structure necessary for such extended nonstop journeys; (3) the need for sleep, a seemingly non-negotiable, organismal requirement; (4) the existence of a seasonal clock influencing physiological changes and migratory movements; and (5) the abilities needed to orient and navigate across the vast oceanic expanse. These topics raise interesting questions about how, mechanistically, birds can accomplish these flights, what the ecological shaping factors are, and what some of the consequences are of these behaviors.

What Are the True Costs of Sustained Energy Expenditure During Trans-Pacific Flights?

From a physiological perspective, the nonstop distance traveled by migrating birds is essentially irrelevant; what matters is the duration of continuous flight exercise. This can be explained with a simple thought experiment.

A hypothetical migrant with a sufficient (imaginary) tailwind could travel thousands of kilometers in a matter of hours, or conversely with a strong headwind (equal to its maximum airspeed) could fly for many hours or days without traveling anywhere—just as birds do in wind tunnels (Guglielmo 2010). Trans-Pacific flights lasting over a week require having sufficient fuel, maintaining life support, and avoiding catastrophic internal damage. This means: (1) carrying enough energy (mostly fat; Jenni and Jenni-Eiermann 1998); (2) maintaining temperature, water, electrolyte, and nutrient (e.g., glucose) homeostasis (Jenni and Jenni-Eiermann 1998, Gerson and Guglielmo 2011); and (3) avoiding or repairing damage from physical and oxidative processes (Guglielmo et al. 2001, Costantini et al. 2007, Skrip et al. 2015, Dick and Guglielmo 2019). Here we focus on energetics to illustrate that, despite decades of research, we remain unable to satisfactorily explain these feats of endurance.

Satellite telemetry and geolocation devices have shown conclusively that medium to large shorebirds can sustain

TABLE 1. Actual and predicted maximum flight durations of trans-Pacific migrant shorebirds. Flight energy expenditure (P_{chem}, W) was predicted from the average of preflight and postflight body mass using $y = 52.6 M_b^{0.74}$ (M_b in kg, Bishop and Butler 2015). Maximum flight duration was predicted from the difference between preflight and postflight body mass assuming fat and wet protein, respectively, contribute 95% and 5% of energy for flight (0.12 g W^{-1}). Actual flight P_{chem} was estimated from the ratio of actual to predicted flight duration and the allometrically predicted P_{chem}. Ratio is the actual flight duration divided by the theoretically predicted flight duration. Data sources indicated below.

Species	Actual max flight duration (days)	Preflight mass (g)	Postflight mass (g)	Predicted P_{chem} (W)	Predicted max flight duration (days)	Actual P_{chem} (W)	Ratio
Limosa lapponica baueri [a,M]	7–9	485	215	24.2	3.9	11.6	2.1
L. haemastica [b,M]	7	430	183	21.9	3.9	12.2	1.8
Arenaria interpres [c,B]	6–7	210	89	12.9	3.2	5.6	2.3
Calidris alba [d,M]	6	100	43	7.4	2.7	3.3	2.2
C. canutus rogersi [e,M]	7–8	240	102	14.2	3.4	6.4	2.2
C. tenuirostris [f,B]	5	233	125	14.7	2.5	7.5	2.0
Pluvialis fulva [g,B]	6–8	260	111	15.1	3.4	7.4	2.0
Numenius madagascariensis [h,M]	7–8	1,200	510	46.8	5.1	31.6	1.5

[a] Gill et al. (2005).
[b] Senner et al. (2014), Walker et al. (2020).
[c] Minton et al. (2011, 2013), Nettleship (2020).
[d] Minton et al. (2013), Lisovski et al. (2016), Macwhirter et al. (2020).
[e] Tomkovich et al. (2013), Baker et al. (2020).
[f] Pennycuick and Battley 2003.
[g] Johnson et al. (2015, 2020).
[h] Driscoll and Ueta (2002), Minton et al. (2013).
[M] Size-dimorphic species, males were used.
[B] Both sexes combined because size monomorphic or to match previous study (*C. tenuirostris*; Pennycuick and Battley 2003).

flights lasting at least 6–9 days (Conklin et al. 2017 and references therein). Based on flight durations and pre- and postflight body masses, Hedenström (2010) calculated that shorebirds like the Bar-tailed Godwit must have incredibly low, time-integrated rates of body mass loss and energy expenditure (chemical power input, P_{chem}) while in flight. These extremely low rates are about one-half or less of those predicted from allometric equations derived from over 50 years of studies on the energetics of bird flight; similar discrepancies are found for other trans-Pacific migrant shorebirds for which we now have empirical tracking data, with actual maximum flight durations about twice those predicted from the allometric equations (Box 1, Table 1). Thus, this simple physiological approach cannot explain trans-Pacific ultra-endurance flight. Flight energy costs during multi-day flights of shorebirds must be much lower than predicted, and since there is no evidence that shorebirds routinely soar or sail the winds during long flights (Senner et al. 2018), we must look for physiological explanations for their ability to maintain flapping flight for so long.

A more sophisticated approach to understanding the energetics of migratory flight is to use highly parameterized simulation models, such as program *Flight* (Pennycuick 2008). In this model, steady aerodynamic theory is used to predict mechanical power output (P_{mech}) from physical principles based on body mass, wing size and shape, characteristics of the flight environment, and various assumed parameters. Using default values for assumed parameters, simulations from the program for Great Knots (*Calidris tenuirostris*) and Bar-tailed Godwits predicted flight durations that were closer to but still a few days shorter than actual flights; however, slightly increasing the value for muscle efficiency or reducing the value for basal metabolic rate (BMR) would eliminate the discrepancies (Box 2). Thus, higher muscle conversion efficiency and lower BMR are two factors that could account for the longer than predicted flight durations in migratory shorebirds (Kvist et al. 2001, Hedh et al. 2020). In fact, we expect strong natural selection for energy efficiency in extreme nonstop migrant birds, which could lead to the evolution of greater muscle conversion efficiency, selective metabolic suppression of noncritical organ systems under extreme conditions, or other yet undescribed physiological strategies. The finding of extreme reductions in the metabolically active body parts of Bar-tailed Godwits starting trans-Pacific migratory flights compared with fueling birds (Piersma et al. 2021a), tallies with this expectation.

The physiological and biochemical adaptations that allow trans-Pacific migrants to successfully budget energy, water, and nutrients to maintain exercise for over a week remain to be discovered. The classic comparative approach using species and populations facing different flight

BOX 1. PREDICTING FLIGHT DURATION OF TRANS-PACIFIC MIGRANT SHOREBIRDS BASED ON ALLOMETRIC EQUATIONS AND ENERGY EXPENDIUTRES

Here we compare actual and allometrically predicted P_{chem} (chemical power input, or rate of energy expenditure) and maximum flight durations of a variety of trans-Pacific migrant shorebirds for which there are definitive tracking data (Table 1). For Bar-tailed Godwits and Great Knots, we used published preflight and postflight body mass; for other species we used preflight and postflight masses that were, respectively, twice the approximate yearly low body mass recorded during breeding or a tropical overwintering period, and 15% lower (assuming shorebirds can double body mass when fueling and survive mass reduction below normal lean mass; van der Meer and Piersma 1994, Piersma 1998). In sexually size-dimorphic species we used males so that results for Bar-tailed Godwits would be comparable to Gill et al. (2005). Using the average of preflight and postflight masses, we predicted P_{chem} from an allometric equation (Table 1; Bishop and Butler 2015). We then predicted maximum flight duration from the difference between preflight and postflight body mass and a rate of body mass loss per unit of P_{chem} (0.12 g W^{-1}) that assumes energy contributions of 95% fat and 5% protein (39 and 5.5 kJ g^{-1}, respectively). This procedure matched known preflight and postflight body compositions of Great Knots and Bar-tailed Godwits. Actual flight durations are about twice the theoretically predicted maxima from this allometric approach (Table 1).

challenges (Feder et al. 2000, Karasov and Martínez del Rio 2007), coupled with empirical physiological measurements of individual shorebirds during these incredible feats of endurance, will be required to solve the puzzle.

How Are Bodies Strategically Restructured Before and During Long-distance Flights?

Odum et al. (1964) argued that, in terms of fueling, migratory birds are like airplanes—structures with a constant shape but a load of fuel (fat) that is variable. However, subsequent analyses of the body composition of shorebirds revealed something quite different: not only the fat loads but also organ and muscle sizes vary greatly between and within seasons (Piersma 1990, Piersma and Jukema 1990, Battley and Piersma 1997, Piersma et al. 1999, Guglielmo and Williams 2003). The discovery of young Bar-tailed Godwits with tiny guts and livers upon southward departure from Alaska came as the clincher concerning restructuring of body components in long-distance migratory birds (Piersma

BOX 2. PREDICTING FLIGHT DURATION USING SIMULATION PROGRAM *FLIGHT*, BASED ON AERODYNAMICS AND PHYSICAL PRINCIPLES

Here we examine the accuracy of program *Flight* (Pennycuick 2008), a highly parameterized simulation model, for predicting mechanical power output (P_{mech}) and flight duration from physical principles based on the body mass, size and shape of the wing, characteristics of the flight environment (e.g., altitude), and various assumed parameters, most notably the body drag coefficient. P_{mech} is only ~20% of P_{chem}; and P_{chem} is calculated by dividing P_{mech} by a muscle conversion efficiency (η_{fm}; usually assumed to be 0.23), adding basal metabolic rate (BMR), and then multiplying the sum by a respiration factor that adds a 10% overhead (Pennycuick 2008). Starting with the initial body composition of the bird (fat, flight muscle, and remaining airframe masses) and an assumed energy contribution of protein (often 5%), calculations are run in 6-min time steps, body composition is updated, and the simulation runs until fat is exhausted. *Flight* has been used to model trans-Pacific migration of Great Knots (Pennycuick and Battley 2003) and Bar-tailed Godwits (Pennycuick and Battley 2003, Gill et al. 2005), but calculations from the program do not explain the known duration of trans-Pacific flights. Using measured departure and arrival body compositions, the simulations showed that the birds could travel the required geographic distances in still air but both studies predicted flight durations (about 5 days for Great Knots and 7 days for Bar-tailed Godwits) that were a few days shorter than what has been documented in tracking studies (Battley et al. 2012, Piersma et al. 2021b).

Because maximal flight durations are known, a more fruitful approach is to model the conditions necessary to achieve the required flight durations rather than geographic distances between departure and arrival locations. Two physiological parameters, η_{fm} and BMR, are of particular interest because they have very large effects on P_{chem}. Using *Flight* version 1.24 with model settings for Bar-tailed Godwits from Gill et al. (2005) and adjusting muscle conversion efficiency η_{fm} from a default value of 0.23 to 0.3, results in a predicted maximum duration of 218 hours (9.1 days); even with a drag coefficient of 0.1, a similar flight duration can be achieved if η_{fm} is 0.35. Similarly, by reducing the BMR factor in *Flight*, the predicted flight duration increases by up to 24 hr in Bar-tailed Godwits. Higher muscle conversion efficiency and lower BMR are two factors that could account for the much longer flight durations in migratory shorebirds than predicted by models with default values for these parameters.

and Gill 1998). The large amounts of subcutaneous and intraperitoneal fat, combined with the relatively small digestive organs (gizzards, livers, kidneys, and guts), equated to the highest relative fat mass (55% of body mass) recorded in birds. In this early study, Piersma and Gill (1998) concluded that "the small size of the nutritional organs of extremely fat Bar-tailed Godwits … is consistent with the suggestion that it is unprofitable and energetically too expensive to carry a digestive machinery over thousands of kilometers of open ocean (Piersma and Lindström 1997)." Sequential sampling has since confirmed that the small digestive machinery follows active atrophy of the organs (Piersma et al. 2021a for Alaska godwits; Landys-Ciannelli et al. 2003 for northward-migrating Bar-tailed Godwits in Europe).

Indeed, changes occur not only during the fueling (Piersma 1998, Battley and Piersma 2005) and flight phases (Battley et al. 2000) but also during the stationary and postflight phases (van Gils et al. 2007, Vézina et al. 2012). Such changes have invited seemingly straightforward interpretations about the importance of a large digestive apparatus to boost nutrient processing during fueling and then growing larger flight muscles, bigger hearts and thicker blood for sustained flight while simultaneously downsizing the digestive tract and other organs less required during the flight itself. Indeed, laboratory studies demonstrated some of the mechanistic processes in such rapid physiological changes, such as how pectoral muscles in Red Knots (*Calidris canutus*) flown in a wind tunnel change in size relative to body mass (Lindström et al. 2000) and how gizzards in captive Red Knots change in size relative to the quality of the diet (Bijleveld et al. 2014, Mathot et al. 2017).

Although research on temporal changes in organ sizes and fat stores in Pacific migrants has ebbed (but see Hua et al. 2013), there is great scope for further discovery, given the extreme nature of shorebird migration in this geographic arena. For example, in a test of the quantitative prediction of gizzard size of Red Knots from northwest Australia upon arrival in China (Battley et al. 2005), Yang et al. (2013) showed that the main bivalve food along the Chinese coast, *Potamocorbula laevis* (Zhang et al. 2019b, Piersma et al. 2021b), turned out to be heavy-shelled but easy to crush, unlike bivalves in other parts of the world. Illuminating the limits to adaptive organ size adjustments, Zhang et al. (2019a) demonstrated how severe food quality reductions at a main staging site in China, with a magnitude not reported elsewhere before, were associated with increased gizzard size in Great Knots. Similar comparisons of physiological plasticity on critical intertidal staging areas elsewhere in the Pacific and in other migratory systems may yield insights about limiting factors that shape migratory pathways.

Sensing of Time: Do Birds Have Seasonal Clocks?

Red Knots that were confined to aviaries, in which prolonged flight was not possible, still increased pectoral muscle mass at the appropriate seasons for migration, even without power training (Dietz et al. 1999). This hints that seasonal change in flight muscle in knots is regulated by an endogenous "calendar." Experiments involving the withholding of timing cues from birds (especially daylight cycles) provide evidence for a capacity of annual time-keeping (see Gwinner 1986 and Helm et al. 2017 for early and recent reviews of this field, respectively). For shorebirds, this was established by the experimental work with Red Knots held under unvarying ambient temperature and photoperiodic conditions (Karagicheva et al. 2016, 2018).

No such experimental work has been carried out in populations crossing the Pacific, but, as a sense of time is a generic trait for all birds (see discussion in Piersma et al. 2005a), such endogenous calendars should surely exist. Indeed, seasonal clocks are likely to underpin the precise individual timing of migratory movements shown in Bar-tailed Godwits (Conklin et al. 2010, 2013), and provide the framework for building an understanding of the timing adjustments found among individual godwits during the nonbreeding season in New Zealand (Conklin et al. 2021). Different seasonal phenotypic traits (e.g., molt, mass gain) within an individual appear driven by clocks of different rigidity (Karagicheva et al. 2016). Evidence for a positive correlation between circannual-period lengths and species-specific adult annual survival rates suggests that long-lived species will benefit from being late chronotypes and initiating breeding at later, relatively safer times (Karagicheva et al. 2018). These findings highlight the considerable scope available for intraspecific and interspecific comparative analyses of calendar traits (both in captivity and in the wild), within and among individuals crossing the Pacific along various migratory pathways, originating at different latitudes with different photoperiodic conditions, and exhibiting different life-history strategies. In this search, the work by Parody-Merino et al. (2019) has suggested that annual-cycle timing is unlikely to be the result of any simple genetic pathway, but rather the sum of many traits plus ontogeny. In addition, seasonal timing may well be influenced by the ways that individual migrants assess the likely upcoming quality of staging habitats along the flyway, in interaction with assessments of the timing of key resources on the breeding grounds (Conklin et al. 2021).

Cognition of Space: How Do Migrants Orient and Navigate During Trans-Pacific Flights?

"Not all those who wander are lost …" (Tolkien 1954). Almost all vertebrate migrants require the cognitive abilities to know the direction in which they are headed (orientation) and how to reach a destination (navigation). Animal cognition includes all the ways in which "animals take in information about the world through the senses, process, retain, and decide to act on it" (Shettleworth

2001). The orientation and navigation mechanisms used by birds, particularly long-distance migratory shorebirds transiting the Pacific, are predicated on a navigational process that requires a map to define position and a compass to tell direction (Abel 1980, 2000; Åkesson et al. 2014, 2017; Mouritsen 2018, Kok et al. 2020).

Migrating for days on end across vast expanses of open ocean where geographic cues for guidance are limited, trans-Pacific migrant shorebirds clearly possess the tools needed for advanced forms of navigation. Many of the tracks of Bar-tailed Godwits (Battley et al. 2012) and Red Knots (Piersma et al. 2021b) followed over the past 15 years were not the shortest, nor the most direct, yet individuals could locate specific destinations (atolls, discrete estuaries, breeding sites) to which they are strongly site-faithful during stationary phases of their annual cycle (Y.-C. Chan et al. personal communication). Individual flight tracks reflect an array of strategies that vary from direct great circle routes (orthodromes) to what appear to be constant compass headings (loxodromes), while others exhibit marked arching tracks that deviate greatly from either orthodrome or loxodrome routes.

Perhaps the strongest evidence that trans-Pacific migrants know their location relative to their destination lies in numerous examples of adaptive wind drift (*sensu* Chapman et al. 2011), as demonstrated by tracks of Bristle-thighed Curlews, Pacific Golden-Plovers, and Whimbrels (*Numenius phaeopus*; Figure 3). The most pronounced example of this occurs among Bar-tailed Godwits during their migration from the Yellow Sea to Alaska (Figure 4). Here, godwits timed departures with favorable winds associated with synoptic (i.e. broad-scale weather) events embedded in the North Pacific storm track (Gill et al. 2014). Flying eastward along this storm track with strong tail winds, birds tended to track well south (1,000–2,600 km) of the direct 5,300-km-long route. After availing themselves of advantageous winds for some 4,500 km of their flights, godwits showed abrupt course corrections to reorient northeastward towards their goal.

Godwits also exhibited adaptive wind drift with corresponding course corrections when migrating north from New Zealand to the Yellow Sea and south from Alaska to New Zealand (Figure 4), but the deviations were less pronounced. During the southward flight, most birds left on south to southeast flows and drifted southeast for the initial 1,500–2,500 km of their flights (Gill et al. 2009, 2014). Such flows took godwits laterally up to 1,500 km from an orthodrome route to their goal and into or through the zone (approximately 50–30°N) of Westerlies, further promoting eastward drift. But once under the influence of the southwest-flowing trade winds, they reoriented accordingly and continued on a mostly orthodrome track to New Zealand and eastern Australia. This regular course deviation reflected a consistent behavioral choice in orientation to capitalize on wind drift through predictable alternating zones of winds.

Such pronounced course corrections suggest that birds are using orientation and navigation mechanisms other than the inclination compass, which would only allow them to distinguish between "poleward" and "equatorward" directions (Wiltschko and Wiltschko 1972, Åkesson et al. 2014, 2017). Birds in general also use celestial cues such as the stars, the sun, and patterns of skylight polarization as compass mechanisms (Åkesson et al. 2014, 2017), and many species appear to be able to transfer information from one type of compass to another (e.g., Cochran et al. 2004). Navigational maps are less well understood but may be based on physical features or cues from the Earth's magnetic field, wave and wind patterns, and olfactory and infrasonic stimuli (Alerstam 1976, Åkesson and Hedenström 2007, Hagstrum 2013, Thiebot et al. 2020). Maps can be considered mosaic in nature, such as a series of landscape features or other cues that have become recognized through past experience, or gradient in nature, such as isolines of magnetic field intensity and inclination where they form a bi-coordinate grid (Wallraff 1974, Åkesson et al. 2014).

Hedenström (2010) used the movements of Bar-tailed Godwits (Gill et al. 2009, Battley et al. 2012) for a case study of the likely cues for orientation and navigation used by transoceanic migrants. Given the largely southward route that godwits take from Alaska to nonbreeding areas in New Zealand and eastern Australia, he postulated that godwits could simply be using an inclination compass for orientation except for near the equator, where they would need to use other, possibly celestial, cues. However, an inclination compass would not work for the godwits' other two migratory legs (i.e. New Zealand and Australia nonbreeding to Yellow Sea staging, Yellow Sea staging to Alaska breeding; Battley et al. 2012), during which they would need some form of a bi-coordinate map to guide direction (Åkesson et al. 2014). A geomagnetic map would work, especially if the angular difference between isolines for field intensity and inclination is large, which is the case for the last half of the migration of godwits from New Zealand to the Yellow Sea and the initial migration from the Yellow Sea to Alaska (Boström et al. 2012). However, for the initial southward migration from Alaska to Hawaii (~3,500 km) the angular differences along the migration corridor are so small that bi-coordinate navigation would be impossible or extremely difficult (Boström et al. 2012:1,044) and birds would likely have to rely on a different navigational tool.

Given that most trans-Pacific migrations involve multi-day flights that span large blocks of latitude and longitude, it is likely that godwits and other trans-Pacific migrants use time-compensated celestial cues (stars and sun compass) for their primary map, as found in numerous other species of migratory birds (Åkesson et al. 2014). Additional

information could be gained from wave patterns, which in northern and southern parts of the Pacific are driven by seasonally structured macro-scale wind fields (Crowe 2018). Especially during approaching storms or when birds are engaged in adaptive wind drift (Green et al. 2004, Chapman et al. 2011), the wave patterns could help visual orientation (Alerstam 1976) or yield infrasound cues, likely from both prevailing winds (Figure 2) and those associated with synoptic systems (Hagstrum 2013, Weimerskirch and Prudor 2019, Thiebot et al. 2020, Zeyl et al. 2020). Skylight polarization could also be used (Åkesson et al. 2014), but it remains unclear how such information could be used with a time-compensated sun compass (Muheim et al. 2014).

Trans-Pacific migrants are true navigators and, in fact, almost always behave as if they have a Geographical Positioning System (GPS) on board (cf. Thorup and Holland 2009), the nature of which represents one of the great mysteries in biology (Hedenström 2010, Hedenström and Lindström 2014, Muheim et al. 2014, Mouritsen 2018, Barrie 2019, Kok et al. 2020). Advances in remote-tracking technologies and improved interfaces for integrating migration tracks with relevant environmental factors (e.g., Kemp et al. 2012, Fernandez-Lopez and Schliep 2019) will surely contribute to the unraveling of this mystery. This provides a rich scope for comparison between deviations from expectations during cross-ocean flights and those along geographic leading lines such as coasts and over land, both within and among populations and across species. Such observational studies would provide fertile ground for further physiological and experimental work (i.e. blocking specific sensors, etc.).

How Do Marathon Migrants Cope with (a Lack of) Sleep?

In a review of sleep in flying animals, Rattenborg (2017) concluded, "[I]f for some reason sleep is not possible during flapping flight, then species that primarily rely on this flight mode (e.g., brant, shorebirds, and songbirds) might not sleep on the wing." A lack of proper sleep is indeed suggested by the observations made on shorebirds after their arrival in New Zealand. Citing Beth Brown (in OSNZ News 37, December 1985), Schwilch et al. (2002) recounted, "[O]n 21 September newly arrived godwits and knots kept separate from those which had overwintered. While the latter fed on the falling tide, two flocks of recent arrivals slept on. Next day, many more had arrived and the pattern was repeated." Such observations suggest that, after long flights, migrants need not only to refuel but also to catch up on sleep (see also Fuchs et al. 2009, Nemeth 2009). The Red Knots and Bar-tailed Godwits that "slept on" as the intertidal feeding areas became exposed seemed to have prioritized sleep over feeding and vigilance. In this way, they "paid" for catching up on something of which they had apparently incurred a shortage. This would represent an important consequence of the extremely long

migrations by trans-Pacific migrants. However, it is also clear that we have overestimated minimum short-term sleep requirements of animals, as demonstrated by weeks-long periods of little or no sleep during the intensely demanding reproductive season of Arctic-nesting shorebirds (Lesku et al. 2012).

It has been commonly proposed that multi-day flights might involve uni-hemispheric sleep, which has been shown to occur in soaring flight (Rattenborg et al. 2016) and is associated in other taxa with some continuous activities, such as swimming (Rattenborg et al. 2017). We expect, however, that the more constant demands of transoceanic powered flight, which include not only near-constant flapping but engagement with critical systems for orientation and weather monitoring, might exceed the capabilities afforded by uni-hemispheric sleep. Thus, transoceanic flights might be another instance of "adaptive sleep loss," involving no sleep at all for the duration. The recent miniaturization of sleep-recording devices for use on free-living birds is poised to help answer fundamental questions about the needs and processes of sleep during migration. The Pacific theater, given the potential extreme length of sleepless periods even relative to other transoceanic flights, presents us with great research opportunities (Rattenborg et al. 2017, van Hasselt et al. 2020).

ONTOGENY OF MIGRATORY BEHAVIOR

Unless one thinks that birds "simply" follow a genetic blueprint, or program, to carry out their trans-Pacific migrations, a program that is enacted even during the first migration (see review in Piersma et al. 2020), it is interesting to consider that there may be developmental elements to this extreme migratory behavior. In this section, we first ask what governs an individual bird's choice of its initial migratory pathway and then assess the extent to which a bird can alter its routine based on experience accrued over numerous migrations. To what extent do the demonstrated alterations in timing and routes of migration imply cognition of and adjustment to their inherently complex and variable aerosphere? Lastly, we address how adjustment to timing of migration and routes taken may result in seasonal interactions with molt and reproduction (Senner et al. 2015).

How Do Individual Migration Routines Develop Across Time and Space?

As Geertz (1973) profoundly observed, "[W]e all begin with the natural equipment to live a thousand kinds of life but end in the end having lived only one." What makes one life different from another, even in identical twins? How and why can individuals born from the same parents, or in the same area, develop such a great variety of seasonal routines (Verhoeven et al. 2019, 2021a)? To what
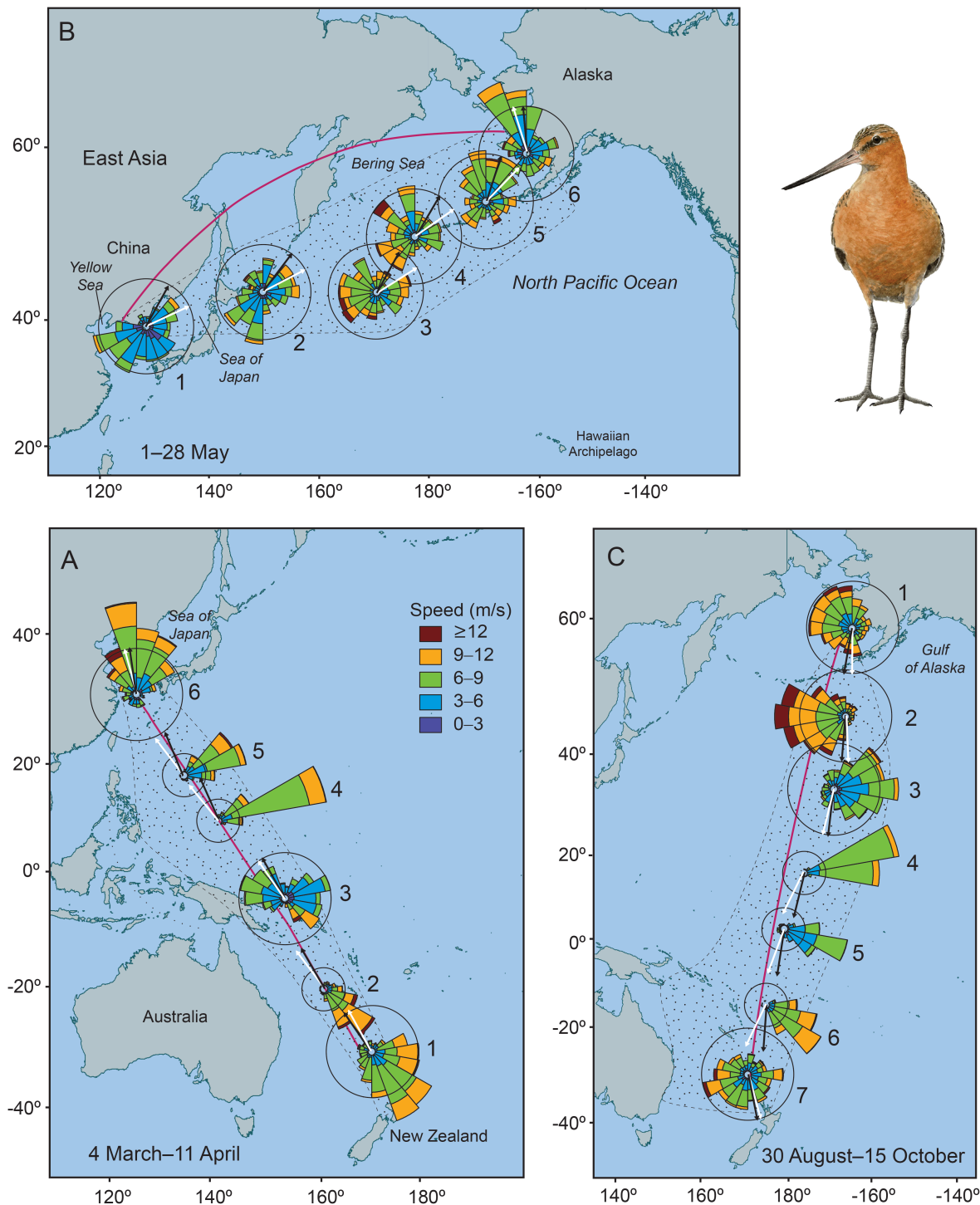
FIGURE 4. Wind rose plots for selected points along migration corridors of 24 satellite-tracked (2006–2010) Bar-tailed Godwits (*L. lapponica baueri*) that show daily mean wind conditions that occurred during each migration period: (A) New Zealand to the Yellow Sea, (B) Yellow Sea to Alaska, and (C) Alaska to New Zealand and eastern Australia (Gill et al. 2014). Plots depict near-surface (10 m above sea level) wind data (Risien and Chelton 2006, 2008; from Climatology of Global Ocean Winds at http://numbat.coas.oregonstate.edu/cogow/) that have been vector-averaged and spatially smoothed over 0.5° latitude and 0.5° longitude grid cells for all dates between first godwit departures and last arrival at the destination between 1999 and 2009. Colors indicate wind speeds, and the length of the sectors extending radially from the center of each rose reflects the relative frequency of winds from that direction. For example, a sector converging to the center of the rose from the northwest indicates the wind is blowing from the northwest. The scale of wind roses varies for legibility, but open circles around each wind rose are scaled to depict 10% frequency of occurrence. The black arrow

extent does ecological context cause this type of variation (Badyaev 2009, Duckworth 2010)?

The development of birds from hatchling to fledgling to mature adult is probably best seen as a strongly intertwined web of reciprocal interactions between a developing organism and its environment: "incremental development" (Bateson 2005, Duckworth 2009, 2010, Frankenhuis and Panchanathan 2011, Panchanathan and Frankenhuis 2015). So far, empirical investigations of the mechanisms to help steer young birds (i.e. those not flying in family groups) along a migration track from the area of birth to a nonbreeding area have focused on genetic aspects. These studies provided evidence for the inheritance, or genomic correlates, of a *clock* for the timing of fueling and flight (e.g., Pulido 2007, Maggini and Bairlein 2010, Pulido and Berthold 2010, Mueller et al. 2011, Bazzi et al. 2015, Saino et al. 2015) and a *compass* for the direction of migration (Helbig 1991, 1996)—the two mechanisms assembled in an inherited *clock-and-compass* system (Berthold 1996, Mouritsen 1998). To explain seasonal migration in birds that supposedly receive no parental guidance during their initial migration away from the area of birth, such as in the Common Cuckoo (*Cuculus canorus*; Willemoes et al. 2014), it was proposed that specific geographic goal areas are genetically inherited (Rabøl 1978, Thorup and Rabøl 2001, Thorup et al. 2003). Yet Weimerskirch et al. (2015), grappling with the interindividual variation of annual routines in Wandering Albatrosses (*Diomedea exulans*), suggested that, rather than being a heritable character, "the individual strategy probably develops from experience during the long immature stage when birds have to learn foraging skills and locate productive waters to which they return subsequently." That the well-explored genetic inheritance pathway is insufficient to explain individual patterns of variation in seasonal migration is especially clear for birds migrating in family groups. Among them, geese and cranes may fully rely on social learning of the relevant ecological conditions during the development of their migration routines (Harrison et al. 2010, Mueller et al. 2013).

The multiple migratory flyways that occur within the Pacific Basin provide some unique opportunities to investigate where shorebirds fall along this gradient between inheritance and learning. Precise descriptions of the individual development of a seasonal migration routine by birds of particular populations, including the variation among individuals (Verhoeven et al. 2019) and how juveniles may differ from older birds (Meyburg et al. 2017, Verhoeven et al. 2018), are mostly lacking for shorebirds migrating across the Pacific, with one notable exception. Sharp-tailed Sandpipers (*Calidris acuminata*) breed on the east Siberian tundra, but only juveniles appear to move east (Handel and Gill 2010) for rapid fueling in southwestern Alaska (Lindström et al. 2011). Most adults appear to leave the Siberian tundra to reach the southern nonbreeding grounds (ephemeral freshwater wetlands in Australia) more directly along a coastal flyway across East Asia (Handel and Gill 2010). The juveniles, which accrue huge fat stores in Alaska (Lindström et al. 2011), reach Australia after a trans-Pacific migration. That juveniles fly separately from adults hints at a "cuckoo-like" story of inherited factors being more important than information learned from experienced conspecifics. How can we find out and would it be different in other species? Battley et al. (2020) showed that the individually consistent timing of northbound migration by Bar-tailed Godwits depends on wintering location and latitude, with juveniles "finding" this location by exploring during early life. Are the first southward migration and subsequent migrations also shaped by social learning and other experiences? For want of in-depth studies, at this point, we turn to some insightful anecdotes.

Consider Alaska Peninsula estuaries, where each autumn three godwit species stage for migration following nesting in Alaska, often in mixed flocks, and where juveniles usually depart after adults (Gill and McCaffery 1999, Ruthrauff et al. 2020, D. R. Ruthrauff and R. E. Gill, Jr., personal observation). The three species have very disparate migration routes, which lead them to nonbreeding areas in New Zealand/Australia (Bar-tailed Godwit; Battley et al. 2012), South America (Hudsonian Godwit *Limosa haemastica*; Senner et al. 2014), and the Pacific coast of the United States (Marbled Godwit *Limosa fedoa*; Ruthrauff et al. 2019). Surprisingly, Hudsonian Godwits are vagrants to the Hawaiian Archipelago (Pyle and Pyle 2017) and irregular visitors to eastern Australia and New Zealand, well west of their normal migration corridor. Because their flights to and from South America are similar in distance to those of Bar-tailed Godwits, Hudsonian Godwits staging with flocks of Bar-tailed Godwits should have lipid stores sufficient to accompany their congeners successfully on 10,000-km-long flights across the Pacific. Joining southward flights of Bar-tailed Godwits likely also explains the 4 records of Marbled Godwits in the Hawaiian Archipelago (Pyle and Pyle 2017). Marbled Godwits are medium-distance migrants and reaching Hawaii is probably at the limit of their flight range

---

emanating from the center of each rose represents the geographic bearing from that location to the destination; the white arrow is the average track bearing of all birds nearest that location. Sample points were selected 300 km past the departure site, 300 km before the destination, and at intervening locations where migratory corridors bisected major wind fields and convergence zones (see Figure 2). Red lines denote great circle routes. Lightly stippled areas define the migration corridors of the tracked godwits (Gill et al. 2014). Map is a Mercator projection. Original illustration of Bar-tailed Godwit by Keith Woodley.

(~4,000 km); this would account for the absence of records farther south in Oceania. Scattered reports of both Bar-tailed and Hudsonian godwits within the wintering range of Marbled Godwits (Hamilton et al. 2007; californiabirds.org; oregonbirding.org/oregon-bird-records-committee/) likely reflect similar congeneric associations. Juveniles predominate among autumn records of vagrant godwits for all three species. These occurrences suggest that social learning, especially among young birds, can override an inherited *clock-and-compass* system. It is easy to imagine the occasional godwit of any of these species becoming integrated into late-staging flocks of congeners. Despite the three godwit species having different migration destinations and routes, the social nature of flocking and the abrupt, en masse departures may be stronger motivators for the onset and orientation of migration than any endogenously programmed stimulus (Helm et al. 2006).

Even if most adult Bar-tailed Godwits and other shorebirds are gone before the juveniles set off, it is possible that a few late adults may provide guidance for some or all of the juvenile flocks. If a successful first migration across the Pacific would indeed require guidance by experienced flock mates, this would put a premium on juveniles being prepared physiologically to migrate with adults. Early-departing young would have much better chances to survive long-distance flights than those departing later after most adults had migrated. Further studies of tagged juveniles in various social groups throughout the season will help elucidate the mechanisms through which individual migratory routines become established.

How Do Individuals Assess and Adjust to the Pacific's Complex Aerosphere?

The importance of winds as a selection factor in bird migration cannot be overstated (Alerstam 1979, 2011, Åkesson and Hedenström 2000, Shamoun-Baranes et al. 2017), and probably nowhere on Earth is the aerosphere as dynamic and yet structured as over the Pacific Basin (Ahrens 2016). At the macro-scale this structure begins with 3 well-defined and essentially closed circulation cells symmetric about the equator, each spanning about 30° of latitude and reaching heights of 10–15 km at the equator but becoming progressively shallower towards the poles. The circulation within and between these cells produces several discrete zonal belts of wind and pressure (e.g., northern and southern hemisphere Westerlies and Trade Winds; Figure 2, after Gill et al. 2014) throughout the lower (<10 km) troposphere, where migration occurs. Within the Pacific Basin, these belts of wind and pressure have greater linearity compared to other regions of the Earth in terms of fluid dynamics, resulting in flows that are considered more predictable by atmospheric scientists (Lee and Kim 2003). But does this predictability hold true for birds as well, and, if so, at what temporal and spatial scales?

Extreme shorebird migrations across the Pacific Basin traverse between 3 and 6 of these zonal wind belts, and success of a nonstop flight is dependent upon an individual's decision as to when and where to fly. Within each zonal belt winds can change (1) daily through convection, especially near the tropics, (2) weekly to monthly through recurring and shifting patterns of pressure and circulation (e.g., Pacific–North American, Western Pacific, Eastern Pacific–North Pacific patterns; subtropical jet stream; and Madden–Julian and Arctic Oscillations), and (3) interannually or decadally in association with phases of large-scale modes of oceanic–atmospheric variability (e.g., Western Pacific Monsoon, El Niño–Southern Oscillation [ENSO], and Pacific Decadal Oscillation [PDO]; Mantua and Hare 2002, Di Lorenzo et al. 2010, Chand and Walsh 2011, Smith et al. 2012, Wang et al. 2012, Feldstein and Franzke 2017).

Atmospheric patterns that affect changes in weather at weekly to monthly time intervals are particularly important for migrating birds, especially the Madden–Julian Oscillation (tropical Pacific; Zhang 2013) and the subtropical jet stream (North Pacific; Lee and Kim 2003). Both of these features affect the location, strength, and structure of broad-scale storms (disturbances), especially in the North Pacific between May and October. The strength of the jet determines the predictability of where and when disturbances will occur (Lee and Kim 2003), but cyclogenesis generally originates in the warm Japanese current and storms gain in intensity as they move eastward across the Pacific into the Gulf of Alaska (Mesquita et al. 2010). Such movement creates patterns of strong general airflow accompanied by troughs and/or ridges and, if birds time their departure from staging areas appropriately, they can capitalize on favorable wind assistance during both eastward (spring) and southward (autumn) migrations (Gill et al. 2014).

Indeed, use of winds by birds has been shown to be highly adaptive in terms of timing between and within seasons (Gill et al. 2009, 2014), routes (Newton 2008, Åkesson and Bianco 2015, Kranstauber et al. 2015), and altitude (Gill et al. 2014, Senner et al. 2019, Lindström et al. 2021), at least to the extent to which birds can predict and discern conditions favorable for long-distance migration. Properly timed decisions will maximize wind profitability and thus reduce energetic costs of migration; conversely, poor decisions or unpredictable weather events will threaten survival (e.g., Watts et al. 2021). Thus, regular long-distance, transoceanic migrants must have the cognitive abilities necessary to assess the variability in atmospheric patterns, evaluate the spatial and temporal extent of these patterns and their associated winds, and incorporate this information into decisions that minimize the risk and optimize the benefits of their annual flights. Studies have shown that Bar-tailed Godwits and other shorebirds do in fact integrate such cues when transiting the Pacific. Not only did satellite-tracked

godwits select favorable winds at all their primary departure sites during their annual cycle (Gill et al. 2009, 2014, Conklin and Battley 2011), but the days they selected for departure also conferred the greatest possible overall wind assistance throughout the remainder of their flights (Gill et al. 2014). Such behavior suggests that there exists an unexplained cognitive mechanism that allows godwits and other trans-Pacific migrants to assess changes in weather conditions that are linked (teleconnected) across widely separated atmospheric regions (Gill et al. 2014, Feldstein and Franzke 2017). Landbird and shorebird migrations across large expanses of the Atlantic Basin are likely similarly linked to birds' cognition of atmospherically teleconnected winds (Richardson 1978, Nigam and Baxter 2015, Carneiro et al. 2020, Watts et al. 2021).

To minimize the cost of transport, trans-Pacific migrant shorebirds should also exhibit adaptive flexibility in their response to en route conditions vertically in the air column (Alerstam and Lindström 1990, Hedenström 2010, Hedenström and Åkesson 2017, Senner et al. 2019, Lindström et al. 2021). For Bar-tailed Godwits previously tracked across the Pacific, technology was not yet sufficient to determine altitude of the birds during flight. Models suggested, however, that optimal flight efficiency would have depended significantly upon active shifts in altitude to maximize wind assistance, and that overall net wind assistance would have been obtained at flight altitudes at or above 3,000 m (Gill et al. 2014). Recently, studies by Senner et al. (2018) of Black-tailed Godwits (*Limosa limosa*) and Lindström et al. (2021) of Great Snipe (*Gallinago media*) migrating between Europe and Africa confirmed such shifts, with diel changes of over 5,000 m altitude.

The behavioral responsiveness of trans-Pacific migrants to spatial shifting of storm tracks, temporal periods of cyclogenesis, and cues associated with stochastic events at departure sites does, however, appear to leave room for improvement. This was evident from case studies of 2 Bar-tailed Godwits that departed with favorable winds but were overtaken by rapidly developing cyclones in which they flew through prolonged periods of strong headwinds (Gill et al. 2009). In both instances, the birds eventually continued on their migrations but with apparent carry-over effects (see also Watts et al. 2021 for Whimbrel in the Atlantic). One northward-migrating godwit did not nest upon reaching the breeding grounds but did successfully migrate back south, while the other southward migrant stopped its migration on a small atoll in the tropical Pacific, 1,600 km short of New Zealand, where its transmitter went silent and the bird presumably died.

Many intriguing questions remain to be answered about how extreme migrant shorebirds choose when to depart and which route to take in navigating vast expanses of ocean. Some birds departed from Alaska when local winds were in opposition over the first few hundred kilometers of their flight, but beyond that they entered long stretches of favorable winds over the North Pacific, resulting in net wind assistance for the entire flight (Figure 4). This implies cognition of not only large-scale seasonal atmospheric patterns but also the variation in synoptic features (e.g., shifting storm tracks) associated with these teleconnected patterns. What are the cues and their limits that govern departure decisions and how is learning involved to fine-tune this complex decision-space? To what extent have the godwits and other extreme endurance migrants buffered the range and duration of their flights (cf. Hedenström 2010) through adjustments of fuel deposition rates, catabolism of protein, water balance, altitudinal wind selection, metabolic costs, and so on? How will projected future changes in atmospheric patterns and their teleconnections affect the frequency and strength of broad-scale weather systems at departure and throughout the flight corridors across the Pacific and over other expansive ecological barriers? The Pacific Basin, by virtue of its complex aerosphere, provides a unique laboratory in which to address such questions for multiple species.

Do Long-distance Migrants Show Reversible State and Other Carry-over Effects?

In a photographic study of uniquely marked Bar-tailed Godwits, Conklin and Battley (2012) showed that individuals arriving late in New Zealand after crossing the Pacific delayed the initiation of wing molt but partially compensated for the delay by increasing the growth rate of the feathers. Delays in arrival (and wing molt) of more than a month did not affect the extent of breeding plumage at northward departure half a year later, nor the timing of this departure. In this example, the timing of southward migration, therefore, carried over to affect the wing molt but not preparations for the subsequent migration and breeding. Carry-over effects denote evidence for circumstances encountered sometime in life affecting subsequent performance (Harrison et al. 2011, O'Connor et al. 2014). These include effects at the scale of the life cycle, such as the circumstances experienced at hatch and differences in the ecological and social contexts during development (Senner et al. 2015), as well as effects occurring at the annual scale, subject to year-to-year variation in environmental conditions (i.e. seasonal interactions; Marra et al. 1998), to which individuals can respond by repeatedly altering phenotypes (Senner et al. 2015). Problems incurred sometime in life may be dissipated so that later performance is not affected (Inger et al. 2010, Legagneux et al. 2012), but earlier life conditions may also lead to a more permanent stratification in higher- and lower-quality individuals (Studds and Marra 2005, Sedinger et al. 2011). To understand this process, the precise developmental origins of individual differences need scrutiny (Senner et al. 2015).

Conklin and Battley (2012) tried to assess the individual adjustments to environmental conditions that would, alone or cumulatively, affect trade-offs and fitness (Senner et al. 2015). Despite these adjustments apparently being common and widespread (Harrison et al. 2011), such "reversible state effects" (defined as the "reversible changes in functional traits resulting from life-history trade-offs during adulthood that affect fitness"; Senner et al. 2015) are surprisingly rare in the extreme migrants of concern here (Conklin and Battley 2012, Senner et al. 2014). To explain this puzzling fact, Conklin et al. (2017) proposed that "severe natural selection, particularly during early life, … quickly removes low-performing individuals and results in populations with a narrow and elevated spectrum of individual quality." Swift et al. (2020) showed that individual Hudsonian Godwits using intertidal nonbreeding habitats in Chile with high godwit densities had comparably better predeparture body condition than individuals foraging in bays with lower densities, a difference that was associated with higher return rates to the Alaska breeding grounds and higher breeding success. This work, however, did not unambiguously show reversible state effects: such individual variation could still have had developmental origins. The exciting field of organismal cross-seasonal interactions thus calls for more such detailed longitudinal studies of individual performance and development, as well as for comparative studies using the worldwide variation in migration strategies found in species such as the Red Knot and Bar-tailed Godwit (Piersma 2007). Studies of the Pacific migrants, which offer the most extreme cases, will be particularly enlightening.

EVOLUTION AND PERSISTENCE OF MIGRATORY BEHAVIOR

The existence of week-long transoceanic flights requires not just the proper environmental and geographic conditions to support it, but individuals that can recognize the 'opportunity' and are properly positioned to benefit from it. From an evolutionary perspective, such a phenomenon raises many questions: How did this behavior evolve? How long has this been going on? Will it persist under rapid and widespread habitat modification and climate change? In this section, we discuss what we know about the recent evolutionary history of shorebird species with populations crossing the Pacific, and the ecological conditions in the Pacific region that enable the presence and persistence of extreme long-distance nonstop flights.

Can Phylogeography Reveal the Evolution of Trans-Pacific Migrations?

The range of avian migratory behavior forms an unbroken continuum, from sedentary through short-distance migration, to extreme long-jump strategies (Piersma 1987).

Migration is thought to evolve through gradual dispersal into regions with different resources and conditions (Salewski and Bruderer 2007, Winger et al. 2019), and may be subject to extension and contraction amid long-term climate oscillations (Zink and Gardner 2017). For this reason, we generally assume that both the need and capacity for extended nonstop flights arose incrementally. Two unique aspects of the Pacific make this an intriguing region to explore the origin of such flights. First, unlike most Arctic regions, Beringia (which includes breeding ranges of all trans-Pacific migratory shorebirds) was largely ice-free during the LGM (Kaufman and Manley 2004), and therefore could have been continuously occupied throughout recent glaciations. Second, southward migration routes from these breeding areas soon encounter at least 3,000 km of land-free ocean expanse. These two aspects mean that, unlike continental migration routes, recent northward expansion of breeding areas was unlikely to contribute to the origin or upscaling of nonstop trans-Pacific flights.

For Bar-tailed Godwits, several conceivable historical scenarios could have led to a direct Alaska–New Zealand flight. Hedenström (2010) envisioned two such scenarios: (1) a continental Palearctic population expanded its breeding and nonbreeding ranges eastward into the Pacific, or (2) an Alaska-breeding population initially migrated to east Asia but gradually shifted its nonbreeding grounds southeastward into Australasia. Both scenarios involve incremental colonization, with each step requiring ever-longer overwater flights and imposing increasing selection for endurance-flight capabilities.

Mayr (1953) invoked a different type of incremental change, arguing that "it seems inconceivable that a migration into or through the central Pacific should have evolved through natural selection if the configuration of land and water had always been exactly the same as today." He envisioned a Pacific Ocean with many archipelagos, now smaller or totally submerged, that previously provided "stepping stones" across the Pacific, and the disappearance of these fostered the evolution of long nonstop flights along historical migration routes. Thus, endurance-flight capacity arose *in situ*, rather than through colonization. Mayr (1953) specifically mentioned periods of the Tertiary (>2.6 million years ago) when such stepping stones were probable, predicting an ancient origin for present-day trans-Pacific migrations. However, periods of dramatically lower sea levels, and greatly enlarged land masses in both Beringia and the South Pacific, also occurred during more recent periods of global cooling, such as the LGM, implying that some upscaling of flights could have occurred in just the last 12,000–18,000 years of rising sea levels. This could have additionally involved the gradual southward drift of nonbreeding areas, if land masses of the mid-Pacific were previously more suitable for intertidal specialists such as Bar-tailed Godwits. Alternatively, Newton (2008) proposed an *in situ* hypothesis that would require no

change in the landforms of the Pacific. For example, a population originally migrating from Alaska to Australasia on an indirect, short-hopping route along coastal Asia could have undergone progressive corner-cutting, involving increasingly longer oceanic flights and a gradual abandonment of previous stepping stones, eventually resulting in a single, direct nonstop flight.

These various scenarios all assume that the essential capacity for trans-Pacific flights was a direct product of the geography and environmental conditions of the Pacific theater. However, we see that in some shorebirds, extended nonstop flights occur without any discernible barrier such as oceans or other inhospitable terrain (e.g., Klaassen et al. 2011, Lislevand et al. 2017). In fact, at least nine species make nonstop flights >5,000 km along the largely land-based flyways of the Americas, compared with seven species crossing from Beringia to islands in the Pacific (Conklin et al. 2017). This implies that nonstop flights can be an equivalent or preferable solution even if intermediate options are available. Therefore, it is possible that the extreme nonstop flights required to cross the Pacific were simply "imported" from another region. For example, Hudsonian Godwits make multiple nonstop flights of 6,000–10,000 km on a journey that follows landmasses of the Americas, even well into the continental interior (Senner et al. 2014), overflying wetland habitats used for stopover and wintering by congeneric Marbled Godwits (Olson et al. 2014). One can imagine these birds expanding their breeding or nonbreeding ranges westward and applying their existing long-jump migration strategy to a new transoceanic route. Such an innovation might occur suddenly, by one or a few migratory flocks being blown off course to discover a new and sustainable migration. Here, we require no incremental scenario specific to the Pacific theater because the essential upscaling occurred elsewhere.

Trapped in the present as we are, how can we discern among possible evolutionary hypotheses? For this sort of inquiry, we require tools that reach into the past, such as combining molecular methods with reconstructions of historical climate and habitat conditions (i.e. phylogeography; Avise et al. 1987, Knowles and Maddison 2002). Ongoing developments in genomic methods provide ever-increasing resolution for exploring recent historical processes (Brito and Edwards 2009). Hedenström (2010) mentions that a phylogeographic study would shed light on our question; indeed, if Alaska-breeding *baueri* Bar-tailed Godwits were a young offshoot of the eastern Palearctic subspecies *menzbieri*, it would argue for his eastward-expansion scenario, and calculation of a population divergence time might then represent a ceiling on how long godwits have been crossing the Pacific.

However, there are several reasons to expect the question is not so easily answered. As stated earlier, Beringia was unglaciated at the LGM, and perhaps continuously occupied by migratory species for millions of years (McLaughlin et al. 2020). Conversely, this does not necessarily imply that trans-Pacific migration itself is very old or was slow to evolve. Evidence is growing that birds can pioneer new migration routes quickly and have done so quite recently. For example, the Red Knot subspecies *rufa* and *islandica* breed in areas of Arctic Canada that were glaciated and unavailable at the LGM; these populations are virtually indistinguishable in neutral genetic variation (Buehler and Baker 2005, Conklin et al. 2022), yet they use different flyways and have a nearly three-fold difference in migration distance (Piersma 2011a). This implies colonization of current breeding areas followed by discovery of a new trans-Atlantic migration route to Europe during just the last few thousand years (Buehler et al. 2006, Conklin et al. 2022).

Phylogeography would be best applied to the evolution of transoceanic flights in a comparative framework, including both widely distributed species that have at least one trans-Pacific migratory population (e.g., Bar-tailed Godwits and Ruddy Turnstones), and those for which the migration might have imposed isolation associated with speciation (e.g., Bristle-thighed Curlew vs. continental *Numenius* species). Such inquiry should involve genomic approaches coupled with reconstructions of historical climate and habitat conditions (ecological niche modeling; e.g., Wauchope et al. 2017). Assuming that a species' ecological requirements are relatively conserved over time (Peterson et al. 1999), we may then discover how long circumstances associated with contemporary migrations have existed, and when and where similar conditions might have occurred in the past. This may also reveal whether trans-Pacific migration relies on rare, potentially temporary, circumstances for its appearance and persistence, or if it is a routine development, robust to environmental changes and open to discovery by multiple evolutionary paths.

How Have Trans-Pacific Migrations Been Shaped by Cross-hemispheric Food and Predator Landscapes?

Although we may have given a different impression in this review so far, in ecological terms long-distance migration is more about fueling than about flight (Lindström et al. 2019). Migratory birds fuel their migrations by consuming excess food (Lindström 2003, Piersma et al. 2005b, van Gils et al. 2005, Rakhimberdiev et al. 2018) and storing the energy from the food as fat (Jenni and Jenni-Eiermann 1998). Access to predictably abundant, high-quality food resources around the Pacific Rim undoubtedly facilitated the evolution of long-distance migration in the region. For many shorebirds and waterbirds, such resources take the form of benthic invertebrates that are exploited along the region's extensive intertidal margins (MacKinnon et al. 2012). Given the impressive scale of the nonstop avian migrations in the

Pacific region, one might assume correspondingly impressive attributes related to the benthic food resources that fuel these migrations. Surprisingly, beyond a comparative study on food availability for Western Sandpipers (*Calidris mauri*) along the Pacific shores of the Americas (Mathot et al. 2007) and the important discovery that in the Pacific Basin biofilm may be grazed by sandpipers (Kuwae et al. 2008, 2012), there is scant empirical evidence on this topic. Site-specific assessments notwithstanding (e.g., Powers et al. 2002, Battley et al. 2011, Hickey et al. 2015, Mathot et al. 2018), there is no synoptic perspective on the abundance and distribution of benthic invertebrate resources in the Pacific Basin, and a notable paucity of information from certain key sites (e.g., Alaska, eastern Australia, New Zealand) hampers such efforts. Numerous site-specific studies elsewhere have clearly established the connection between the quality and abundance of benthic resources and shorebird distributions in general (e.g., Quaintenne et al. 2010, Piersma 2012, Bijleveld et al. 2016), but such studies are rare in the Pacific Basin (Piersma et al. 1993, but see Mathot et al. 2007). Typically (but not always, see Bom et al. 2018), research focuses sampling efforts only where birds occur (e.g., Ruthrauff et al. 2013, Choi et al. 2017), and often the presence of birds alone is taken as evidence of suitable food resources (e.g., Gill and Handel 1990).

Complicating the assumption that a presence of shorebirds reflects suitable benthic resources, is the role that predators play in shaping the distribution of long-distance migrants throughout their annual cycle (Lank et al. 2003, Ydenberg et al. 2007). In fact, it was studies in the Pacific region, notably on Western Sandpipers, that first articulated how falcon (Falconidae) predators may shape the timing of migration and the use of sites (Ydenberg et al 2004, Pomeroy et al. 2006). Thus, does an absence of foraging shorebirds at seemingly suitable migratory staging sites mean that food resources are not present to support these migrants, or instead that the risk from predation outweighs the benefits accrued while foraging (see discussion in van Gils et al. 2004)? Rich intertidal areas in western Alaska have relatively low predation pressure during autumn staging (Handel and Gill 1992, Lindström et al. 2011), and a notable characteristic of intertidal sites in New Zealand is a lack of avian predators, such as eagles and hawks (Accipitridae) and falcons, that might hunt and disturb shorebirds. An absence of predation pressure would ensure that exhausted Bar-tailed Godwits arriving from Alaska could recuperate and regain body condition in a safe, benign environment, and would also facilitate foraging for fueling up for nonstop flights from New Zealand to the Yellow Sea. Interestingly, individuals of the *menzbieri* subspecies of Bar-tailed Godwit embark on nonstop flights of 4,000–5,000 km (Battley et al. 2012) despite an abundance of avian predators on the staging area in northwestern Australia. Such contrasts between foraging opportunities, predation danger, and time constraints would provide rich grounds for insightful ecological comparisons.

What Is the Future of Trans-Pacific Migrations Given Rapid Environmental Change?

We now raise our final question: What might the future hold for trans-Pacific shorebird migrations? Conklin et al. (2017) stated that "the most extreme shorebird migrations rely on abundant but difficult-to-access resources; the high minimum individual performance required for survival predicts that degradation of these resource hot-spots will propel rapid population collapse, rather than incremental declines in condition or performance." Recent large-scale intertidal land claim schemes along the coast of East Asia (Ma et al. 2014, Murray et al. 2014, Melville et al. 2016) are unintentionally providing sobering insights into the theory of "high minimum performance" requirements in Pacific migrants. The reclamation and degradation of sites in the Yellow Sea region correspond with declining vital rates (Conklin et al. 2016, Piersma et al. 2016) and declining numbers (Studds et al. 2017, Wang et al. 2018) of the migratory birds in the region.

The monitoring of long-distance migratory shorebirds and their benthic food resources in the Yellow Sea at Yalu Jiang, China, over a 6-year period, demonstrated a sudden near-complete disappearance of the shorebirds' primary prey resources (Zhang et al. 2018). The surprising finding that the use of the site remained relatively unchanged was interpreted to reflect a lack of alternative sites available to the birds (Zhang et al. 2018). Zhang et al. (2019a) further demonstrated that Great Knots increased the size of their gizzards over this same period to facilitate the consumption of the low-quality, thick-shelled prey that now dominate the site. Thus, long-distance migratory shorebirds to some extent manage to accommodate drastic changes in the abundance or quality of food resources, but such changes may nevertheless come at the expense of decreased survival (Rakhimberdiev et al. 2018).

How can the migrants of the Pacific, and indeed the migratory birds of the world, cope with rapid anthropogenically driven loss and change of staging areas throughout their annual cycles (Iwamura et al. 2013)? Similarly, how will global sea level rise affect the integrity of these critical areas (Murray et al. 2019)? How do birds deal with changes in the temporal and spatial characteristics of their Arctic breeding habitats (Wauchope et al. 2017), in conjunction with simultaneous changes in staging and nonbreeding areas (van Gils et al. 2016, Rakhimberdiev et al. 2018)? Such questions become ever more pressing in the face of unprecedented changes in especially the East Asian part of the Pacific Basin (e.g., Barter 2002, Ma et al. 2014, MacKinnon et al 2012, Murray et al. 2014, Melville et al. 2016, Zhang et al. 2018).

GENERAL DISCUSSION

The Pacific Basin provides a superb and unique natural laboratory for learning about multiple facets of migratory

behavior, and our understanding of the mechanisms, stimuli, and consequences of this behavior can be increased by continuing and expanding research on transoceanic migrant shorebirds at various time scales. These long-lived shorebird species provide special opportunities to address important questions about how individual birds respond to environmental change occurring over the course of decades and the mechanisms that they employ to do so (e.g., Battley et al. 2020, Conklin et al. 2021). When, during their annual cycles, is mortality highest (Senner et al. 2019)? Or is it equal across the year as would be the expectation when populations have adjusted to a particular situation (Rakhimberdiev et al. 2015)? Do individuals learn new ecological settings, especially during early life, so that adjustments to environmental change occur across generations (Verhoeven et al. 2018, Gill et al. 2019), are they engaged in life-long learning (Sergio et al. 2014), or is migratory behavior genetically so 'tied up' and fixed that large populations and enough time are required for natural selection to do the hard work (Piersma 2011a)? Comparisons of juveniles and adults during southward migration should help us tease apart the factors in this relevant interplay between learned and genetic mechanisms for timing, orientation, and navigation (Jablonka and Lamb 2014, Verhoeven et al. 2021b).

As we have seen, the duration of nonstop flights during migration challenges the current understanding of flight costs and should provide opportunities to further explore the energetics of flight. The spatial and temporal characteristics of these flights, mapped by ever smaller and more sophisticated tracking devices (Chan et al. 2019, Piersma et al. 2021b), enable explorations on the cognitive aspects of traveling half of the globe (e.g., Kok et al. 2020), i.e. how birds are listening and responding to the vast and complex three-dimensional atmospheric landscape across not only the Pacific but also other broad oceanographic regions. Continued individual-based studies on survival and reproduction (e.g., Conklin et al. 2016, Piersma et al. 2016) may illuminate reversible state and other types of seasonal carry-over effects (Senner et al. 2015) and fitness consequences of different behavioral choices of birds during migration. In fact, ongoing comparative demographic studies in the Pacific region are doing just that (Weiser et al. 2020).

Comparisons among species or populations using different migratory routes (e.g., Lagassé et al. 2020) will shed light on the limitations of nonstop flights under different atmospheric conditions. For example, carefully constructed comparative studies of the northward migration routes of species or populations may reveal why some fly straight north across the Pacific (Bristle-thighed Curlews, Hawaii-wintering Pacific Golden-Plovers) whereas others do not (Bar-tailed Godwits, Australia-wintering plovers). Is it impossible for New Zealand-wintering Bar-tailed Godwits to complete a direct return flight to breeding grounds in Alaska? If it is, is this a legacy (due to deep histories of route-taking) or is it a true physiological limitation

(birds that tried were selected out of the population)? Complementary fruitful comparisons could be made between the long-distance migrants staging in coastal Alaska before embarking on southward trans-Pacific nonstop flights and related shorebirds such as Rock Sandpipers (*Calidris ptilocnemis*), which remain to overwinter in Alaska and are thus subjected to a different set of extreme conditions (Ruthrauff et al. 2013, 2018).

If indeed these most extreme shorebird migrants are primarily high-quality individuals that rely on abundant but very patchy resources, it paradoxically means that even while individuals may not be operating close to the edge, populations may (Conklin et al. 2017). Now that the migrations across and around the Pacific appear threatened by rapid anthropogenic change (Ma et al. 2014, Studds et al. 2017), continued screening of individuals, populations, and the resources they depend on, at a great range of locales, is necessary to understand the extent to which these birds can achieve real-time adjustments to new environmental contexts, both in positive (Tibbitts et al. 2020) and negative ways (Zhang et al. 2018, 2019a). Clearly, the relationships between food resources, their consumers, and the predators that in turn exploit the consumers is complex, and the paucity of information on the interplay of these factors across this region currently precludes rigorous investigation of these important topics.

The rich portfolio of studies reviewed in this paper demonstrates that the tools to describe migration systems comprehensively and comparatively do currently exist: sampling of food resources; counting, tracking, and monitoring the survival of individuals and populations; enumerating the effects of predators; and lifetime-tracking of (necessarily smaller samples of) individuals. For trans-Pacific migrants, the spatial scale over which such work must be implemented is daunting. Nevertheless, the rapid pace and massive scale of anthropogenic change in the Pacific Basin means that such information is critical. Solid science and beguiling stories can help generate the 'public will' to promote conservation of these long-distance migrants. Comparative research within the Pacific and across other complex migratory arenas should yield important insights about the inherent capabilities of migrating birds, their behavioral plasticity and limiting factors, and the past, current, and future evolution of migratory pathways.

ACKNOWLEDGMENTS

LITERATURE CITED

Able, K. P. (1980). Mechanisms of orientation, navigation, and homing. In Animal Migration, Orientation, and Navigation (S. A. Gauthreaux, Jr., Editor). Academic Press, New York, NY, USA. pp. 283–373.

Able, K. P. (2000). The concepts and terminology of bird navigation. Journal of Avian Biology 32:174–183.

Ahrens, C. D. (2016). Meteorology Today: An Introduction to Weather, Climate, and the Environment, 11th edition. Thomson Brooks/Cole, Belmont, CA, USA.

Åkesson, S., and G. Bianco (2015). Assessing vector navigation in long-distance migrating birds. Behavioral Ecology 27:865–875.

Åkesson, S., and A. Hedenström (2000). Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47:140–144.

Åkesson, S., and A. Hedenström (2007). How migrants get there: Migratory performance and orientation. BioScience 57:123–133.

Åkesson, S., J. Boström, M. Liedvogel, and R. Muheim (2014). Animal navigation. In Animal Movements Across Scales (L.-A. Hansson and S. Åkesson, Editors). Oxford University Press, Oxford, UK. pp. 151–178.

Åkesson, S., M. Ilieva, J. Karagicheva, E. Rakhimberdiev, B. Tomotani, and B. Helm (2017). Timing avian long-distance migration: From internal clock mechanisms to global flights. Philosophical Transactions of the Royal Society B 372:20160252.

Alerstam, T. (1976). Do birds use waves for orientation when migrating across the sea? Nature 259:205–207.

Alerstam, T. (1979). Wind as selective agent in bird migration. Ornis Scandinavica 10:76–93.

Alerstam, T. (2011). Optimal bird migration revisited. Journal of Ornithology 152:5–23.

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: The relative importance of time, energy, and safety. In Bird Migration: Physiology and Ecophysiology (E. Gwinner, Editor). Springer-Verlag, Berlin, Germany. pp. 331–351.

Avise, J., J. Arnold, R. Ball, E. Bermingham, T. Lamb, J. Neigel, C. Reeb, and N. Saunders (1987). Intraspecific phylogeography—the mitochondrial-DNA bridge between population genetics and systematics. Annual Review of Ecology, Evolution, and Systematics 40:593–612.

Badyaev, A. V. (2009). Evolutionary significance of phenotypic accommodation in novel environments: An empirical test of the Baldwin effect. Philosophical Transactions of the Royal Society B 364:1125–1141.

Badyaev, A. V. (2018). Evolutionary transitions in controls reconcile adaptation with continuity of evolution. Seminars in Cell & Developmental Biology 88:36–35.

Baker, A. J., P. González, R. I. G. Morrison, and B. A. Harrington (2020). Red Knot (*Calidris canutus*), version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.redkno.01

Baker, R. H. (1951). The avifauna of Micronesia, its origin, evolution, and distribution. University of Kansas Publications, Museum of Natural History 3:1–359.

Barr, J. (2003). On metaphysics and Polynesian navigation. In Seeing God Everywhere: Essays on Nature and Sacred (B. McDonald, Editor). World Wisdom, Inc., Bloomington, IN, USA. pp. 161–170.

Barrie, D. (2019). Supernavigators: Exploring the Wonders of How Animals Find Their Way. The Experiment, New York, NY, USA.

Barter, M. (2002). Shorebirds of the Yellow Sea: Importance, Threats and Conservation Status. Wetlands International Global Series 9, International Wader Studies 12, Canberra, Australia. 104 pp.

Bateson, P. (2005). The return of the whole organism. Journal of Bioscience 30:31–39.

Battley, P. F., and T. Piersma (1997). Body composition of Lesser Knots (*Calidris canutus rogersi*) preparing to take off on migration from northern New Zealand. Notornis 44:137–150.

Battley, P. F., and T. Piersma (2005). Adaptive interplay between feeding ecology and features of the digestive tract in birds. In Physiological and Ecological Adaptations to Feeding in Vertebrates (J. M. Starck and T. Wang, Editors). Science Publishers, Enfield, NH, USA. pp. 201–228.

Battley, P. F., T. Piersma, M. W. Dietz, S. Tang, A. Dekinga, and K. Hulsman (2000). Empirical evidence for differential organ reductions during trans-oceanic bird flight. Proceedings of the Royal Society of London B 267:191–196.

Battley, P. F., D. I. Rogers, J. A. van Gils, T. Piersma, C. J. Hassell, A. Boyle, and H.-Y. Yang (2005). How do Red Knots *Calidris canutus* leave Northwest Australia in May and reach the breeding grounds in June? Predictions of stopover times, fuelling rates and prey quality in the Yellow Sea. Journal of Avian Biology 36:494–500.

Battley, P. F., D. S. Melville, R. Schuckard, and P. F. Ballance (2011). *Zostera muelleri* as a structuring agent of benthic communities in a large intertidal sandflat in New Zealand. Journal of Sea Research 65:19–27.

Battley, P. F., N. Warnock, T. L. Tibbitts, R. E. Gill, Jr., T. Piersma, C. J. Hassell, D. C. Douglas, D. M. Mulcahy, B. D. Gartrell, R. Schuckard, D. S. Melville, and A. C. Riegen (2012). Contrasting extreme long-distance migration patterns in Bar-tailed Godwits *Limosa lapponica*. Journal of Avian Biology 43:21–32.

Battley, P. F., J. R. Conklin, Á. M. Parody-Merino, P. A. Langlands, I. Southey, T. Burns, D. S. Melville, R. Schuckard, A. C. Riegen, and M. A. Potter (2020). Interacting roles of breeding geography and early-life settlement in godwit migration timing. Frontiers in Ecology and Evolution 8:52.

Bazzi, G., R. Ambrosini, M. Caprioli, A. Constanzo, F. Liechti, E. Gatti, L. Gianfranceschi, S. Podofillini, A. Romano, M. Romano, C. Scandolara, et al. (2015). *Clock* gene polymorphism and scheduling of migration: A geolocator study of the Barn Swallow *Hirundo rustica*. Scientific Reports 5:12443.

Berthold, P. (1996). Control of Bird Migration. Chapman & Hall, London, UK.

Bijleveld, A. I., G. Massourakis, A. van der Marel, A. Dekinga, B. Spaans, J. A. van Gils, and T. Piersma (2014). Personality drives physiological adjustments and is not related to survival. Proceedings of the Royal Society B 281:20133135.

Bijleveld, A. I., R. B. MacCurdy, Y.-C. Chan, E. Penning, R. M. Gabrielson, J. Cluderay, E. L. Spaulding, A. Dekinga, S. Holthuijsen, J. ten Horn, M. Brugge, et al. (2016). Understanding spatial distributions: Negative density-dependence in prey causes predators to trade-off prey quantity with quality. Proceedings of the Royal Society B 283:20151557.

Bishop, C. M., and P. J. Butler (2015). Flight. In Sturkie's Avian Physiology, 6th edition (C. G. Scanes, Editor). Elsevier, London, UK. pp. 919–974.

Block, B. A., I. D. Jonsen, S. J. Jorgensen, A. J. Winship, S. A. Shaffer, S. J. Bograd, E. L. Hazen, D. G. Foley, G. A. Breed, A.-L. Harrison, J. E. Ganong, et al. (2011). Tracking apex predator movements in a dynamic ocean. Nature 475:86–90.

Bom, R. A., J. de Fouw, R. H. G. Klaassen, T. Piersma, M. S. S. Lavaleye, B. J. Ens, T. Oudman, and J. A. van Gils (2018). Food web consequences of an evolutionary arms race: Molluscs subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds. Journal of Biogeography 45:342–354.

Boström, J. E., S. Åkesson, and T. Alerstam (2012). Where on earth can animals use a geomagnetic bi-coordinate map for navigation? Ecography 35:1039–1047.

Brito, P. H., and S. V. Edwards (2009). Multilocus phylogeography and phylogenetics using sequence-based markers. Genetica 135:439–455.

Buehler, D. M., and A. J. Baker (2005). Population divergence times and historical demography in Red Knots and Dunlins. The Condor 107:497–513.

Buehler, D. M., A. J. Baker, and T. Piersma (2006). Reconstructing palaeoflyways of the late Pleistocene and early Holocene Red Knot *Calidris canutus*. Ardea 94:485–498.

Bull, P. C. (1948). Field notes on waders in the south-west Pacific with special reference to the Russell Islands. Emu 47:165–176.

Burger, A. E., and S. A. Shaffer (2008). Application of tracking and data-logging technology in research and conservation of seabirds. The Auk 125:253–264.

Carneiro, C., T. G. Gunnarsson, and J. A. Alves. 2020. Linking weather and phenology to stopover dynamics of a long-distance migrant. Frontiers in Ecology and Evolution 8:145.

Chan, Y.–C., T. L. Tibbitts, T. Lok, C. J. Hassell, H.–B. Z. Ma, Z. W. Zhang, and T. Piersma (2019). Filling knowledge gaps in a threatened shorebird flyway through satellite tracking. Journal of Applied Ecology 56:2305–2315.

Chand, S. S., and K. J. E. Walsh (2011). Influence of ENSO on tropical cyclone intensity in the Fiji Region. Journal of Climate 24:4096–4108.

Chapman, J. W., R. H. G. Klaassen, V. A. Drake, S. Fossette, G. C. Hays, J. D. Metcalfe, A. M. Reynolds, D. R. Reynolds, and T. Alerstam (2011). Animal orientation strategies for movement flows. Current Biology 21:R861–R870.

Choi, C.-Y., P. F. Battley, M. A. Potter, Z. Ma, D. S. Melville, and P. Sukkaewmanee (2017). How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species. The Auk: Ornithological Advances 134:76–91.

Cochran, W. W., H. Mouritsen, and M. Wikelski (2004). Migrating songbirds recalibrate their magnetic compass daily from twilight cues. Science 304:405–408.

Conklin, J. R., and P. F. Battley (2011). Impacts of wind on individual migration schedules of New Zealand Bar-tailed Godwits. Behavioral Ecology 22:854–861.

Conklin, J. R., and P. F. Battley (2012). Carry-over effects and compensation: Late arrival on non-breeding grounds affects wing moult but not plumage or schedules of departing Bar-tailed Godwits. Journal of Avian Biology 43:252–263.

Conklin, J. R., P. F. Battley, M. A. Potter, and J. W. Fox (2010). Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. Nature Communications 1:67.

Conklin, J. R., P. F. Battley, and M. A. Potter (2013). Absolute consistency: Individual versus population variation in annual cycle schedules of a long-distance migrant bird. PLoS One 8:e54535.

Conklin, J. R., T. Lok, D. S. Melville, A. C. Riegen, R. Schuckard, T. Piersma, and P. F. Battley (2016). Declining adult survival of New Zealand Bar-tailed Godwits during 2005–2012 despite apparent population stability. Emu 116:147–157.

Conklin, J. R., N. R. Senner, P. F. Battley, and T. Piersma (2017). Extreme migration and the individual quality spectrum. Journal of Avian Biology 48:19–36.

Conklin, J. R., S. Lisovski, and P. F. Battley (2021). Advancement in long-distance bird migration through individual plasticity in departure. Nature Communications 12:4780.

Conklin, J. R., Y. I. Verkuil, P. F. Battley, C. J. Hassell, J. ten Horn, J. A. Johnson, P. S. Tomkovich, A. J. Baker, T. Piersma, and M. C. Fontaine (2022). Global flyway evolution in Red Knots

Calidris canutus and genetic evidence for a Nearctic refugium. Molecular Ecology in press. Authorea preprint: https://doi.org/10.22541/au.162597680.07818696/v1

Costantini, D., M. Cardinale, and C. Carere (2007). Oxidative damage and anti-oxidant capacity in two migratory bird species at a stop-over site. Comparative Biochemistry and Physiology C 144:363–371.

Crowe, A. (2018). Pathway of the Birds: The Voyaging Achievements of Māori and Their Polynesian Ancestors. University of Hawai'i Press, Honolulu, HI, USA.

Cunliffe, B. (2017). On the Ocean: The Mediterranean and the Atlantic from Prehistory to AD 1500. Oxford University Press, New York, NY, USA.

Dick, M. F., and C. G. Guglielmo (2019). Flight muscle protein damage during endurance flight is related to energy expenditure but not dietary polyunsaturated fatty acids in a migratory bird. Journal of Experimental Biology 222:187708.

Dietz, M. W., T. Piersma, and A. Dekinga (1999). Body-building without power training: Endogenously regulated pectoral muscle hypertrophy in confined shorebirds. Journal of Experimental Biology 202:2831–2837.

Di Lorenzo, E., K. M. Cobb, J. C. Furtado, N. Schneider, B. T. Anderson, A. Bracco, M. A. Alexander, and D. J. Vimont (2010). Central Pacific El Niño and decadal climate change in the North Pacific Ocean. Nature Geoscience 3:762–765.

Driscoll, P. V., and M. Ueta (2002). The migration route and behaviour of Eastern Curlews *Numenius madagascariensis*. Ibis 144:E119–E130.

Duckworth, R. A. (2009). The role of behavior in evolution: A search for mechanism. Evolutionary Ecology 23:513–531.

Duckworth, R. A. (2010). Evolution of personality: Developmental constraints on behavioral flexibility. The Auk 127:752–758.

Feder, M. A., A. F. Bennett, and R. B. Huey (2000). Evolutionary physiology. Annual Review of Ecology and Systematics 31:315–341.

Feinberg, R. (2020). People, birds, canoes, and seafaring in the Pacific Islands. Český lid 107:335–350. Institute of Ethnology, Czech Academy of Sciences, Prague, Czech Republic. https://doi.org/10.21104/CL.2020.3.03

Feldstein, S., and C. Franzke (2017). Atmospheric teleconnection patterns. In Nonlinear and Stochastic Climate Dynamics (C. Franzke and T. O'Kane, Editors). Cambridge University Press, New York, NY, USA. pp. 54–104.

Fernandez-Lopez, J., and K. Schliep (2019). rWind: Download, edit and include wind data in ecological and evolutionary analysis. Ecography 42:804–810.

Frankenhuis, W. E., and K. Panchanatha (2011). Balancing sampling and specialization: An adaptationist model of incremental development. Proceedings of the Royal Society B 278:3558–3565.

Fuchs, T., D. Maury, F. R. Moore, and V. P. Bingman (2009). Daytime micro-naps in a nocturnal migrant: An EEG analysis. Biology Letters 5:77–80.

Geertz, C. (1973). The Interpretation of Cultures: Selected Essays. Basic Books, New York, NY, USA.

Gerson, A. R., and C. G. Guglielmo (2011). Endurance flight at low ambient humidity increases protein catabolism in migratory birds. Science 333:1434–1436.

Gill, J. A., J. A. Alves, and T. G. Gunnarsson (2019). Mechanisms driving phenological and range change in migratory species. Philosophical Transactions of the Royal Society B 374:20180047.

Gill, R. E., Jr., and C. M. Handel (1990). The importance of subarctic intertidal habitats to shorebirds: A study of the central Yukon-Kuskokwim Delta, Alaska. The Condor 92:709–725.

Gill, R. E., Jr., and P. D. Jorgensen (1979). A preliminary assessment of the timing and migration of shorebirds along the northcentral Alaska Peninsula. Studies in Avian Biology 2:110–120.

Gill, R. E., Jr., and B. J. McCaffery (1999). Bar-tailed Godwits *Limosa lapponica* in Alaska: A population estimate from the staging grounds. Wader Study Group Bulletin 88:49–54.

Gill, R. E., Jr., M. R. Petersen, and P. D. Jorgensen (1981). Birds of the northcentral Alaska Peninsula, 1976–1980. Arctic 34:286–306.

Gill, R. E., Jr., T. Piersma, G. Hufford, R. Servranckx, and A. Riegen (2005). Crossing the ultimate ecological barrier: Evidence for an 11,000-km-long nonstop flight from Alaska to New Zealand and eastern Australia by Bar-tailed Godwits. The Condor 107:1–20.

Gill, R. E., Jr., T. L. Tibbitts, D. C. Douglas, C. M. Handel, D. M. Mulcahy, J. C. Gottschalck, N. Warnock, B. J. McCaffery, P. F. Battley, and T. Piersma (2009). Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? Proceedings of the Royal Society B 276:447–457.

Gill, R. E., Jr., D. C. Douglas, C. M. Handel, T. L. Tibbitts, G. Hufford, and T. Piersma (2014). Hemispheric-scale wind selection facilitates Bar-tailed Godwit circum-migration of the Pacific. Animal Behaviour 90:117–130.

Green, M., T. Alerstam, G. A. Gudmundsson, A. Hedenström, and T. Piersma (2004). Do Arctic waders use adaptive wind drift? Journal of Avian Biology 35:305–315.

Guglielmo, C. G. (2010). Move that fatty acid: Fuel selection and transport in migratory birds and bats. Integrative and Comparative Biology 50:336–345.

Guglielmo, C. G., and T. D. Williams (2003). Phenotypic flexibility of body composition in relation to migratory state, age, and sex in the Western Sandpiper (*Calidris mauri*). Physiological Biochemical Zoology 76:84–98.

Guglielmo, C. G., T. Piersma, and T. D. Williams (2001). A sport-physiological perspective on bird migration: Evidence for flight-induced muscle damage. Journal of Experimental Biology 204:2683–2690.

Gwinner, E. (1986). Circannual Rhythms: Endogenous Annual Clocks in the Organization of Seasonal Processes. Springer-Verlag, Berlin, Germany.

Hagstrum, J. T. (2013). Atmospheric propagation modeling indicates homing pigeons use loft-specific infrasonic 'map' cues. Journal of Experimental Biology 26:687–699.

Hamilton, R. A., M. A. Patten, and R. A. Erickson (Editors) (2007). Rare Birds of California. California Bird Records Committee. Western Field Ornithologists, Camarillo, CA, USA.

Handel, C. M., and R. E. Gill, Jr. (1992). Roosting behavior of premigratory Dunlins (*Calidris alpina*). The Auk 109:57–72.

Handel, C. M., and R. E. Gill, Jr. (2010). Wayward youth: Trans-Beringian movement and differential southward migration by juvenile Sharp-tailed Sandpipers. Arctic 63:273–288.

Harris, P. T., M. Macmillan-Lawler, J. Rupp, and E. K. Baker (2014). Geomorphology of the oceans. Marine Geology 352:4–24.

Harrison, X. A., T. Tregenza, R. Inger, K. Colhoun, D. A. Dawson, G. A. Gudmundsson, D. J. Hodgson, G. J. Horsburgh,

G. McElwaine, and S. Bearhop (2010). Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. Molecular Ecology 19:5484–5496.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop (2011). Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18.

Hedenström, A. (2010). Extreme endurance migration: What is the limit to nonstop flight? PLoS Biology 8:e1000362.

Hedenström, A., and S. Åkesson (2017). Adaptive airspeed adjustments and compensation for wind drift in the Common Swift: Differences between day and night. Animal Behaviour 127:117–123.

Hedenström, A., and Å. Lindström (2014). Migration and flight strategies in animals: New insights from tracking migratory journeys. In Animal Movements Across Scales (L.-A. Hansson and S. Åkesson, Editors). Oxford University Press, Oxford, UK. pp. 73–89.

Hedh, L., C. G. Guglielmo, L. C. Johansson, J. E. Deakin, C. C. Voigt, and A. Hedenström (2020). Measuring power input, power output and energy conversion efficiency in un-instrumented flying birds. Journal of Experimental Biology 223:jeb223545.

Helbig, A. J. (1991). Inheritance of migratory direction in a bird species: A cross-breeding experiment with SE- and SW-migrating Blackcaps (Sylvia atricapilla). Behavioral Ecology and Sociobiology 28:9–12.

Helbig, A. J. (1996). Genetic basis, mode of inheritance and evolutionary changes of migratory directions in Palearctic warblers (Aves: Sylviidae). Journal of Experimental Biology 199:49–55.

Helm, B., T. Piersma, and H. P. van der Jeugd (2006). Sociable schedules: Interplay between avian seasonal and social behaviour. Animal Behaviour 72:245–262.

Helm, B., M. E. Visser, W. Schwartz, N. Kronfeld-Schor, M. Gerkema, T. Piersma, and G. Bloch (2017). Two sides of a coin: Ecological and chronobiological perspectives of timing in the wild. Philosophical Transactions of the Royal Society B 372:20160246.

Hickey, R. J., G. B. Pearson, and T. Piersma (2015). Advances in large-scale mudflat surveying: The Roebuck Bay and Eighty Mile Beach, western Australia examples. In Environmental Management and Governance: Advances in Coastal and Marine Resources (C. W. Finkl and C. Makowski, Editors). Springer International Publishing, Switzerland, pp. 275–289.

Hogan, J. A. (1994). The concept of cause in the study of behavior. In Causal Mechanisms of Behavioural Development (J. A. Hogan and J. J. Bolhuis, Editors). Cambridge University Press, Cambridge, UK. pp. 3–15.

Hogan, J. A. (2017). The Study of Behavior: Organization, Methods, and Principles. Cambridge University Press, Cambridge, UK.

Hua, N., T. Piersma, and Z. Ma (2013). Three-phase fuel deposition in a long-distance migrant, the Red Knot (Calidris canutus piersmai), before the flight to High Arctic breeding grounds. PLoS One 8:e62551.

Inger, R., X. A. Harrison, G. D. Ruxton, J. Newton, K. Colhoun, G. A. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop (2010). Carry-over effects reveal reproductive costs in a long-distance migrant. Journal of Animal Ecology 79:974–982.

Inglis, J. T. (Editor) (1993). Traditional Ecological Knowledge: Concepts and Cases. International Program on Traditional Ecological Knowledge, International Development Research Centre, Ottawa, ON, Canada.

Iwamura, T., H. P. Possingham, I. Chades, C. Minton, N. J. Murray, D. I. Rogers, E. A. Treml, and R. A. Fuller (2013). Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proceedings of the Royal Society B 280:20130325.

Jablonka, E., and M. J. Lamb (2014). Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life. MIT Press, Cambridge, MA, USA.

Jenni, L., and S. Jenni-Eiermann (1998). Fuel supply and metabolic constraints in migrating birds. Journal of Avian Biology 29:521–528.

Johnson, O. W., L. Fielding, J. P. Fisher, R. S. Gold, R. H. Goodwill, A. E. Bruner, J. F. Furey, P. A. Brusseau, N. H. Brusseau, P. M. Johnson, J. Jukema, et al. (2012). New insight concerning transoceanic migratory pathways of Pacific Golden-Plovers (Pluvialis fulva): The Japan stopover and other linkages as revealed by geolocators. Wader Study Group Bulletin 119:1–8.

Johnson, O. W., R. R. Porter, L. Fielding, M. F. Weber, R. S. Gold, R. H. Goodwill, P. M. Johnson, A. E. Bruner, P. A. Brusseau, N. H. Brusseau, K. Hurwitz, and J. W. Fox (2015). Tracking Pacific Golden-Plovers Pluvialis fulva: Transoceanic migrations between non-breeding grounds in Kwajalein, Japan and Hawaii and breeding grounds in Alaska and Chukotka. Wader Study 122:4–11.

Johnson, O. W., P. G. Connors, and P. Pyle (2020). Pacific Golden-Plover (Pluvialis fulva), version 1.0. In Birds of the World (P. G. Rodewald and B. K. Keeney, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.pagplo.01

Karagicheva, J., E. Rakhimberdiev, A. Dekinga, M. Brugge, A. Koolhaas, J. ten Horn, and T. Piersma (2016). Seasonal time keeping in a long-distance migrating shorebird. Journal of Biological Rhythms 31:509–521.

Karagicheva, J., E. Rakhimberdiev, A. Saveliev, and T. Piersma (2018). Annual chronotypes functionally link life histories and life cycles in birds. Functional Ecology 32:2369–2379.

Karasov, W. H., and C. Martínez del Rio (2007). Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins. Princeton University Press, Princeton, NJ, USA.

Kaufman, D. S., and W. F. Manley (2004). Pleistocene Maximum and Late Wisconsinan glacier extents across Alaska, U.S.A. In Quaternary Glaciations – Extent and Chronology, Part II: North America (J. Ehlers and P. L. Gibbard, Editors). Developments in Quaternary Science 2, Elsevier, Amsterdam, The Netherlands. pp. 9–27.

Kemp, M. U., E. E. van Loon, J. Shamoun-Baranes, and W. Bouten (2012). RNCEP: Global weather and climate data at your fingertips. Methods in Ecology and Evolution 3:65–70.

Kinsky, F. C., and J. C. Yaldwyn (1981). The Bird Fauna of Niue Island, South-west Pacific, with Special Notes on the White-tailed Tropic Bird and Golden Plover. National Museum of New Zealand, Miscellaneous Series no. 2, Wellington, New Zealand. 49 pp.

Klaassen, R. H. G., T. Alerstam, P. Carlsson, J. W. Fox, and Å. Lindström (2011). Great flights by Great Snipes: Long and fast non-stop migration over benign habitats. Biology Letters 7:833–835.

Knowles, L. L., and W. P. Maddison (2002). Statistical phylogeography. Molecular Ecology 11:2623–2635.

Kok, E. M. A., T. L. Tibbitts, D. C. Douglas, P. W. Howey, A. Dekinga, B. Gnep, and T. Piersma (2020). A Red Knot as a Black Swan: How a single bird shows navigational abilities during repeat crossings of the Greenland Icecap. Journal of Avian Biology 51:e02464.

Kranstauber, B., R. Weinzieri, M. Wikelski, and K. Safi (2015). Global aerial flyways allow efficient traveling. Ecology Letters 18:1338–1345.

Kuang, F., J. T. Coleman, C. J. Hassell, K-S. K. Leung, G. Maglio, W. Ke, C. Cheng, J. Zhao, Z. Zhang, and Z. Ma (2020). Seasonal and population differences in migration of Whimbrels in the East Asian–Australasian Flyway. Avian Research 11:24.

Kuwae, T., P. G. Beninger, P. Decottignies, K. J. Mathot, D. R. Lund, and R. W. Elner (2008). Biofilm grazing in a higher vertebrate: The Western Sandpiper, *Calidris mauri*. Ecology 89:599–606.

Kuwae, T., E. Miyoshi, S. Hosokawa, K. Ichimi, J. Hosoya, T. Amano, T. Moriya, M. Kondoh, R. C. Ydenberg, and R. W. Elner (2012). Variable and complex food web structures revealed by exploring missing trophic links between birds and biofilm. Ecology Letters 15:347–356.

Kvist, A., Å. Lindström, M. Green, T. Piersma, and G. H. Visser (2001). Carrying large fuel loads during sustained bird flight is cheaper than expected. Nature 413:730–732.

Lack, D. (1959). Migrations across the sea. Ibis 101:374–399.

Lagassé, B. J., R. B. Lanctot, M. Barter, S. Brown, C.-Y. Chiang, C.-Y. Choi, Y. N. Gerasimov, S. Kendall, J. R. Liebezeit, K. S. Maslovsky, A. Matsyna, et al. (2020). Dunlin subspecies exhibit regional segregation and high site fidelity along the East Asian–Australasian Flyway. The Condor: Ornithological Applications 122:duaa054.

Laland, K. N., K. Sterelny, J. Odling-Smee, W. Hoppitt, and T. Uller (2011). Cause and effect in biology revisited: Is Mayr's proximate–ultimate dichotomy still useful? Science 334:1512–1516.

Landys-Ciannelli, M. M., T. Piersma, and J. Jukema (2003). Strategic size changes of internal organs and muscle tissue in the Bar-tailed Godwit during fat storage on a spring stopover site. Functional Ecology 17:151–179.

Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg (2003). Effects of predation danger on migration strategies of sandpipers. Oikos 103:303–319.

LaSorte, F. A., D. Fink, W. M. Hochachka, and S. Kelling (2016). Convergence of broad-scale migration strategies in terrestrial birds. Proceedings of the Royal Society B 283:20152588.

Lee, S., and H.-K. Kim (2003). The dynamical relationship between subtropical and eddy-driven jets. Journal of Atmospheric Sciences 60:1490–1503.

Legagneux, P., P. L. Fast, G. Gauthier, and J. Bêty (2012). Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proceedings of the Royal Society B 279:876–883.

Lesku, J. A., N. C. Rattenborg, M. Valcu, A. L. Vyssotski, S. Kuhn, F. Kuemmeth, W. Heidrich, and B. Kempenaers (2012). Adaptive sleep loss in polygynous Pectoral Sandpipers. Science 337:1654–1658.

Lindström, Å. 2003. Fuel deposition rates in migrating birds: Causes, constraints and consequences. In Avian Migration (P. Berthold, E. Gwinner, and E. Sonnenschein, Editors). Springer-Verlag, Berlin, Germany. pp. 307–320.

Lindström, Å., A. Kvist, T. Piersma, A. Dekinga, and M. W. Dietz (2000). Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. Journal of Experimental Biology 203:913–919.

Lindström, Å., R. E. Gill, Jr., S. E. Jamieson, B. McCaffery, L. Wennerberg, M. Wikelski, and M. Klaassen (2011). A puzzling migratory detour: Are fueling conditions in Alaska driving the movement of juvenile Sharp-tailed Sandpipers? The Condor 113:129–139.

Lindström, Å., T. Alerstam, and A. Hedenström. 2019. Faster fuelling is the key to faster migration. Nature Climate Change 9:288–289.

Lindström, Å., T. Alerstam, A. Andersson, J. Bäckman, P. Bahlenberg, R. Bom, R. Ekblom, R. H. G. Klaassen, S. Korniluk, S. Sjöberg, and J. K. M. Weber (2021). Extreme altitude changes between night and day during marathon flights of Great Snipes. Current Biology 31:3433–3439.

Lislevand, T., M. Briedis, O. Heggøy, and S. Hahn (2017). Seasonal migration strategies of Common Ringed Plovers *Charadrius hiaticula*. Ibis 159:225–229.

Lisovski, S., K. Gosbell, M. Christie, B. J. Hoye, M. Klaassen, I. D. Stewart, A. J. Taysom, and C. Minton (2016). Movement patterns of Sanderling (*Calidris alba*) in the East Asian–Australasian Flyway and a comparison of methods for identification of crucial areas for conservation. Emu 116:168–177.

Ma, Z., D. S. Melville, J. Liu, Y. Chen, H. Yang, W. Ren, Z.-W. Zhang, T. Piersma, and B. Li (2014). Rethinking China's new great wall. Science 346:912–914.

MacKinnon, J., Y. I. Verkuil, and N. J. Murray (2012). IUCN situation analysis on East and Southeast Asian intertidal habitats, with particular reference to the Yellow Sea (including the Bohai Sea). Occasional Paper of the IUCN Species Survival Commission No. 47. IUCN, Gland, Switzerland, and Cambridge, UK.

Macwhirter, R. B., P. Austin-Smith, Jr., and D. E. Kroodsma (2020). Sanderling (*Calidris alba*), version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.sander.01

Maggini, I., and F. Bairlein (2010). Endogenous rhythms of seasonal migratory body mass changes and nocturnal restlessness in different populations of Northern Wheatear *Oenanthe oenanthe*. Journal of Biological Rhythms 25:268–276.

Mantua, N. J., and S. R. Hare (2002). The Pacific Decadal Oscillation. Journal of Oceanography 58:35–44.

Marks, J. S., T. L. Tibbitts, R. E. Gill, Jr., and B. J. McCaffery (2020). Bristle-thighed Curlew (*Numenius tahitiensis*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.brtcur.01

Marra, P. P., K. A. Hobson, and R. T. Holmes (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Mathot, K. J., B. D. Smith, and R. W. Elner (2007). Latitudinal clines in food distribution correlate with differential migration in the Western Sandpiper. Ecology 88:781–79.

Mathot, K. J., A. Dekinga, and T. Piersma (2017). An experimental test of state–behaviour feedbacks: Gizzard mass and foraging behaviour in Red Knots. Functional Ecology 31:1111–1121.

Mathot, K. J., T. Piersma, and R. W. Elner (2018). Shorebirds as indicators and integrators of mudflat ecology. In Mudflat Ecology (P. G. Beninger, Editor). Aquatic Ecology Series 7, Springer Nature, Switzerland. pp. 309–338.

Mayr, E. (1953). On the origin of bird migration in the Pacific. Proceedings of the 7th Pacific Science Congress 4:387–394.

Mayr, E. (1961). Cause and effect in biology: Kinds of causes, predictability, and teleology are viewed by a practicing biologist. Science 134:1501–1506.

McLaughlin, J. F., B. C. Faircloth, T. C. Glenn, and K. Winker (2020). Divergence, gene flow, and speciation in eight lineages of trans-Beringian birds. Molecular Ecology 29:3526–3542.

Melville, D. S., Y. Chen, and Z. Ma (2016). Shorebirds along the Yellow Sea coast of China face an uncertain future—a review of threats. Emu 116:100–110.

Mesquita, M. D., D. E. Atkinson, and K. I. Hodges (2010). Characteristics and variability of storm tracks in the North Pacific, Bering Sea, and Alaska. Journal of Climate 23:294e31.

Meyburg, B.-U., U. Bergmanis, T. Langgemach, K. Graszynski, A. Hinz, I. Börner, C. Meyburg, and W. M. G. Vansteelant (2017). Orientation of native versus translocated juvenile Lesser Spotted Eagles (*Clanga pomarina*) on the first autumn migration. Journal of Experimental Biology 220:2765–2776.

Minton, C., K. Gosbell, P. Johns, M. Christie, M. Klaassen, C. Hassell, A. Boyle, R. Jessop, and J. Fox (2011). Geolocator studies on Ruddy Turnstones *Arenaria interpres* and Greater Sandplovers *Charadrius leschenaultii* in the East Asian–Australasia Flyway reveal widely different migration strategies. Wader Study Group Bulletin 118:87–96.

Minton, C., K. Gosbell, P. Jones, M. Christie, M. Klaassen, C. Hassell, A. Boyle, R. Jessop, and J. Fox (2013). New insights from geolocators deployed on waders in Australia. Wader Study Group Bulletin 120:37–46.

Mouritsen, H. (1998). Modelling migration: The clock-and-compass model can explain the distribution of ringing recoveries. Animal Behaviour 56:899–907.

Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. Nature 558:50–59.

Mueller, J. C., F. Pulido, and B. Kempenaers (2011). Identification of a gene associated with avian migratory behaviour. Proceedings of the Royal Society B 278:2848–2856.

Mueller, T., R. B. O'Hara, S. J. Converse, R. P. Urbanek, and W. F. Fagan (2013). Social learning of migratory performance. Science 341:999–1002.

Muheim, R., J. Boström, S. Åkesson, and M. Liedvogel (2014). Sensory mechanisms of animal orientation and navigation. In Animal Movements Across Scales (L.-A. Hansson and S. Åkesson, Editors). Oxford University Press, Oxford, UK. pp. 179–194.

Murray, N. J., R. S. Clemens, S. R. Phinn, H. P. Possingham, and R. A. Fuller (2014). Tracking the rapid loss of tidal wetlands in the Yellow Sea. Frontiers in Ecology and the Environment 12:267–272.

Murray, N. J., S. R. Phinn, M. De Witt, R. Ferrari, R. Johnston, M. B. N. Clinton, D. Thau, and R. A. Fuller (2019). The global distribution and trajectory of tidal flats. Nature 565:222–225.

Nemeth, Z. (2009). Observation of daytime sleep-like behavior in a migratory songbird during stopover. Wilson Journal of Ornithology 212:644–646.

Nettleship, D. N. (2020). Ruddy Turnstone (*Arenaria interpres*), version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.rudtur.01

Newton, I. (2008). The Migration Ecology of Birds. Academic Press, London, UK.

Nigam, S., and S. Baxter (2015). Teleconnections. In Encyclopedia of Atmospheric Sciences, Elsevier, Amsterdam, The Netherlands. pp. 90–109. https://doi.org/10.1016/B978-0-12-382225-3.00400-X

NOAA (2020). Ocean Facts. National Ocean Service, National Oceanic and Atmospheric Administration, U.S. Department of Commerce. https://oceanservice.noaa.gov/facts/ (accessed 2/28/2020)

Nunn, P. D. (2009). Vanished Islands and Hidden Continents of the Pacific. U. Hawai'i Press, Honolulu, HI, USA.

O'Connor C., D. R. Norris, G. T. Crossin, and S. J. Cooke (2014). Biological carry-over effects: Linking common concepts and mechanisms in ecology and evolution. Ecosphere 5:1–11.

Odum, E. P., C. E. Connell, and D. L. Hicks (1964). Homeostasis of the nonfat components of migrating birds. Science 143:1037–1039.

Olson, B. E., K. A. Sullivan, and A. H. Farmer (2014). Marbled Godwit migration characterized with satellite telemetry. The Condor 116:185–194.

Panchanathan, K., and W. E. Frankenhuis (2015). The evolution of sensitive periods in a model of incremental development. Proceedings of the Royal Society B 283:20152439.

Parody-Merino, Á. M., P. F. Battley, J. R. Conklin, and A. E. Fidler (2019). No evidence for an association between Clock gene allelic variation and migration timing in a long-distance migratory shorebird (*Limosa lapponica baueri*). Oecologia 191:843–859.

Pennycuick, C. J. (2008). Modelling the Flying Bird. Academic Press, London, UK.

Pennycuick, C. J., and P. F. Battley (2003). Burning the engine: A time-marching computation of fat and protein consumption in a 5420-km non-stop flight by Great Knots *Calidris tenuirostris*. Oikos 103:323–332.

Peterson, A. T., J. Soberón, and V. Sánchez-Cordero (1999). Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Piersma, T. (1987). Hop, skip, or jump? Constraints on migration of Arctic waders by feeding, fattening, and flight speed. Limosa 60:185–194.

Piersma, T. (1990). Pre-migratory "fattening" usually involves more than the deposition of fat alone. Ringing and Migration 11:113–115.

Piersma, T. (1998). Phenotypic flexibility during migration: Optimization of organ size contingent on the risks and rewards of fueling and flight? Journal of Avian Biology 29:511–520.

Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. Journal of Ornithology 148 (Suppl. 1):S45–S59.

Piersma, T. (2011a). Flyway evolution is too fast to be explained by the modern synthesis: Proposals for an 'extended' evolutionary research agenda. Journal of Ornithology 152 (Suppl. 1):S151–S159.

Piersma, T. (2011b). Why marathon migrants get away with high metabolic ceilings: Towards an ecology of physiological restraint. Journal of Experimental Biology 214:295–302.

Piersma, T. (2012). What is habitat quality? Dissecting a research portfolio on shorebirds. In Birds and Habitat: Relationships

in Changing Landscapes (R. J. Fuller, Editor). Cambridge University Press, Cambridge, UK. pp. 383–407.

Piersma, T. (2018). Ornithology from the flatlands: The logic to questions about birds (and other topics). Ardea 106:1–3.

Piersma, T., and R. E. Gill, Jr. (1998). Guts don't fly: Small digestive organs in obese Bar-tailed Godwits. The Auk 115:196–203.

Piersma, T., and J. Jukema (1990). Budgeting the flight of a long-distance migrant: Changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. Ardea 78:315–337.

Piersma, T., and Å. Lindström (1997). Rapid reversible changes in organ size as a component of adaptive behaviour. Trends in Ecology and Evolution 12:134–138.

Piersma, T., and J. A. van Gils (2011). The Flexible Phenotype: A Body-centred Integration of Ecology, Physiology, and Behaviour. Oxford University Press, Oxford, UK.

Piersma, T., P. de Goeij, and I. Tulp (1993). An evaluation of intertidal feeding habitats from a shorebird perspective: Towards comparisons between temperate and tropical mudflats. Netherlands Journal of Sea Research 31:503–512.

Piersma, T., G. A. Gudmundsson, and K. Lilliendahl (1999). Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. Physiological and Biochemical Zoology 72:405–415.

Piersma, T., J. Perez-Tris, H. Mouritsen, U. Bauchinger, and F. Bairlein (2005a). Is there a "migratory syndrome" common to all migrant birds? Annals of the New York Academy of Sciences 1046:282–293.

Piersma, T., D. I. Rogers, P. M. González, L. Zwarts, L. Niles, I. D. L. S. do Nascimento, C. D. T. Minton, and A. J. Baker (2005b). Fuel storage rates before northward flights in Red Knots worldwide: Facing the severest ecological constraint in tropical intertidal environments? In Birds of Two Worlds: Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 262–273.

Piersma, T., T. Lok, Y. Chen, C. J. Hassell, H.-Y. Yang, A. Boyle, M. Slaymaker, Y.-C. Chan, D. S. Melville, Z.-W. Zhang, and Z. Ma (2016). Simultaneous declines in survival of three shorebird species signals a flyway at risk. Journal of Applied Ecology 53:479–490.

Piersma, T., A. H. J. Loonstra, M. A. Verhoeven, and T. Oudman (2020). Rethinking classic starling displacement experiments: Evidence for innate or for learned migratory directions? Journal of Avian Biology 51:e02337.

Piersma, T., R. E. Gill, Jr., and D. R. Ruthrauff (2021a). Physiomorphic transformation in extreme endurance migrants: Revisiting the case of Bar-tailed Godwits preparing for trans-Pacific flights. Frontiers in Ecology and Evolution 9:685764.

Piersma, T., E. M. A. Kok, C. J. Hassell, H.-B. Peng, Y. I. Verkuil, G. Lei, J. Karagicheva, E. Rakhimberdiev, P. W. Howey, T. L. Tibbitts, and Y.-C. Chan (2021b). When a typical jumper skips: Itineraries and staging habitats used by Red Knots (Calidris canutus piersmai) migrating between northwest Australia and the New Siberian Islands. Ibis 163:1235–1251.

Pomeroy, A.C., R.W. Butler, and R. C. Ydenberg (2006), Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. Behavioral Ecology 17:1041–1045.

Powers, S. P., M. A. Bishop, J. H. Grabowski, and C. H. Peterson (2002). Intertidal benthic resources of the Copper River Delta, Alaska, USA. Journal of Sea Research 47:13–23.

Pulido, F. (2007). The genetics and evolution of avian migration. Bioscience 57:165–174.

Pulido, F., and P. Berthold (2010). Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. Proceedings of the National Academy of Sciences USA 107:7341–7346.

Pyle, R. L., and P. Pyle (2017). The Birds of the Hawaiian Islands: Occurrence, History, Distribution, and Status, version 2. B. P. Bishop Museum, Honolulu, HI, USA. http://hbs.bishopmuseum.org/birds/rlp-monograph/

Quaintenne, G., J. A. van Gils, P. Bocher, A. Dekinga, and T. Piersma (2010). Diet selection in a molluscivore shorebird across Western Europe: Does it show short- or long-term intake rate-maximization? Journal of Animal Ecology 79:53–62.

Rabøl, J. (1978). One-direction orientation versus goal area navigation in migratory birds. Oikos 30:216–223.

Rakhimberdiev, E., P. J. van den Hout, M. Brugge, B. Spaans, and T. Piersma (2015). Seasonal mortality and sequential density dependence in a migratory bird. Journal of Avian Biology 46:332–341.

Rakhimberdiev, E., S. Duijns, J. Karagicheva, C. J. Camphuysen, V. R. S. Castricum, A. Dekinga, R. Dekker, A. Gavrilov, J. ten Horn, J. Jukema, A. Saveliev, et al. (2018). Food abundance at refuelling sites can mitigate Arctic warming effects on a migratory bird. Nature Communications 9:4263.

Rattenborg, N. C. (2017). Sleeping on the wing. Interface Focus 7:20160082.

Rattenborg, N. C., B. Voirin, S. M. Cruz, R. Tisdale, G. Dell'Omo, H.-P. Lipp, M. Wikelski, and A. L. Vyssotski (2016). Evidence that birds sleep in mid-flight. Nature Communications 7:12468.

Rattenborg, N. C., H. O. de la Iglesia, B. Kempenaers, J. A. Lesku, P. Meerlo, and M. F. Scriba (2017). Sleep research goes wild: New methods and approaches to investigate the ecology, evolution and functions of sleep. Philosophical Transactions of the Royal Society B 372:20160251.

Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: A review. Oikos 30:224–272.

Richter-Gravier, R. (2019). Manu narratives of Polynesia: A comparative study of birds in 300 traditional Polynesian stories. Ph.D. dissertation, University of Otago, Dunedin, New Zealand.

Risien, C. M., and D. B. Chelton (2006). A satellite-derived climatology of global ocean winds. Remote Sensing of Environment 105:221–236.

Risien, C. M., and D. B. Chelton (2008). A global climatology of surface wind and wind stress fields from eight years of QuikSCAT scatterometer data. Journal of Physical Oceanography 38:2379–2413.

Ruthrauff, D. R., R. E. Gill, Jr., and T. L. Tibbitts (2013). Coping with the cold: An ecological context for the abundance and distribution of Rock Sandpipers during winter in upper Cook Inlet, Alaska. Arctic 66:269–278.

Ruthrauff, D. R., A. Dekinga, R. E. Gill, Jr., and T. Piersma (2018). Energetic solutions of Rock Sandpipers to harsh winter conditions rely on prey quality. Ibis 160:397–412.

Ruthrauff, D. R., T. L. Tibbitts, and R. E. Gill, Jr. (2019). Flexible timing of annual movements across consistently used sites by Marbled Godwits breeding in Alaska. The Auk: Ornithological Advances 136:1–11.

Ruthrauff, D. R., Z. M. Pohlen, and H. M. Wilson (2020). Aerial surveys of shorebirds at pre-migratory staging sites in western

Alaska, 2018–2019. U.S. Geological Survey data release. https://doi.org/10.5066/P9ZS5Y6N

Ruthrauff, D. R., C. M. Harwood, T. L. Tibbitts, N. Warnock, and R. E. Gill, Jr. (2021). Diverse patterns in migratory timing, site use, and site fidelity by Alaska-breeding Whimbrels. Journal of Field Ornithology 92:156–172.

Saino, N., G. Bazzi, E. Gatti, M. Caprioli, J. G. Cecere, C. D. Possenti, A. Galimberti, V. Orioli, L. Bani, D. Rubolini, L. Gianfranceschi, and F. Spina (2015). Polymorphism at the *Clock* gene predicts phenology of long-distance migration in birds. Molecular Ecology 24:1758–1773.

Salewski, V., and B. Bruderer (2007). The evolution of bird migration—a synthesis. Naturwissenschaften 94:268–279.

Schwilch, R., T. Piersma, N. Holmgren, and L. Jenni (2002). Do migratory birds need a nap after a long non-stop flight? Ardea 90:149–154.

Sedinger, J. S., J. L. Schamber, D. H. Ward, C. A. Nicolai, and B. Conant (2011). Carry-over effects associated with winter location affect fitness, social status, and population dynamics in a long-distance migrant. American Naturalist 178:E110–E123.

Senner, N. R., W. M. Hochachka, J. W. Fox, and V. Afanasyev (2014). An exception to the rule: Carry-over effects do not accumulate in a long-distance migratory bird. PLoS One 9:e86588.

Senner, N. R., J. R. Conklin, and T. Piersma (2015). An ontogenetic perspective on individual differences. Proceedings of the Royal Society B 282:20151050.

Senner, N. R., M. Stager, M. A. Verhoeven, Z. A. Cheviron, T. Piersma, and W. Bouten (2018). High-altitude shorebird migration in the absence of topographical barriers: Avoiding high air temperatures and searching for profitable winds. Proceedings of the Royal Society B 285:20180569.

Senner, N. R., M. A. Verhoeven, J. M. Abad-Gómez, J. A. Alves, J. C. E. W. Hooijmeijer, R. A. Howison, R. Kentie, A. H. J. Loonstra, J. A. Masero, A. Rocha, M. Stager, and T. Piersma (2019). High migratory survival and highly variable migratory behavior in Black-tailed Godwits. Frontiers in Ecology and Evolution 7:96

Sergio, F., A. Tanferna, R. De Stephanis, L. J. Jiménez, J. Blas, G. Tavecchia, D. Preatoni, and F. Hiraldo (2014). Individual improvements and selective mortality shape lifelong migratory performance. Nature 515:410–413.

Shamoun-Baranes, J., F. Liechti, and W. M. G. Vansteelant (2017). Atmospheric conditions create freeways, detours and tailbacks for migrating birds. Journal of Comparative Physiology A 203:509–529.

Shettleworth, S. J. (2001). Animal cognition and animal behaviour. Animal Behaviour 61:277–286.

Skrip, M. M., U. Bauchinger, W. Goymann, L. Fusani, M. Cardinale, R. R. Alan, and S. R. McWilliams (2015). Migrating songbirds on stopover prepare for, and recover from, oxidative challenges posed by long-distance flight. Ecology and Evolution 5:3198–3209.

Smith, I. N., A. F. Moise, and R. A. Colman (2012). Large-scale circulation features in the tropical western Pacific and their representation in climate models. Journal of Geophysical Research 117(D4):D04109.

Sonsthagen, S. A., T. L. Tibbitts, R. E. Gill, Jr., I. Williams, and S. L. Talbot (2015). Spatial genetic structure of Bristle-thighed Curlews (*Numenius tahitiensis*): Breeding area differentiation not reflected on the non-breeding grounds. Conservation Genetics 16:223–233.

Studds, C. E., and P. P. Marra (2005). Nonbreeding habitat occupancy and population processes: An upgrade experiment with a migratory bird. Ecology 86:2380–2385.

Studds, C. E., B. E. Kendall, N. J. Murray, H. B. Wilson, D. I. Rogers, R. S. Clemens, K. Gosbell, C. J. Hassell, R. Jessop, D. S. Melville, D. A. Milton, et al. (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nature Communications 8:14895.

Swift, R. J., A. D. Rodewald, J. A. Johnson., B. A. Andres, and N. R. Senner (2020). Seasonal survival and reversible state effects in a long-distance migratory shorebird. Journal of Animal Ecology 89:2043–2055.

Thiebot, J.-B., N. Nakamura, Y. Toguchi, N. Tomita, and K. Ozaki (2020). Migration of Black-naped Terns in contrasted cyclonic conditions. Marine Biology 167:83.

Thompson, M. C. (1973). Migratory patterns of Ruddy Turnstones in the central Pacific region. Living Bird 12:5–23.

Thorup, K., and R. A. Holland (2009). The bird GPS—long-range navigation in migrants. Journal of Experimental Biology 212:3597–3604.

Thorup, K., and J. Rabøl (2001). The orientation system and migration pattern of long-distance migrants: Conflict between model predictions and observed patterns. Journal of Avian Biology 32:111–119.

Thorup, K., T. Alerstam, M. Hake, and N. Kjellén (2003). Can vector summation describe the orientation system of juvenile Ospreys and Buzzards? An analysis of ring recoveries and satellite tracking. Oikos 103:350–359.

Tibbitts, T. L., D. R. Ruthrauff, J. G. Underwood, and V. P. Patil (2020). Factors promoting the recolonization of Oahu, Hawaii, by Bristle-thighed Curlews. Global Ecology and Conservation 21:e00785.

Tinbergen, N. (1963). On aims and methods of ethology. Zeitschrift für Tierpsychologie 20:410–433.

Tolkien, J. R. R. (1954). The Lord of the Rings: The Fellowship of the Ring. Houghton-Mifflin, New York, NY, USA.

Tomkovich, P. S., R. R. Porter, E. Y. Loktionov, and L. J. Niles (2013). Pathways and staging areas of Red Knots *Calidris canutus rogersi* breeding in southern Chukotka, Far Eastern Russia. Wader Study Group Bulletin 120:181–193.

Turner, J. S. (2007). The Tinkerer's Accomplice: How Design Emerges from Life Itself. Harvard University Press, Cambridge, MA, USA.

U.S. Geological Survey (USGS) Alaska Science Center (2019). USGS Alaska Science Center wildlife tracking data collection. U.S. Geological Survey data release. https://doi.org/10.5066/P9VYSWEH

van der Meer, J., and T. Piersma (1994). Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. Physiological Zoology 67:305–329.

van Gils, J. A., P. Edelaar, G. B. Escudero, and T. Piersma (2004). Carrying capacity models should not use fixed prey density thresholds: A plea for using more tools of behavioural ecology. Oikos 104:197–204.

van Gils, J. A., P. F. Battley, T. Piersma, and R. Drent (2005). Reinterpretation of gizzard sizes of Red Knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. Proceedings of the Royal Society B 272:2609–2618.

van Gils, J. A., A. Dekinga, P. J. van den Hout, B. Spaans, and T. Piersma (2007). Digestive organ size and behavior of Red Knots (*Calidris canutus*) indicate the quality of their benthic food stocks. Israel Journal of Ecology and Evolution 53:329–346.

van Gils, J. A., S. Lisovski, T. Lok, W. Meissner, A. Ożarowska, J. de Fouw, E. Rakhimberdiev, M. Y. Soloviev, T. Piersma, and M. Klaassen (2016). Body shrinkage due to Arctic warming reduces Red Knot fitness in tropical wintering range. Science 352:819–821.

van Hasselt, S. J., G.-J. Mekenkamp, J. Komdeur, G. Allocca, A. L. Vyssotski, T. Piersma, N. C. Rattenborg, and P. Meerlo (2020). Seasonal variation in sleep homeostasis in migratory geese: A rebound of NREM sleep following sleep deprivation in summer but not in winter. Sleep 2020:1–14.

Verhoeven, M. A., A. H. J. Loonstra, J. C. E. W. Hooijmeijer, J. A. Masero, T. Piersma, and N. R. Senner (2018). Generational shift in spring staging site use by a long-distance migratory bird. Biology Letters 14:20170663.

Verhoeven, M. A., A. H. J. Loonstra, N. R. Senner, A. D. McBride, C. Both, and T. Piersma (2019). Variation from an unknown source: Large inter-individual differences in migrating Black-tailed Godwits. Frontiers in Ecology and Evolution 7:31.

Verhoeven, M. A., A. H. J. Loonstra, A. D. McBride, C. Both, N. R. Senner, and T. Piersma (2021a). Migration route, stopping sites, and non-breeding destinations of adult Black-tailed Godwits breeding in southwest Fryslân, The Netherlands. Journal of Ornithology 162:61–76.

Verhoeven, M. A., A. H. J. Loonstra, A. D. McBride, W. Kaspersma, J. C. E. W. Hooijmeijer, C. Both, N. R. Senner, and T. Piersma (2021b). Age-dependent timing and routes demonstrate developmental plasticity in a long-distance migratory bird. Journal of Animal Ecology. doi:10.1111/1365-2656.13641

Vézina, F., T. D. Williams, T. Piersma, and R. I. G. Morrison (2012). Phenotypic compromises in a long-distance migrant during the transition from migration to reproduction in the High Arctic. Functional Ecology 26:500–512.

Walker, B. M., N. R. Senner, C. S. Elphick, and J. Klima (2020). Hudsonian Godwit (*Limosa haemastica*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.hudgod.01

Wallraff, H. G. (1974). Das Navigationssystem der Vögel. R. Oldenbourg Verlag, München, Germany.

Wang, C., C. Deser, J.-Y. Yu, P. DiNezio, and A. Clement (2012). El Niño and Southern Oscillation (ENSO): A review. In Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment (P. W. Glynn, D. Manzello, and I. C. Enochs, Editors). Springer, Berlin, Germany. pp. 3–19.

Wang, X., F. Kuang, K. Tan, and Z. Ma (2018). Population trends, threats, and conservation recommendations for waterbirds in China. Avian Research 9:14.

Watts, B. D., F. M. Smith, C. Hines, L. Duval, D. Hamilton, T. Keyes, J. Paquet, L. Pirie-Dominix, J. Rausch, B. Truitt, B. Winn, and P. Woodward (2021). Whimbrel populations differ in trans-Atlantic pathways and cyclone encounters. Scientific Reports 11:12919.

Wauchope, H. S., J. D. Shaw, Ø. Varpe, E. G. Lappo, D. Boertmann, R. B. Lanctot, and R. A. Fuller (2017). Rapid climate-driven loss of breeding habitat for Arctic migratory birds. Global Change Biology 23:1085–1094.

Weimerskirch, H., and A. Prudor (2019). Cyclone avoidance behaviour by foraging seabirds. Scientific Reports 9:5400.

Weimerskirch, H., K. Delord, A. Guitteaud, R. A. Phillips, and P. Pinet (2015). Extreme variation in migration strategies between and within Wandering Albatross populations during their sabbatical year, and their fitness consequences. Scientific Reports 5:8853.

Weiser, E. L., R. B. Lanctot, S. C. Brown, H. R. Gates, J. Bêty, M. L. Boldenow, R. W. Brook, G. S. Brown, W. B. English, S. A. Flemming, S. E. Franks, et al. (2020). Annual adult survival drives trends in Arctic-breeding shorebirds but knowledge gaps in other vital rates remain. The Condor: Ornithological Applications 122:duaa026.

Whaanga, H., P. Wehi, M. Cox, T. Roa, and I. Kusabs (2018). Māori oral traditions record and convey indigenous knowledge of marine and freshwater resources. New Zealand Journal of Marine and Freshwater Research 52:487–496.

Willemoes, M., R. Strandberg, R. H. G. Klaassen, A. P. Tøttrup, V. Vardanis, P. W. Howey, K. Thorup, M. Wikelski, and T. Alerstam (2014). Narrow-front loop migration in a population of the Common Cuckoo *Cuculus canorus*, as revealed by satellite telemetry. PLoS One 9:e83515.

Williams, T. C., and J. M. Williams (1999). The migration of birds over the Pacific Ocean. In Acta XXII Congressus Internationalis Ornithologici (N. Adams and R. Slotow, Editors). BirdLife South Africa, Johannesburg, South Africa. pp. 1948–1957.

Wiltschko, W., and R. Wiltschko (1972). Magnetic compass of European Robins. Science 176:70–74.

Winger, B. M., G. G. Auteri, T. M. Pegan, and B. C. Weeks (2019). A long winter for the Red Queen: Rethinking the evolution of seasonal migration. Biological Reviews 94:737–752.

Woodley, K. (2009). Godwits: Long-haul Champions. Penguin Group, Rosedale, North Shore, New Zealand.

Yang, H.-Y., B. Chen, Z. Ma, N. Hua, J. A. van Gils, Z.-W. Zhang, and T. Piersma (2013). Economic design in a long-distance migrating molluscivore: How fast-fuelling Red Knots in Bohai Bay, China, get away with small gizzards. Journal of Experimental Biology 216:3627–3636.

Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith, and J. Ireland (2004). Western Sandpipers have altered migration tactics as Peregrine Falcon populations have recovered. Proceedings Royal Society B 271:1263-1269.

Ydenberg, R. C., R. W. Butler, and D. B. Lank (2007). Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. Journal of Avian Biology 38:523–529.

Zeyl, J. N., O. den Ouden, C. Köpp, J. Assink, J. Christensen-Dalsgaard, S. C. Patrick, and S. Clusella-Trulla (2020). Infrasonic hearing in birds: A review of audiometry and hypothesized structure–function relationships. Biological Reviews 95:1036–1054.

Zhang, C. (2013). Madden–Julian oscillation: Bridging weather and climate. Bulletin American Meteorological Society 94:1849–1870.

Zhang, S.-D., Z. Ma, C.-Y. Choi, H.-B. Peng, Q.-Q. Bai, W.-L. Liu, D. S. Melville, P. He, Y.-C. Chan, J. A. van Gils, and T. Piersma (2018). Persistent use of a shorebird staging site in the Yellow Sea despite severe declines in food resources implies a lack of alternatives. Bird Conservation International 28:534–548.

Zhang, S.-D., Z. Ma, C.-Y. Choi, H.-B. Peng, D. S. Melville, T.-T. Zhao, Q.-Q. Bai, W.-L. Liu, Y.-C. Chan, J. A. van Gils, and T. Piersma (2019a). Morphological and digestive adjustments buffer performance: How staging shorebirds cope with severe food declines. Ecology and Evolution 9:3868–3878.

Zhang, S.-D., Z. Ma, C.-C. Feng, D. S. Melville, J. A. van Gils, and T. Piersma (2019b). Individual diet differences in a molluscivore shorebird are associated with the size of body instruments for internal processing rather than for feeding. Journal of Avian Biology 50:e02255.

Zink, R. M., and A. S. Gardner (2017). Glaciation as a migratory switch. Science Advances 3:e1603133.