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In this series, coordinated by Thomas Mondain-Monval (UK Centre for Ecology & Hydrology, *thoval@ceh.ac.uk*), invited authors discuss themes in wader/shorebird biology, ecology or conservation that arise from publications other than *Wader Study*.

Flying high or flying low? How wind shapes flight altitude for migratory waders

Birds light up weather radars across the globe during their seasonal migrations. Together, they appear to flow across the landscape in response to wind conditions, their movements visibly intensifying when winds are favorable and fading away as winds deteriorate[1,2]. Their vertical movements, too, can be wind-dependent. Radar-based studies have shown that migrating birds mostly fly within 2,000 m of ground level[3], but they sometimes venture into higher air layers to take advantage of jet streams[4,5]. Flows of migrants also appear to adjust their altitude dynamically as conditions change, escaping energy-draining headwinds by climbing until winds improve[6,7]. It is no surprise, then, that wind is generally assumed to be a central abiotic force shaping in-flight migratory behavior and one of the strongest predictors of flight altitude[8].

While radar-based studies often focus on large-scale patterns evident across diverse groups of migrating birds, a number of studies are now testing how well these patterns hold for more specific taxonomic groups – including waders. Waders can travel exceptionally long distances during migration[9], and many cross open oceans that are largely unmonitored by weather radar networks. How waders adjust altitude during these crossings could differ from the altitude adjustments observed by weather radars elsewhere. Distinctive morphological or physiological adaptations for long-distance flight could also separate wader behavior from average trends, altering how they mitigate risks, minimize energetic costs, and ultimately respond to the wind conditions they encounter along the way.

Recent work by Galtbalt and colleagues in the East Asian-Australasian flyway[10] offers a look into these possibilities. Their team examined ongoing flight altitude adjustments for two migratory waders: Far Eastern Curlew *Numenius madagascariensis* and Whimbrel *Numenius phaeopus*. Both are long-distance migrants, commuting thousands of kilometers each year between non-breeding sites in Australia and breeding sites in northern China and eastern Siberia. Using high-resolution GPS transmitters, the team tracked individuals throughout their northbound and southbound migrations. For each recorded location, they compared atmospheric conditions in the air layer where the bird actually flew – including available wind support, cloud cover, air temperature, and relative humidity – with conditions elsewhere in the vertical air column.

The team expected wind support to have a positive effect on how high their tracked birds flew. In fact, wind support was an important predictor of flight altitude for both species: birds were more likely to occupy an altitude if wind support was higher. But the team also found an even stronger negative effect when they used altitude itself as an explanatory variable. In other words, their tracked birds preferred low-altitude flight, and this preference was an even more important predictor of flight altitude than wind. Though they occasionally climbed to higher altitudes, the birds spent the majority of the time

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[10] Galtbalt, B., A. Lilleyman, J.T. Coleman, C. Cheng, Z. Ma, D.I. Rogers, B.K. Woodworth, R.A. Fuller, S.T. Garnett & M. Klaassen. 2021. Far eastern curlew and whimbrel prefer flying low – wind support and good visibility appear only secondary factors in determining migratory flight altitude. *Movement Ecology* 9: 32.

(75%) flying no higher than 1,000 m above ground level. Odds ratios, which measure the likelihood of occurrence, showed that, for each unit increase in altitude, the birds' presence was dramatically less likely: 89% less likely for Far Eastern Curlew and 92% less likely for Whimbrel, regardless of local wind conditions.

Other atmospheric conditions played a smaller role in altitude selection or no distinguishable role at all. The interaction between air temperature and altitude, for example, had a significant but smaller effect for both species, revealing that they preferred to fly at low altitudes particularly when those layers were cool. Cloud cover, which may interfere with visibility, appeared to affect only Far Eastern Curlew; they avoided layers with cloud cover, though this effect was also small. Relative humidity, which may impact evaporative water loss during flight, had no significant effect on flight altitude for either species.

So why is flying low such an important migratory strategy for these species? Galtbalt *et al.* suggested that it may be a way to reduce the total energetic or metabolic costs of migratory flight. While higher altitudes might occasionally offer the best tailwinds, the air in these layers is thinner, generally drier, and less dense – features that affect breathing and reduce the lift produced by flapping wings. Over long distances, flying at high altitudes could accelerate water loss and increase the total energy that birds spend on migration. Plus, frequent climbing to check on wind conditions could be costly, particularly for large-bodied waders like Far Eastern Curlew and Whimbrel. On the other hand, navigation could also explain a strong preference for low altitudes. Galtbalt *et al.* pointed out that flying low likely provides more precise visual cues about travel speed and direction than flying at high altitudes. For birds on the move, these cues indicate how far off course they may be drifting, allowing them to make corrections along the way[11]. Given the long distances traveled by both these species, this seems like an intriguing possibility.

Equally intriguing is the takeaway, echoed here and in other individual-based altitude tracking studies, that no single rule of thumb governs in-flight behavior for all migrating birds or for all locations along their routes. Senner *et al.*[12], for example, found that Black-tailed Godwits *Limosa limosa* often traveled at extremely high altitudes, and they changed altitude dynamically to reach better winds and cooler air temperatures. Sjöberg *et al.*[13] found that, for migrating Great Reed Warblers *Acrocephalus arundinaceus* flying over the Mediterranean Sea and the Sahara Desert, altitude changes followed a more consistent pattern. These songbirds climbed steeply at sunrise, cruised at high altitudes throughout the day, and dropped lower at sunset – a pattern that could not be explained by wind or air temperature, and one that reversed the broad radar-based trend of flying higher at night[3]. Of course, neither of these patterns was replicated in the birds tracked by Galtbalt *et al.* Distinctive costs and risks, inherent to species themselves or the geographic routes they travel, are likely driving distinctive strategies.

Documenting the full range of these strategies will require tracking changes in flight altitude in different kinds of migratory birds. But even species that have already been the subject of tracking studies continue to raise questions. Galtbalt *et al.* found that their models explained more than 60% of the variability in flight altitude in their study – a higher percentage than conventional models based only on wind support could explain. That still leaves room for other, yet-unidentified factors that may also be contributing to flight altitude. Underlying geography may be one: both species in this study generally flew higher over land than they did over sea. That may be because land crossings are inherently more risky, perhaps due to elevated predation pressure[13] or disorienting sensory inputs[14]. There is also much left to learn about how birds navigate, and how altitude-dependent navigational mechanisms may shift in importance as birds travel over land or sea. Down the road, building a fuller understanding of these factors could allow us to more accurately model the current spatial distribution of migratory waders. And, as atmospheric conditions continue to shift and wind energy projects begin moving into flyways, it can also help us better predict how waders will respond to changes in the aerial environment in the years to come.

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