IN FOCUS

Encountering extreme weather during migration: individual strategies and their consequences

The way that animal populations respond to changing weather conditions is a major focus of current research, fuelled by the need to predict the future consequences of climatic changes. Severe weather events can provide valuable opportunities to uncover the mechanisms through which weather influences population demography but opportunities to track individual responses to such events are rare. *Senner et al.* report on an exceptional opportunity to address this issue, when their detailed studies of a migratory shorebird population were interrupted by an extreme weather event that coincided with spring migration, a key period in the annual cycle of migratory species. Through tracking of individuals across the migratory range, *Senner et al.* show that, while individual schedules were severely disrupted by the harsh weather, with many individuals undertaking reverse migrations and experiencing delayed breeding, breeding success was unaffected. This study highlights the complexities involved in predicting the ecological consequences of extreme weather events, and the key role of behavioural flexibility in mitigating the costs to individuals.

Harsh weather events have the potential to drive population trends through their impacts on demography, but our capacity to quantify individual and population-level responses to harsh weather is inevitably constrained by the rarity of these events. In addition, as individual responses to weather conditions can vary greatly (Coulson *et al.* 2001), quantifying their impact requires tracking of individuals through periods of varying weather conditions. Consequently, our understanding of the impacts of severe weather on populations has relied heavily on long-term demographic studies in which occasional harsh weather events have been encountered (Coulson *et al.* 2001, Duriez *et al.* 2012).

Migratory species can be particularly susceptible to harsh weather, as their seasonal movements can mean that conditions at key locations (eg migratory stopover sites that are used by many individuals over a short period of time) may have far-reaching impacts on populations. For example, a series of years with drought conditions in the Sahel region in the 1980s have been linked to low survival rates in several migratory species undertaking this desert crossing (Peach *et al.* 1991, Szép 1995). Recent developments in satellite-tracking of individuals during migratory journeys are also providing evidence of high levels of mortality associated with headwinds and dust storms during Sahara crossings, again highlighting the potential for weather conditions during key periods of the annual cycle to impact population demography (Strandberg *et al.* 2009; Hays 2014, Klaassen *et al.* 2014). In this issue, *Senner et al.* report the findings of the situation they encountered in 2013, when their study of the migration and breeding ecology of black-tailed godwits (*Limosa limosa limosa*), a species that is rapidly declining across Europe (Birdlife International 2004), coincided with a period of exceptionally cold weather during spring migration, a key period in the annual cycle of migratory species.

The return migration of migratory species to the breeding grounds in spring is a period characterised by rapid and highly repeatable individual movements (Lourenço *et al.* 2011, Tøttrup *et al.* 2012, Gill *et al.* 2014). Early arrival is frequently correlated with higher breeding success (Marra, Hobson & Holmes 1998, Gunnarsson *et al.* 2005), and repeatable timing of individual migration means that pairs are highly synchronized in their arrival (Gunnarsson *et al.* 2004). Given this apparent strong selection on individual timing of spring migration and the benefits of early breeding, severe weather during this period might be expected to be particularly disruptive.

Through tracking of individual godwits with satellite tags and colour-rings, *Senner et al.* show that the period of harsh weather in March 2013, when temperatures dropped more than 10°C across western Europe and snow fell as far south as central France, caused widespread disruption to godwit migration and breeding. Many individuals undertook reverse migrations and returned to more southerly areas where they remained for around three weeks, until the weather improved. The more favourable conditions that these individuals sought out resulted in substantial energetic savings, and those individuals that remained in the breeding areas increased foraging rates to offset the resulting energetic costs. However, despite these costs and the associated delayed arrival on the breeding grounds, there was no evidence of any impact on subsequent breeding success or survival. In fact, both nest survival and fledging success were higher in the interrupted year than in the following year.

Given the benefits of early arrival for breeding success that are common in migratory species, the lack of an effect of delayed breeding on productivity is perhaps surprising. *Senner et al.* discuss the potential for the cold conditions to have also delayed the emergence of the insect prey required for chick growth, and thus for chick growth to be aligned with prey availability despite the delay in breeding. As productivity of meadow birds has also been closely linked to farming operations in the agricultural landscapes of western Europe (Kleijn *et al.* 2010), the effects of the cold weather on farming operations may also be relevant. Identifying the mechanisms linking weather and productivity will clearly be key to understanding these patterns and predicting the consequences of future changes in weather patterns.

This study highlights the complex relationships linking weather and population demography. The weather conditions experienced in western Europe in March 2013, although severe and occurring at a key time of year for migratory birds, were sufficiently short-term to allow breeding to occur. While individuals in this study clearly experienced substantial energetic and/or flight costs as a result of encountering harsh weather conditions, their flexibility in responding to these conditions appears to have been sufficient to limit any demographic consequences. Other studies have reported demographic changes in response to harsh weather events (eg Robinson, Baillie & Crick 2007, Duriez *et al* .2012), and longer extreme weather events, such as the harsh winter of 1962/63 in western Europe, have been linked to much more severe impacts on populations and ecosystems (Crisp 1964). The opportunities afforded by severe weather events to quantify individual, demographic and population responses to these conditions are invaluable, and can provide key insights into potential impacts of future climatic change. Long-term studies provide unique opportunities to observe these events and to uncover the mechanistic basis of consequent changes in individual fitness and population demography.

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