Population decline of waders and vigilance behaviour in the Eurasian Curlew

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Abstract

Global biodiversity loss is continuing, and birds such as the waders Eurasian Curlew, Northern Lapwing, Oystercatcher, Redshank, and Common Snipe, are no exception. These birds occupy a wide variety of habitats during the breeding and non-breeding winter season and are in turn exposed to a variety of threats, most of which stem from human activity. By developing our understanding of the threats to waders, we can work to mitigate their effects and improve survival rates of waders. One habitat that is under threat is high tide roost sites, which are vital for wintering waders as they offer protection from predators and allow birds to rest and conserve energy when their low tide feeding areas are not available. However, wader roost behaviour and their response to threats is still poorly understood, particularly in endangered species such as Eurasian Curlew. Vigilance behaviours can be used as a visible measure of the effect of disturbance and can give insight into the perceived threat levels from disturbance sources. In Chapter 1, the current understanding of the drivers of population decline of waders is reviewed, including the role of habitat loss and land use change, the reduction in reproductive success, the non-breeding winter season, and the impact of recreational disturbance. Low productivity rates are the dominant reason for wader decline, driven by a combination of factors that lead to an overall negative impact on nesting habitat, food availability, predation rates, nest destruction, and vegetation change. Similarly, waders at coastal wintering sites face increased survival pressures from low temperatures and extreme weather, the effects of which are compounded by the additional energy expenditure from recreational disturbance, and the loss of food sources and roost sites from land use change. We identify gaps in knowledge surrounding the reduction of predation in the breeding season and the mechanisms behind the effects of low temperatures on waders in the winter period, as well as issues with current efforts to slow population declines. In Chapter 2, vigilance behaviour of Eurasian Curlews is investigated, to test whether environmental and anthropogenic disturbances influence behaviour and long-term population trends. We measured the individual and group level behaviour of Eurasian Curlews at winter roost sites on the Isle of Man, and analysed these behaviours against environmental temperature, wind speed, group size, and the frequency of anthropogenic disturbance. We also analysed the effect of environmental temperature on long-term winter populations of Eurasian Curlew on the Isle of Man. Vigilance behaviour increased with group size and wind speed, but declined in low temperatures, however anthropogenic disturbance did not correspond to changes in vigilance behaviour, and we did not find correlation between temporal variation and environmental temperatures.

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Declaration

I declare that this thesis is my own work, except where acknowledged, and has not been submitted in substantially the same form for the award of a higher degree elsewhere.

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Chapter 1

Drivers of the decline in UK waders

Abstract

The ongoing global biodiversity crisis is characterised by rapidly declining populations of many species across the world. In the UK, one group of particular concern are the waders, including Eurasian Curlew, Common Snipe, Northern Lapwing, Redshank, and Oystercatcher. Declines in these species are not the result of any one driver, but rather a myriad of contributing factors that together impact waders in the breeding and non-breeding seasons. Productivity rates are limited by the availability of suitable habitat, stemming from the modification of the agricultural landscape through agricultural intensification, while increased predation, livestock stocking density, and the draining of grasslands reduce the survival of wader chicks. In winter, extreme weather increases survival pressures on waders, and loss of feeding grounds and increased anthropogenic disturbance increase mortality. In this review, we demonstrate the synergistic relationship between these factors that is leading to wader decline and identify measures to halt or reverse this trend.

Introduction

We are currently experiencing a global biodiversity crisis, a rapidly occurring mass extinction event in the Anthropocene, that is predominantly driven by human activity (Ceballos *et al*., 2010; Naggs, 2017). The IUCN currently categorises 926 species as extinct and 81 species as extinct in the wild since 1500 AD, but these numbers are thought to be higher as for many species there is a lack of data or a need for re-assessment; others may remain undiscovered (Ceballos *et al*., 2010; IUCN, 2024). The populations of many extant species also continue to decline, and in the last 75 years alone, monitored wildlife populations have decreased in size by an estimated 73% (WWF, 2024). In Europe, 19% of species face risk of extinction, including 18% of vertebrate species (Hochkirch *et al.,* 2023).

To prevent further loss of biodiversity, we need to understand not just the leading factors which are impacting wildlife, but to determine how different species respond to these changes, which is greatly impacted by their biological traits and adaptations (Chichorro *et al*., 2019; Chichorro *et al*., 2022). In turn, such traits inform behaviours, and by measuring the behaviour of a species alongside its population dynamics, it is possible to develop improved population models and improve the understanding of the drivers of population change (Sumpter & Broomhead, 2001; Morales *et al.*, 2010; Bro-Jorgensen *et al.,* 2019).

As the global biodiversity decline continues, avifauna populations have not been spared. Worldwide, approximately 48% of bird species populations are thought to be in decline (Lees et al., 2022), and in Europe, there has already been an estimated decline of 17-19% in bird abundance since 1980 (Burns *et al.,* 2021). If allowed to continue, these trends are expected to result in the extinction of 6-14% of bird species by 2100 (Sekercioglu *et al*., 2004). This, in turn, could have major impacts on ecological systems across the world (Gaston, 2022). This is because birds perform a wide variety of ecosystem services, including controlling insect pest populations (Diaz-Siefer *et al*., 2022), pollination (Sekercioglu, 2011), seed dispersal (Garcia *et al*., 2010), scavenging (Peisley *et al*., 2017), and ecosystem engineering (Wenny *et al*., 2011), as well as other less common services (Whelan *et al*., 2008). Not only do these processes increase efficiency in ecosystem services, support biodiversity, and fulfil ecological niches, but they also provide economic value for humans (Whelan *et al*., 2008; Wenny *et al*., 2011; Whelan *et al*., 2015; Gaston, 2022). This value is most visible in association with agriculture, through their consumption of pests reducing the need for pesticides, the use of guano as fertilizer, and with tourism that is generated by bird watching (Whelan *et al*., 2008; Wenny *et al*., 2011; Whelan *et al*., 2015; Gaston, 2022).

Ground nesting birds are particularly at risk compared with other bird species, with 74% of ground-nesting species being in decline versus 41% of other bird species (McMahon *et al*., 2020). Species which frequently use grassland and farmland habitats are also being heavily impacted (Burns *et al.,* 2021). In the British Isles, wading birds occupy some of the habitats experiencing the most change by human activity, coastal areas, agricultural land, and grassland. In fact, this situation is not unique to the British Isles, with similar landscape level changes occurring across Europe, where waders are amongst the most threatened species groups as identified by the Birdlife European Red

List of Birds (2021). In this study, we focused on Northern Lapwing *Vanellus vanellus* (hereafter Lapwing), Redshank *Tringa totanus,* Common Snipe *Gallinago gallinago* (hereafter Snipe), Oystercatcher *Haematopus ostralegus,* and Eurasian Curlew *Numenius arquata,* (hereafter collectively referred to as waders). These are wading birds (belonging to the suborder Charadrii) that breed predominantly in arable, grassland, or moorland areas, and in the non-breeding season migrate to coastal habitats such as wetlands, estuaries, and coastal farmland, and are all red or amber listed in the UK Birds of Conservation Concern (Stanbury *et al.,* 2021; Heywood *et al.,* 2023; Woodward *et al.,* 2024). The non-breeding populations of these species see increases at the end of the breeding season as birds migrate to the British Isles from Northern and Eastern Europe (Woodward *et al.*, 2024). Despite these seasonal influxes, both breeding and winter populations of waders in the UK have decreased in the last 60 years (Heywood *et al.* 2024; Woodward *et al.*, 2024) (Table 1). The latest trends for UK bird's species are summarised in the Birds of Conservation Concern 5 (BoCC5) publication (Table 1) (Stanbury *et al.,* 2021).

Table 1. Species assessments of waders from Birds of Conservation Concern UK 5 (BoCC 5) (Stanbury et al., 2021) with qualifying criteria and global threat status from the IUCN Red List of Threatened species (IUCN, 2024). The wader species listed are Oystercatcher *Haematopus ostralegus*, Lapwing *Vanellus vanellus*, Curlew *Numenius arquata*, Common Snipe *Gallinago gallinago*, and Redshank *Tringa totanus*. These species are classified as wading birds (suborder Charadrii) that breed predominantly in arable, grassland, or moorland areas. This table also includes rates of change of breeding and non-breeding populations in the UK from Heywood et al. (2024) and Woodward et al. (2024). Productivity rates refer to the proportion of chicks surviving to their first year, unless stated otherwise. The qualifying criteria for conservation status of BoCC 5 as defined by Stanbury et al., (2021) includes; ERLOB: European Red List status, concerning species which are threatened in Europe under IUCN guidelines, BL & WL: non-breeding localisation (Species were considered localised if more than 50% of the UK population was found at ten or fewer sites in either the breeding (BL) or the non-breeding (WL) season), BR & WR: Breeding and non-breeding international importance. Species were considered of international importance if the UK holds at least 20% of the European population in either the breeding (BI) or the nonbreeding (WI) season, BDp/BDMp: Breeding population decline, a severe decline of >50% (BDp) or moderate decline >25% but <50% (BDMp) over 25 years (1) or since 1969 (2), BDr/BDMr: breeding range decline, a severe decline of >50% (BDr) or moderate decline >25% but <50% (BDMr) between 1988-91 and 2007-11 (1) or 1968-71 and 2007-11 (2), WDp/WDMp: Non-breeding population decline, a severe decline of >50% (WDp) or moderate decline >25% but <50% (WDMp) over 25 years (1) or since 1969 (2).

Species	**BoCC5 Conservation status**	**BoCC Qualifying criteria**	**IUCN threat status**	**Current rate of change -UK breeding population**	**Current rate of change -UK non-breeding population**	**Productivity rate**
Oystercatcher *Haematopus ostralegus*	Amber	ERLOB, WL, WI, BI	Vulnerable (VU)	-21% (1995 – 2022)	-21% (1996/97 – 2021/22)	~0.39 (to age 5) (Siriwardena *et al.,* 1998)
Lapwing *Vanellus vanellus*	Red	BDp1, BDr1, BDMr2, WR	Vulnerable (VU)	-62% (1967-2022)	-46% (1996/97-2021/22)	~0.56 (Siriwardena *et al.,* 1998)
Curlew *Numenius arquata*	Red	BDp2; BDMp1, WDMp1, BI	Endangered (EN)	-50% (1995 – 2022)	-32% (1996/97-2021/22)	~0.25 (chicks fledged per nest) (Cook *et al.*, 2021)
Common Snipe *Gallinago gallinago*	Amber	ERLOB, WDMp1, BDMr2	Vulnerable (VU)	No change (1995 – 2022)	Data unavailable	~0.48 (Siriwardena *et al.,* 1998)
Redshank *Tringa totanus*	Amber	ERLOB, BDMp1, BDMr1/2, WI	Vulnerable (VU)	-49% (1995-2022)	-19% (1996/97-2021/22)	~0.47 (Siriwardena *et al.,* 1998)

Causes of population decline

Declines in populations of wading birds are due to a variety of causes which may vary between geographic regions and, in some cases, may be due to compounding effects of multiple causes. The main contributing factors to the population decline of waders in the UK are the reduction in reproductive success, and the reduction in over-winter survival. These changes are predominantly driven by habitat loss and land-use change, agricultural intensification, and anthropogenic disturbance. In this review, we analyse existing literature regarding the decline of waders in the UK, with reference to studies of these species in similar landscapes elsewhere in Europe.

Reduction in reproductive success

Much of the decline in wader populations can be attributed to the lack of breeding productivity, which means that breeding adults are not producing enough viable offspring to replace themselves. In a review of data from 1909-2020, Viana *et al*. (2023) suggested that low productivity rates were the leading cause of the decline of Eurasian Curlews across their European range, as adult survival had remained relatively stable over that period (Pakanen, 2023). In the UK, productivity of Eurasian Curlews has been estimated at 0.25 chicks fledged per nest, whilst a minimum productivity of 0.43 chicks fledged per nest is needed to maintain a stable population (Cook *et al*., 2021). Similarly low levels of breeding productivity have been found in Eurasian Curlew populations across Europe (Roodbergen *et al*., 2012; Brown *et al*., 2015). Declines in productivity have also been recorded in other wader populations including Snipe, Lapwing, and Redshank (Table 1) (Siriwardena *et al.,* 1998; Newton, 2004; Roodbergen *et al*., 2012).

Agricultural intensification and habitat loss

Across farmland bird species, population declines have been stronger than those seen in other bird groups, a trend that has been recorded across Europe since 1980 (Rigal *et al*., 2023). Agriculture and its associated processes are globally the most frequently reported threat towards farmland birds and are much more heavily reported in Europe than other potential threats (Dougles *et al*., 2023). Agricultural intensification has been heavily linked to the decline of wader species, as its effects on the landscape and ecology of farmland alters habitat features and food chains (Fig. 1) (Newton, 2004; Ausden & Bolton, 2012; Johannesdottir *et al.*, 2017).

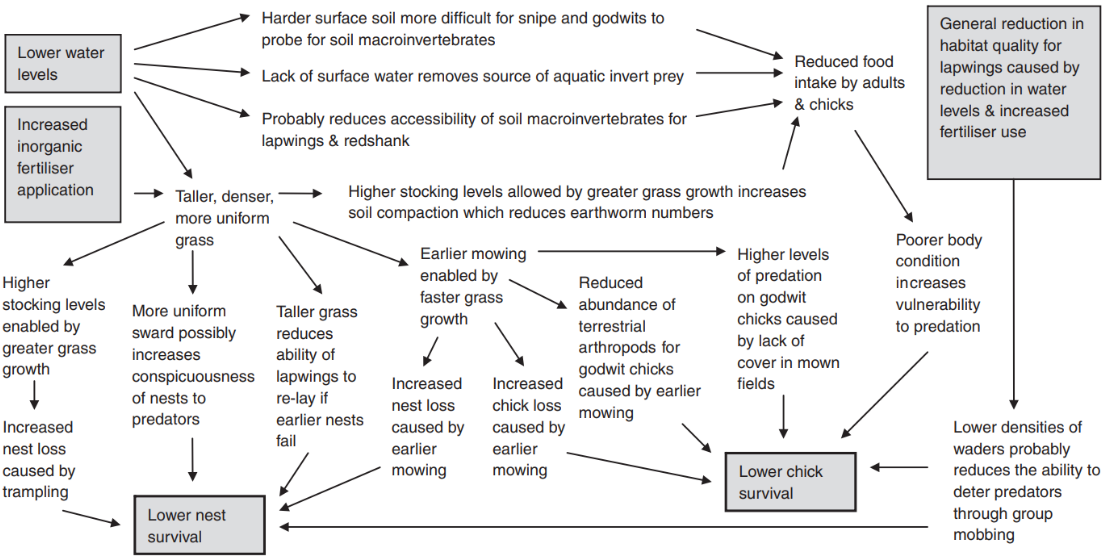

Figure 1. The mechanism through which agricultural intensification is thought to impact habitat quality for waders on lowland wet grassland. Figure taken from Ausden & Bolton, (2012).

The change in management of farmland habitats used by waders and other farmland bird species has been heavily linked to declines in populations, as farming moves away from semi-natural habitat to enclosed farmland (Franks *et al.,* 2017), and from mixed crop farms towards large scale monocultures for crops or pasture (Newton, 2004). The restructuring of farmland has also been linked to declines in these species due to loss of food sources, as the removal of hedgerows to provide larger fields, increased uses of herbicides and pesticides, and further land drainage, all to aid in increased crop production, also result in reduced invertebrate diversity and abundance (Fig. 1) (Newton, 2004).

A key determinant of nest location for breeding waders is vegetation height, and preferences vary in wader species (Tichit *et al*., 2005). Some birds prefer taller grasses for increased protection from predators, to help disguise the nest and because of the invertebrate food source that grasses provide, whereas other species prefer shorter sward or bare soil, as this gives the parents better visibility of potential threats to the nest (Olsen & Schmidt, 2004; Tichit *et al*., 2005; Van der Wal & Palmer, 2008;

Mandema *et al.,* 2014; Laidlaw *et al.,* 2016; Bell & Calladine, 2017; Moller *et al.,* 2018; van den Berg, 2024). Eurasian Curlews use areas of tall vegetation such as grasses for nest protection (Valkama *et al*., 1998; Newton, 2004), whereas Lapwings and Oystercatchers prefer shorter vegetation between 5-10 cm for their nests (Mandema *et al.,* 2014; Bell & Calladine, 2017; van den Berg, 2024). In fact, Lapwings have even been recorded abandoning nests in corn fields when vegetation has grown a metre during the breeding season, as they are no longer able to detect potential predators (Korner *et al.,* 2024). With increased use of fertilisers on farmland, the growth of vegetation occurs much faster, making it unsuitable habitat for breeding waders earlier in the breeding season (van den Berg, 2024).

For species such as Lapwing that prefer shorter vegetation, the application of cattle grazing has been found to increase breeding numbers, as this maintains a suitable sward height for their needs, as well as reducing rates of predation, making vigilance behaviours more effective for birds on the nest (Olsen & Schmidt, 2004; Laidlaw *et al.,* 2016). However, this approach can be damaging to wader populations as intensive livestock grazing resulting in especially short sward heights has been found to decrease the productivity of several wader species. Oystercatchers and Redshanks were found to nest more frequently in grassland habitat that had a higher vegetation canopy height, which correlated with the lower stocking density of livestock (Mandema *et al.,* 2014; Bell & Calladine, 2017). This is possibly due to the reduction in nest cover of shorter vegetation, as the decreased productivity in some wader species when avian predator population were high was correlated with high intensity grazing (Van der Wal & Palmer, 2008; Moller *et al.,* 2018).

The draining of wet grassland also contributes to reduced habitat suitability as the drier soils result in shorter vegetation and changes to vegetation community assemblage, which provide less cover as well as a decrease in availability of insects, which are a key food source (Smart *et al*., 2006; Moller *et al.,* 2018; Silva-Monteiro *et al*., 2022). Farmland with areas of shallow flooding have been found to attract much higher densities of nesting Lapwings, and later higher levels of chick field use (Eglinton *et al*., 2008). For birds such as Eurasian Curlew, Oystercatcher, and Redshank that use long beaks to probe into the substrate to forage, the penetrability of wet soils provides greater foraging success as well as greater availability of their target invertebrates (Smart *et al*., 2006).

Changes in the frequency and timing of farming practices have also been linked to farmland bird declines. Ploughing now often occurs in late summer, which removes spilled grain and seed that is used as a winter food source by farmland birds. The timing of silage cutting has also changed to allow for multiple cuttings in one year, as grass growth in early spring has increased with warming temperatures, meaning the first cut is now in direct conflict with the Curlew nesting period. The increased frequency of silage cutting to store as winter food then reduces habitat cover for chicks, which increases predation risk, and exposes them to large farm machinery which can destroy nests and chicks (Berg *et al*., 1992; Valkama *et al*., 1998; Newton, 2004; Wilson *et al*., 2004).

Grassland-breeding waders are now more dependent on unimproved grassland, moorland, and wetlands, as these habitats offer vegetation and food types that is more suited to their needs (Green *et al*., 1990; Hoodless *et al.,* 2010). Due to the broadness and complexity of the impact of agricultural intensification on waders using farmland, there is no singular solution to improve diversity and abundance of waders. There is also a variety of preferences across the waders species in relation to habitat management, in particular sward height and vegetation cover, which supports the needs for a varied approach to habitat management (Valkama *et al*., 1998; Newton, 2004; Olsen & Schmidt, 2004; Tichit *et al.,* 2005; Mandema *et al.,* 2014; Bell & Calladine, 2017; van den Berg, 2024). The distribution of many farmland bird species including waders has been positively linked to increased heterogeneity of agricultural landscapes, which supports bird abundance and overall greater biodiversity (Pickett & Siriwardena, 2011). To better support breeding wader populations, heterogeneity on UK farmland should be promoted further, as this would not only provide habitat for waders, but a wide range of species too (Benton *et al*., 2003; Martin *et al*., 2020). Approaches for increasing habitat heterogeneity include reverting from the large, continuous fields currently used towards mosaics of different fields connected by non-cropped areas, such as ponds, field margins, low hedges, and fallow land. By utilising a more open structure in planting of crops to provide space for nesting, and provisioning fields with dense vegetation and sparse vegetation, as well as varying sward height, there are habitats to suit a variety of waders, as well as the necessary food provisions and support for wider biodiversity (Benton *et al*., 2003; Bell & Calladine, 2017).

To combat the effects of agricultural intensification, governing bodies and environmental organisations have offered agri-environment schemes in many countries across Europe, including the UK. These schemes provide financial incentives, knowledge, and guidelines for the agricultural sector and individual farmers to improve habitat management for the benefit of biodiversity (Vickery et al., 2004; Hiron et al., 2013). The practices that they encourage focus on farmland bird diversity and abundance, in particular features such as old stone buildings and stone walls, grassland habitats, and increased food provisions for farmland birds other than waders, as well as improving insect populations (Kleijn et al., 2004; Birrer et al., 2007; Baker et al., 2012; Prince et al., 2012; Hiron et al., 2013; Roilo et al., 2022). However, these practices were less effective in more complex habitats with arable, grassland, and woodland blocks, and in some cases saw little improvement overall to farmland bird populations, potentially due to the large-scale impact of agricultural intensification (Kleijn et al., 2004; Prince et al., 2012; Hiron et al., 2013; Calvi et al., 2018; Roilo et al., 2022). Some strategies that are frequently advocated by these schemes to improve reproductive success of waders may also pose a threat to other wader species, including the removal of rush (Juncus spp.) to provide more suitable nesting habitats and inadvertently increase predation rates of waders due to reduced cover (Kelly et al., 2021). Postponed mowing is also encouraged, for example in the Netherlands, to allow for taller vegetation for breeding waders, but has minimal impact on wader abundance (Verhulst et al., 2007). Including raised groundwater levels to increase flooded areas into agri-environment schemes is likely to have the greatest effect on wader abundance and breeding success (Verhulst et al., 2007).

Predation

A major cause of low rates of reproductive success is predation of eggs or chicks. For example, most breeding failures of Eurasian Curlews and other waders have been attributed to predation (Berg, 1992; Valkama & Currie, 1999; Grant et al., 2001; Macdonald & Bolton, 2008; Amar et al., 2011; Moller et al., 2018, Ewing *et al*., 2023), with predators including Red Fox *Vulpes vulpes*, Hooded Crow *Corvus cornix* and Carrion Crow *Corvus corone*, Weasel *Mustela nivalis,* and raptors such as Common Buzzard *Buteo buteo and* Common Kestrel *Falco tinnunculus,* and in areas where larger predators have been eliminated, the Stoat *Mustela eminea* (Brown *et al.,* 2015; Mason *et al.,* 2018; Zielonka *et al*., 2019). Habitat change, afforestation, and agricultural intensification have also been linked to increased rates of predation. Fragmentation of forest habitats by the expansion of agricultural areas may increase predation of nests, and in several studies, predator numbers were negatively correlated with fragment size, and predators strongly preferred habitat edges (Smedshaug *et al.,* 2001; Cervinka *et al.,* 2011). Livestock may also lead to higher rates of predation, as their disturbance of nesting birds in fields leaves nests exposed to predators (Newton, 2004). The use of lethal predator control to protect ground nesting birds is increasing, and the removal of predators has been shown to maintain or increase wader reproductive success (Bodey *et al.,* 2011). However, this control then provides opportunities for compensation by other uncontrolled predators such as other corvid species and poses ethical issues as well as legal issues for protected raptor species (Bodey *et al.,* 2011; Laidlaw *et al.,* 2020).

Fencing areas to keep out predators at nest and site-level - covering specific plots or fields, has been identified as a potential method for conservation and for improving breeding success on lowland grassland. However, this method is not suitable for larger scale efforts to reduce predator effects on nests across the UK, especially for nest-level fencing, as it requires significant resources, time, and ongoing monitoring and maintenance (Malpas *et al.,* 2013; Ewing *et al.,* 2023). Reductions in the numbers of foxes and crows through predator control have led to an increase in breeding success for Eurasian Curlews, as well as other moorland birds such as Lapwing and Red Grouse *Lagopus lagopus* (Fletcher *et al*., 2010; Baines *et al*., 2022). This increase in productivity also occurred on grouse moors that are managed for grouse shooting, and where predators are controlled as part of this management. Eurasian Curlew productivity was higher at 1.05 fledglings per pair on grouse moors compared to 0.27 fledglings per pair on non-managed moorland without predator control (Baines *et al*., 2022). Managed grouse moors are currently the only areas in the UK experiencing successful landscape-scale predator control leading to increased ground-nesting bird productivity and showing what is possible for the protection of these species with the necessary funding. Inversely, grouse moor management has been linked to declines in raptor species due to illegal persecution and demonstrates the difficulty that comes with balancing the needs of all of the species that use this habitat (Newton, 2020). However, recent work has shown support for the success of grouse moors' maintenance without raptor persecution, which may present opportunities for wader success without predator control (Ludwig *et al.,* 2017). An additional solution to reduce predation, rather than predator control, which is difficult at a large scale, is controlling sward height, which as previously mentioned is important for nest and chick cover and camouflage (Grant *et al.,* 2001; Van der Wal & Palmer, 2008; Kelly *et al*., 2021; Ewing *et al.,* 2023). This is possible with the strategic use of grazing at certain times in the year, to maintain vegetation height at an appropriate level for wader species' preferences.

Forestry

Woodland planting and forestry is a growing concern in the UK when considering the restructuring of habitats typically used by grassland-breeding waders. This afforestation is primarily used to supply timber and wood fuel, and is often characterised by large, dense blocks of tree cover. These areas can host high numbers of predators, including Red Fox and Corvids, compared to the surrounding open landscapes (Valkama *et al.,* 1999). Predation on Curlew nests in areas of mixed farm and woodland was considerably higher than in areas of continuous farmland (Valkama *et al.,* 1999). Over a period of 8-10 years, Douglas et al. (2014) found that Curlew population changes were inversely related to the area of woodland that surrounded nesting sites, likely resulting from increased rates of predation. Oystercatchers are also affected by afforestation, with density of individuals being lower within the 200 m zone from the plantation compared to 700 m away, while Snipe density was shown to increase within 50 m of the plantation edge (Palsdottir *et al*., 2022). The absence of waders from areas adjacent to woodland or plantations further reduces the amount of suitable habitat available for them to breed, and when combined with the increased threat of predation, suggests that current afforestation strategies may pose a significant threat to grassland-breeding waders.

Food availability

Food availability also contributes to low productivity rates of waders. In agricultural grassland, Lapwing chicks feed on invertebrates in soil and low grasses, while Redshank has a similar but less specialised diet (Beintema *et al*., 1990). In contrast, Oystercatchers young have a diet mostly consisting of earth worms and larvae that they probe for in the soil (Beintema *et al*., 1990). Snipes probe in the earth and feed on earthworms, snails, and larvae, (Green *et al*., 1990), with Eurasian Curlews having a similar diet (Navedo *et al.,* 2020). Draining of grassland, re-seeding and use of fertilisers and insecticides lowers the availability of the invertebrates as a food source in these habitats (Wilson *et al.,* 2004). This is because there is no longer suitable habitat for aquatic invertebrates, and the short vegetation resulting from livestock grazing is negatively correlated with grassland invertebrate abundance that is a large part of waders' diets (Silva-Monteiro *et al.,* 2020).

Nest destruction

Another compounding factor in low productivity levels is the direct destruction of eggs, nests, and chicks by other agents. Tilled fields, which are used by waders that prefer open ground for nesting in agricultural areas, are more heavily impacted by modern farming practices that use large scale heavy machinery (Berg, 1992). While farmers are often familiar with their own land and the potential nest locations of local ground-nesting birds, this machinery is often operated by contractors who may have less knowledge of the area and may not provide birds with enough time to escape as the scale of the machinery makes small nests difficult to spot (Berg, 1992). The risk of destruction of nests, eggs, and chicks is a leading cause of reduced productivity for ground nesting birds in farmland such as Stone-curlew and Corncrake (Newton, 2004) and contributes to declines of wader species such as the Eurasian Curlew (Berg, 1992).

Direct destruction is also a risk posed to waders by livestock in farmland habitats, a risk that has been shown to increase with the density of livestock, as the likelihood of a nest being stepped on is greater (Mandema *et al.,* 2013; Sabatier *et al.,* 2015). Horses have been found to more frequently trample nests than cattle, and there was a higher rate of trampling overall near to water troughs, as this is an especially high traffic area

(Mandema *et al*., 2013). Trampling rates were highest at the start of the grazing period, so timing grazing with the breeding season is essential to decrease the risk to breeding waders (Pakanen *et al.,* 2011). However, complete removal of grazers from the landscape is also not the solution. Sabatier *et al*. (2010) found that the absence of or very low intensity grazing had a greater impact on population size than trampling, due to the decline in habitat quality supported by grazing, as vegetation length is important in wader site choice (Valkama *et al*., 1998; Newton, 2004; Olsen & Schmidt, 2004; Tichit *et al.,* 2005; Mandema *et al.,* 2014; Bell & Calladine, 2017; van den Berg, 2024). These findings emphasise the fine balance between the successful cohabitation of livestock and breeding waders, and the risk of nest destruction and loss of suitable breeding habitat.

Reduction in over-winter survival

Most waders move to coastal areas in the non-breeding season, including coastal wetlands, estuaries, beaches, and coastal farmland. These habitats introduce a new set of challenges for waders, including extreme weather, with snow, low temperatures, high winds, and large waves, factors which can also potentially impact food availability at these sites. The frequency with which these birds come into direct contact with human activity can be greater at these habitats, and the rate at which humans are altering these sites with urbanisation, infrastructure, fishing pressure, and recreational activity is increasing. Wader populations in the UK also increase in the non-breeding season, as birds from Northern Europe and Iceland migrate here for our milder winters, so the factors affecting wintering waders in the UK can have far reaching population effects. While there are declines in UK wader populations in the breeding and non-breeding winter seasons (Table 1), these population changes are largely independent from each other, as winter population declines likely reflect changes in European breeding populations (Woodward *et al*., 2022). Despite the challenges associated with these populations, wintering waders are comparatively less studied than those in the breeding season, with factors affecting survival in winter often overlooked.

Low temperatures and extreme weather

Survival rates of waders in winter vary from year to year, and a key factor that has been linked to this variation is temperature. This has been identified in winters with a higher frequency of days with air frost for Eurasian Curlew (Cook *et al*., 2021; Woodward *et al.*, 2022) and Oystercatcher (Durrel *et al.,* 2001). In one study of Lapwings, mean winter soil temperature and total rainfall explained 69% of variation in adult survival rates (Peach *et al*., 1994). The low temperatures in winter increase survival pressures on waders because the energy required to maintain their body temperature in cold weather is greater, so birds must increase their food intake. For birds that are already facing increased survival pressure from other factors, cold temperatures can exacerbate these issues and result in increased mortality (Clark, 2004; Goss-Custard *et al.,* 2006; Clark, 2009). For example, in the years directly following the UK's hunting ban on Eurasian Curlew in 1981, there was a decreased effect of severe weather on survival (Woodward *et al.*, 2022), which suggests that prior to the ban, the weather patterns worked to worsen the decline of populations that were already under pressure from hunting. Similarly, over a 4-year period, Franks *et al*. (2017) found that warmer winters strongly correlated with declines in Eurasian Curlews in Britain, although this was posited to result from a decline in the availability of the invertebrates that Eurasian Curlew feed on due to the temperature change, rather than a direct effect on the birds themselves. These studies provide further support for the role of synergistic factors in the decline of over-wintering success in waders.

Because of the interactions between these survival pressure on waders in winter, food availability is important to maintain populations. With their long, thin beaks, Eurasian Curlew, and Oystercatchers feed mostly on invertebrates in sand and soil, such as earthworms, Oligochaeta, which are a common food source in coastal pastures, as well as bivalves such as mussels and clams (Durrel et al., 2007; Navedo et al., 2020). On low tide feeding areas, they have been recorded feeding on Lanice worms, crabs, lugworms, and small molluscs, but this varies based on habitat, availability, and geographical location (Goss-Custard & Jones, 1976). Prey type may also influence species viability in the non-breeding season. The survival rates of Redshanks have been shown to be strongly related to food availability, as their prey is smaller than that of other waders, so to intake enough energy to survive colder temperatures, they need a large volume of food (Mitchell et al., 2000).

The flock density of foraging Oystercatchers and Eurasian Curlews is closely correlated with food availability (Rands & Barkham, 1981; Goss-Custard et al., 1991; Navedo et al., 2020). For example, Rands & Barkham (1981) found that Oystercatcher flock density was correlated with cockle *Cerastoderma edule* density, and Eurasian Curlew with *Mya arenaria* and *Arenicola marina* density. Declines in cockle and mussel stocks from commercial fishing activity have been linked to mass mortality events in Oystercatchers, as well as longer term reductions in body condition and longer-term survival; highlighting the importance of these food sources to wader populations (Atkinson *et al.,* 2003; Bowgen *et al.,* 2022). Feeding behaviour has also been linked to time of year, with the proportion of Eurasian Curlews and Oystercatchers feeding peaking between November and January, while population densities of Eurasian Curlew were highest in the autumn (Goss-Custard et al., 1977; Burton et al., 2002a). This period is the time when daylight time is shortest, and temperatures are lowest, meaning the individual energy requirements were at their highest (Burton et al., 2002a).

Habitat loss and land use change at coastal sites

The waders' ability to feed at wintering sites is evidently vital to their survival; however, human activity is altering habitats through development and poses a risk to wading birds through the loss of these feeding sites. The loss of feeding sites results in an increase in flock size of birds at other sites, putting a greater strain on prey populations as consumption by waders increases (Goss-Custard, 1977; Bowgen *et al*., 2022). The number of waders makes the prey's population unsustainable, leading to insufficient food availability, which can result in starvation, and the loss of large numbers of waders in the local population (Goss-Custard, 1977; Goss-Custard, 1979; Goss-Custard *et al.,* 1995). Waders' wintering sites are also being impacted at a global scale. Their choice of wintering site is now being impacted by climate change, with European populations moving Northwards in line with temperature increases (Maclean *et al.,* 2008). This range expansion may in future force wintering birds to locations that are less suitable for them in terms of the habitat type and available resources, but with lower climatic temperatures better suited to their physiology, potentially leading to further population declines (Maclean *et al*., 2008).

Disturbance from construction and development may also impact winter waders. Larger scale sources of anthropogenic disturbance such as construction have been shown to reduce Eurasian Curlew densities and feeding activity (Burton *et al*., 2002a). When predicting the possible impact of Barrage construction for renewable energy infrastructure, Austin et al., (1996) predicted population reductions in Lapwing, Curlew, and Redshank between 37.5% and 69% at the developed location. Such developments could change the size of intertidal areas, alter or dry out saltmarshes, and increase the risk of eutrophication, potentially impacting wader food sources, resulting in a loss of important breeding and wintering habitat for wading birds (Clark, 2006; Kadiri *et al*., 2014). The potential disturbance affects from developments such as tidal barrages to waders are broad, and possible mitigations should be considered when planning or considering these projects.

Recreational Disturbance

Coastal roosts are an important site for wintering waders as they provide a safe area for birds to flock together and are often frequently used at high tide when feeding areas are unusable and suitable habitat is limited. However, anthropogenic disturbance in coastal and tidal areas has led to the loss of suitable roost sites and is now being linked to declines in wintering wader populations (Catry *et al.,* 2011). In fact, anthropogenic disturbance has been shown to affect a wide range of species (Collop *et al.*, 2016; Scarton, 2018; Larson *et al*., 2019; Dertien *et al*., 2021).

Recreational disturbance refers to people undertaking recreational activities which may cause disturbance and is the most well-studied disturbance type for winter waders. The most used category of recreational disturbance is humans walking, but dogs, bicycles, aircraft, cars, and watercraft have also been identified as sources in disturbance studies (Kirby *et al*., 1993; Fitzpatrick & Bouchez, 1998; Navedo & Herrera, 2012; Collop *et al.*, 2016; Scarton, 2018; Larson *et al*., 2019; Goodship & Furness, 2022).

Disturbance may be measured indirectly, using landscape features such as footpaths or roads that are associated with disturbance, which when combined with a model that accounted for resource level variation provides preliminary measures for disturbance (Burton, 2007). However, these studies cannot provide enough detail to make a clear conclusion, especially when the amount that humans use these features is not quantified (Burton, 2007). More often, disturbance is measured directly. Species richness has been used as a measure of disturbance effect, with richness decreasing with higher levels of disturbance (Larson *et al*., 2019). To the best of our knowledge, disturbance has not yet been shown to effect local population size of Eurasian Curlew over an extended period (Kirby *et al*., 1993). However, the abundance of ground nesting birds; including wading birds, was found to be more heavily affected by higher rates of recreational disturbance than shrub or tree nesting birds (Larson *et al*., 2019).

The tidal period also appears to play a role in determining the level of disturbance, with disturbance response behaviours increasing at high tide, and decreasing towards low tide (Navedo & Herrera, 2012; Goss-Custard *et al.,* 2019). This is because Eurasian Curlew and other waders often feed on mudflats and areas exposed at lower tides, while humans are typically at higher areas of the intertidal area (Goss-Custard *et al.,* 2019). However, when tides move in, the likelihood of humans coming into the proximity of roosting birds increases (Navedo & Herrera, 2012). It was found that most disturbances occurred when only the upper shore was available at high tides, and therefore foraging time was rarely interrupted by disturbance (Goss-Custard *et al*., 2019). These coastal roosts are an important site for wintering waders as they provide a safe area for birds to flock together when suitable habitat is limited. However, anthropogenic disturbance in coastal and tidal areas has led to the loss of suitable roost sites due to the frequency of disturbance, meaning birds choose other, less resource-rich sites, and is now being linked to declines in wintering wader populations (Catry *et al.,* 2011; Navedo & Herrera, 2012).

One of the most common methods of measuring disturbance sensitivity is flight initiation distance – hereafter referred to as FID. Eurasian Curlews have been determined to have a high sensitivity to disturbance based on FID, with a mean FID of 211-340 m outside the breeding season, a greater distance compared to wading birds in general, with a threshold typically less than 100 m (Smit & Visser, 1993; Dertien *et al*., 2021; Goodship & Furness, 2022). This is in keeping with previous findings on FID, with positive correlations between mean body size and FID (Smit & Visser, 1993; Collop *et al.,* 2016; Scarton, 2018). If moving away, the birds would fly rather than walk, travelling distances between 41 m to 339 m (Smit & Visser, 1993; Fitzpatrick & Bouchez, 1998). The flight distances and time spent in flight as a response to disturbance are typically short for Eurasian Curlews, landing within the study area or returning within 5 minutes, travelling between 38-399 m (Kirby *et al*., 1993; Fitzpatrick & Bouchez, 1998). Wading birds spent <0.01% of foraging time in flight due to disturbance, equivalent to <0.02% of its daily energy requirements and <0.08% of daily foraging time (Goss-Custard *et al*., 2019). While these numbers suggest that the energetic effects of disturbance to wintering waders is minimal, it does not account for other disturbance behaviours such as vigilance which can also increase with disturbance, and result in further foraging time lost (Beauchamp, 2017).

Temperature can also alter energy expenditure and behaviours, as time spent in flight and therefore the amount of time spent foraging that was lost was greater in milder conditions, which Collop *et al*. (2016) proposed was a result of the increased need for energy conservancy in colder conditions. This suggests that the impact of disturbance is in fact less significant in colder weather. Individual variation may also contribute to the cost of disturbance to waders. Van der Kolk *et al.* (2021) proposed that the balance of energy usage and intake would vary between individuals, with less efficient feeders spending more time feeding and therefore are more likely to be disturbed, as well as having less ability to compensate for the effects of this disturbance. Further studies of the full energetic costs of disturbance are required to fully determine its effect on survival of over-wintering waders.

A key consideration when looking at disturbance is how peck rates and feeding success are affected. Flight requires energy, and takes away time needed for feeding, and there is concern that if disturbance increases to a point where energy expended outweighs energy input that it would negatively impact the bird. Larger shorebird species such as Eurasian Curlews have a greater response to disturbance, but this does not reach a threshold where those individuals’ energetic costs altered daily intake (Collop *et al.*, 2016). This is further supported by the finding that in areas where human activity has increased, scan rates also increase but peck rates were unaffected, though Eurasian Curlews will typically stop feeding when disturbed. Overall feeding success increased with human disturbance (Fitzpatrick & Bouchez, 1998). This suggests energy intake and expenditure are relatively unaffected by human activity.

Conclusion

Wader populations are impacted by factors in both breeding and non-breeding seasons that in combination are resulting in their severe decline. In the breeding season, agricultural intensification and its modification of vegetation and wetland habitats used by wading birds to raise young has resulted in loss of suitable nesting habitats and direct mortality by predation, machinery, and livestock, as well as declines in food availability. In the non-breeding season, low temperatures put pressure on waders' energy intake, and when feeding habitats are lost and recreational disturbances increase energy expenditure further, the waders cannot sustain themselves, resulting in further population declines. Efforts such as agri-environment schemes are being made to halt population declines, though the effects are limited, and the changes that would most improve breeding success in waders are not being made. Future research should consider approaches to decrease predation, and ways to minimize the impact of agricultural activity on breeding waders. There is currently limited understanding of the effects of low temperatures and other extreme weather conditions on waders at non-breeding sites, and we need to better understand which conditions most negatively impact waders, and how other survival pressures can be minimised to reduce the effects of extreme weather.

Chapter 2

Vigilance behaviour of Curlews *Numenius arquata* at winter roost sites

Abstract

Anthropogenic activities are leading to declines in a wide range of species, the effects and mechanisms of which can be assessed through not only changes in population size, but also behaviour. Vigilance behaviours, for example, can give insight into perceived threat levels from disturbance from natural or anthropogenic sources. Here, we use vigilance behaviour as a proxy to assess the impact of anthropogenic disturbance and environmental conditions on behaviour and long-term population trends. Data was collected through observation of non-breeding Curlews, a species classified on the IUCN Red List as 'near threatened' following rapid worldwide declines (IUCN, 2024), at winter roost sites on the Isle of Man. Vigilance behaviour frequency and duration in individuals increased with group size and wind speed, and declined in temperatures below 5 °C, while vigilance across the group increased with group size. Vigilance behaviour was not found to be affected by anthropogenic disturbance, and temporal variation in population size did not correspond with environmental factors. We conclude that intra-specific behaviour and environmental factors affect vigilance behaviour, but that the mechanisms are still poorly understood.

Introduction

The world's human population is growing (United Nations, 2024) and with that growth come negative impacts on the environment through a range of processes including increased urbanisation, agricultural intensification, land use change and habitat loss (Mantyka-Pringle et al., 2011; Lawler et al., 2014; Hautier et al., 2015; Emmerson et al., 2016; Theodorou, 2022). Anthropogenic disturbances are discrete events that can result in a change in resource availability or ecological function (Burton et al., 2020), and these have been linked to declines in species richness globally through a range of human activities including disturbance due to recreational activity (Murphy & Romanuk, 2013). When exposed to recreational human disturbance such as walkers, dogs, cars, planes and boats, organisms alter their behaviour in response (Frid & Dill, 2002; Mengak & Dayer, 2020; Wilson et al., 2020; Zhang et al., 2023). This may result in reduced food intake (Ciuti et al., 2012; Lee et al., 2024) a decline in reproduction (Setsaas et al., 2018), stronger fear responses (Tarjuelo et al., 2015, Meisingset et al., 2022), and increased frequency of avoidance behaviours such as flight and vigilance (Frid & Dill, 2002) resulting in an increase in energy expenditure (Collop et al., 2016). Such behavioural changes not only negatively impact the organisms directly, but also have implications for ecosystem functioning, including primary production, nutrient cycling, habitat modification, and pollination and seed dispersal (Burton et al., 2020).

Impact of anthropogenic disturbance on birds

Anthropogenic disturbances have been found to negatively affect functional diversity of birds globally, particularly impacting specialised traits and behaviours such as monophagy, and favouring species that are more capable of adapting to these disturbed habitats (Devictor *et al.,* 2008; Matuoka *et al.,* 2020; Callaghan *et al*., 2024). The decline in functional diversity is in line with loss and fragmentation of habitats, which forces species within a niche to compete more for reduced resources (Matuoka *et al.,* 2020; Brodie *et al*., 2021; Mariano-Neto & Santos, 2023). This also puts more specialised species at higher risk because they have fewer ecological opportunities to exploit if they are forced out of their primary habitat (Reed & Tosh, 2019; Matuoka *et al.,* 2020).

The effects of anthropogenic disturbance are especially important for wetland birds, as habitat loss due to agricultural change and urbanisation have reduced habitat availability for wetland species globally (Hughes, 2004; Stevens & Conway, 2019). Declines in food availability and suitable breeding sites, because of hydrological and vegetation changes, have led to a long-term decline in breeding populations of some wetland bird species (Stevens & Conway, 2019). Recreation activities which provide a direct source of disturbance have also been associated with reduced species richness and abundance, with greater effects on small and ground nesting birds (Larson *et al*., 2019) such as waders and passerines, which have threshold distances for disturbance effects that are considerably smaller than for larger species, or those that nest in trees or shrubs (Dertien *et al*., 2021). Potential recreational disturbances at coastal sites include small boats close to shore, horse riders, surfers and wakeboarders, cyclists, cars, and aircraft, but the most frequent recreational disturbance at coastal sites is walkers, who are often with dogs (Kirby *et al*., 1993). Several studies have evidenced an increased likelihood of disturbance to waders from the presence of dogs (Lafferty *et al*., 2001; McBlain *et al*., 2020). Plovers were found to be more likely to fly from dogs, horses, or crows, than from humans (Lafferty *et al*., 2001), while Oystercatchers *Haematopus ostralegus* showed increased levels of vigilance when exposed to dogs compared to other sources of disturbance (McBlain *et al*., 2020).

During periods of high tide, wading birds such as Curlews *Numenius arquata* (hereafter 'the Curlew') make use of roost sites, where individuals congregate in flocks until feeding sites become available again as the tide recedes. Their behaviour at roosts is primarily resting to conserve energy, as these sites are often lower in food availability than feeding grounds but can provide shelter from weather such as high winds and can offer protection from predation with vegetation and result in the formation of denser flocks as the birds are not foraging (Rosa et al., 2006; Zhang et al., 2021). Increased levels of disturbance at roosts result in a reduction in the number of birds using those sites, and when roost sites are limited, this can be energetically costly, requiring birds to travel further distances to find suitable, undisturbed sites (Rogers *et al.,* 2006). Increased disturbance exposure can also result in increased energy expenditure, which when combined with a decline in food availability and severe weather, may result in reduced fitness (Goss-Custard *et al*., 2006).

Behavioural adaptations to anthropogenic disturbance

Vigilance in ecology is typically defined as the monitoring of potential threats using different sensory modes (Beauchamp, 2017a). The observable behaviours of vigilance, such as stopping foraging, preening or walking to look up and visually scan the surroundings, can be used as a proximal way to measure disturbance effects on an organism (Fitzpatrick & Bouchez, 1998; McBlain et al., 2020; Kong et al., 2021). By measuring changes in the frequency of vigilance behaviours of birds exposed to anthropogenic disturbance, we can better understand the extent to which it alters typical behaviours (Frid & Dill, 2002). However, the variation in vigilance behaviours has also been associated with group size, most often resulting in a decline in vigilance as group size increases (Lima, 1995; Beauchamp, 2003; Beauchamp, 2008; Beauchamp, 2017b). The decrease in vigilance with group size is frequently attributed to the 'many-eyes' hypothesis, which suggests that as group size increases, the number of individuals scanning for predators increases, so they can each spend more time performing non-vigilance behaviours, such as foraging, preening or resting (Lima, 1995; Roberts, 1995; Beauchamp, 2003). The inclusion of group size when measuring the individual vigilance behaviour of Curlews considers the possible behavioural changes associated with larger groups in the 'many-eyes' hypothesis. Studies on vigilance behaviour have predominantly focused on periods when birds are foraging rather than resting and have identified the risk of predation (Watson *et al*., 2007; Fuller *et al.,* 2013; Beauchamp, 2019), foraging strategy (Barbosa, 2002), and competition for food (Lian *et al*., 2007; Beauchamp, 2014) as other potential mechanisms for the group size-vigilance effect.

Impact of environmental conditions

Low temperatures in winter increase survival pressures for many avian species in temperate climates, as increased energy expenditure is required to maintain internal temperatures. This extra demand for energy also comes during weather periods which may make foraging more difficult, such as freezing temperatures, or when food supplies are reduced, so making it even more challenging to balance the energy budget. Birds face a trade-off between increasing their risk of predation and increasing their foraging rate or duration, which might cause a decrease in other behaviours such as roosting, that are not immediately essential for survival (Bonter *et al.,* 2013). In a meta-analysis of recreational disturbance effects, Larson *et al.*, (2016), found greater evidence that human recreation had an effect on birds in winter periods, and that the effects of disturbance predominantly impacted animals negatively. Many of these studies showed negative effects to behaviour, physiology, and abundance, which may make them more vulnerable during periods of low temperatures.

The temperature threshold below which increased energy expenditure is required is termed the 'lower critical temperature' (LCT) and varies between species (Bowgen, 2017). In wading bird species, Bowgen (2017) found that the LCT was positively correlated with body mass. However, food availability and predation risk can also impact body mass. Depending on the availability of food, increased body fat enables the individual to account for the increased energy demands of low temperatures, especially when conditions such as snowfall or frost prevent foraging (Robinson *et al*., 2007; Rogers, 2015). Such fat reserves may, however, increase the risk of predation, as flight initiation or agility may be inhibited, resulting in a trade-off during cold weather (Rogers, 2015).

Study species

This study focuses on the Curlew, a wading bird species which is experiencing rapid global decline that is partially attributed to anthropogenic activity, particularly habitat change and recreation, and are listed as near threatened on the IUCN Red List (Pearce-Higgins *et al.,* 2017; BirdLife International, 2021; Wetlands International, 2016; IUCN, 2024). Curlew in the British Isles have experienced long term population declines, with a decline of 50% in the breeding population between 1995 and 2022 (BTO, 2023) and were identified as the UK's highest conservation priority species in 2015 (Brown *et al*., 2015). In winter, the UK Curlew populations increase with overwintering birds migrating from their breeding grounds in Northern Europe, while the UK breeding birds often move further south, and population size increases to 125,000 individuals (BTO, 2023). However, these winter populations have declined, reducing by 32% between 1996 and 2022, likely due to factors that are affecting the European breeding populations (Woodward *et al.,* 2022; BTO, 2023). Curlews mostly remain in the same area over a given winter, with ranges averaging 5 km^2 (Donnez *et al*., 2023). This gives cause for concern for their ability to respond to environmental changes at coastal roost sites, as they may not move away from disturbed areas and are, therefore, more at risk from the potential effects of anthropogenic disturbance (Donnez *et al*., 2023). Such changes include recreational disturbance, human modifications to habitats through the building of roads and structures, the draining of wetlands, and other intrusive landscape alterations, as well as environmental changes such as declines in food availability and periods of severe weather that may be linked to climate warming (Burton *et al*., 2002b; Godet *et al*., 2011; Bowgen *et al*., 2015).

Curlews have a high sensitivity to direct disturbance, with a mean flight initiation distance in the non-breeding season of 188-340 m (Goodship & Furness, 2022), which is the distance at which a bird begins to escape an approaching disturbance. When exposed to disturbances, Curlews tend to increase rates of vigilance behaviours and may stop foraging or fly away from the site entirely (Fitzpatrick & Bouchez, 1998; Goodship & Furness, 2022). Time spent performing vigilance behaviours by Curlews was also shown to increase with the number of birds within a 10 m radius, and in habitat with a greater amount of vegetative cover, but not on open mudflats, while vigilance frequency was negatively correlated with the number of individuals of other bird species (Zhang *et al.,* 2021). A high density of birds may also affect individual level behaviour in Curlews, as this reduces food availability, an often already limited resource at roost sites, requiring Curlews to spend more time foraging to support energy needs and resulting in a decrease in other behaviours such as vigilance (Cook *et al*., 2021).

However, even with their high sensitivity and potential vulnerability towards anthropogenic disturbance, the relatively large body size and physiology of the Curlew may lessen their susceptibility to low temperatures and extreme weather. Curlews have an LCT of 5 °C, due to their large size, which is lower than other wader species that occupy the same habitats, such as Oystercatcher, Bar-tailed Godwit *Limosa lapponica* and Grey Plover *Pluvialis squatarola* (Bowgen, 2017). This allows Curlews to have comparatively more energy resilience through cold weather periods than other wader species, but despite that, their winter survival rates have declined in recent years in conjunction with severe weather and colder winters (Cook *et al*., 2021; Woodward *et al*., 2022).

The previous studies on the vigilance behaviour of Curlews and the effects of anthropogenic and environmental disturbances have focused on Curlews at their breeding season nest sites or at their non-breeding season foraging habitats. Whereas studies that have focused on Curlews at their roost sites considered the effects of disturbance on habitat usage, roost site selection, and energy expenditure. In this study we address the current lack of understanding of Curlews vigilance behaviour at roost sites, and the extent of the impact of anthropogenic and environmental disturbances on this behaviour.

Hypotheses, questions and predictions

The aim of the study was to understand the effect of anthropogenic disturbance and weather conditions on vigilance behaviour of Curlews, and to establish a better understanding of their behaviour at roost sites. The central hypothesis is that, as in other species, the behaviour of Curlews will be impacted by the frequency of anthropogenic disturbance and environmental variables such as temperature and wind. Three predictions were tested to achieve this: first, that vigilance behaviours would decrease with higher wind speed and lower temperatures, due to the greater energy requirement of these conditions for increased foraging and rest; second, that individual vigilance behaviours would decline with increasing group size, as group size alters perception of risk with the many-eyes hypothesis; and third, that vigilance and avoidance behaviours would increase with the frequency of direct anthropogenic disturbance, because of a greater perceived risk and prioritisation of anti-predation behaviours for safety. In addition, that long-term population size would decrease with lower environmental temperatures, due to the physiological costs of extreme weather conditions.

Methods

Study sites

Data were collected from November 2023 until March 2024 at two sites on the Isle of Man where Curlew roost at high tide over winter (Figure 1). Langness is located on a peninsula on the south-east coast of the Isle of Man (54° 4' 5.3'' N 4° 37' 16.1'' W) and is a rocky shoreline, surrounded by a small area of saltmarsh, with an adjacent road. Most of the peninsula is a maintained golf course and area for dog walking. The surrounding marine environment is a marine nature reserve. At high tide the birds mostly roost on the edge of the saltmarsh adjacent to the sea, and on areas of rocky outcrops. Data collection was taken from a single observation point providing visibility of the full roost and was at least 200 m from the birds to minimise disturbance (Figure 2). Data collection occurred within the time period of an hour before and an hour after hightide at both sites. The site is frequently exposed to potential disturbance, as it is less than 2 km from the island’s airport, and the road that runs parallel to the roost is in regular use by vehicles, walkers and walkers with dogs. The bay is also potentially disturbed by people using boats and by windsurfers. Blue Point is located on the north-west coast of the Isle of Man (54° 23' 2.7'' N 4° 29' 54.5' W) and is composed of a narrow area of rocky shoreline, with an adjacent area of vegetated dunes leading to steep sandy cliffs. The birds normally roost on the exposed shoreline next to the mouth of the Lhen Trench. Observations were taken from a single observation point >300 m from the roost site to minimise disturbance (Figure 2). Potential sources of disturbance at the site are infrequent as it is not near any major settlements, however there is a nearby carpark, and it is used predominantly by people walking dogs.

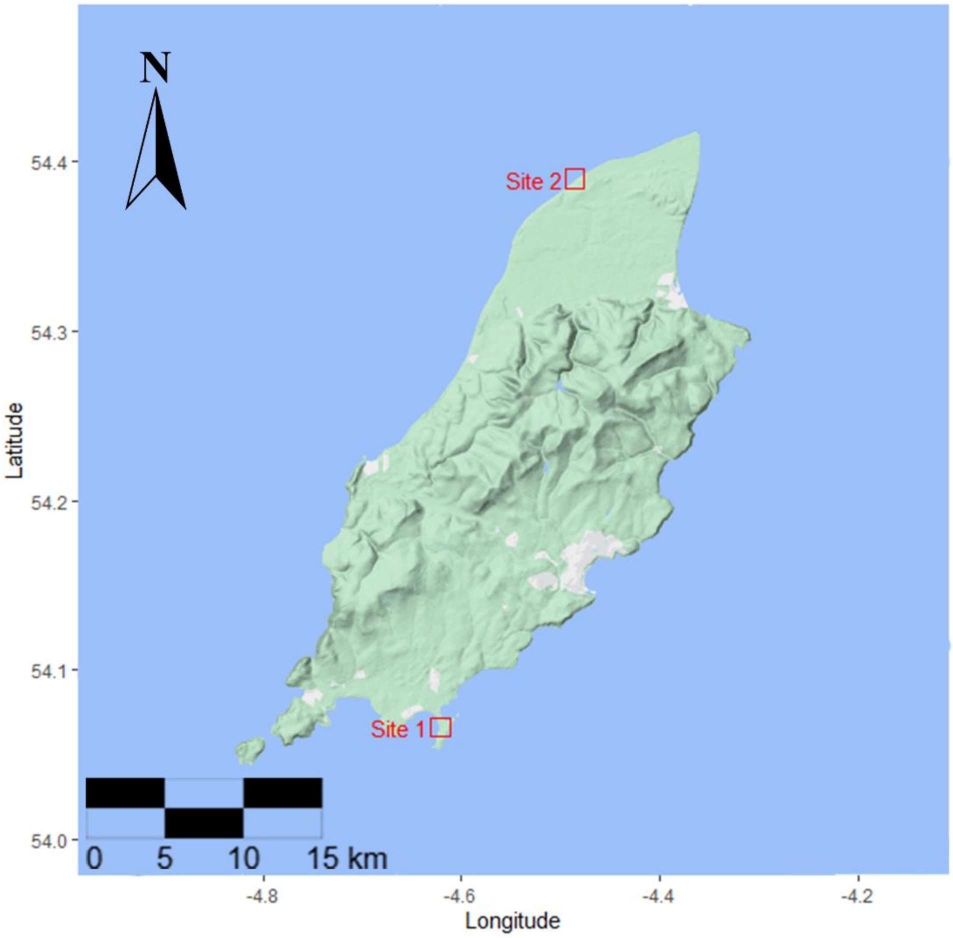

Figure 1. Location of Langness (site 1) and Blue Point (site 2) on the Isle of Man. The red boxes indicate the area covered by individual site satellite views shown in Figure 2.

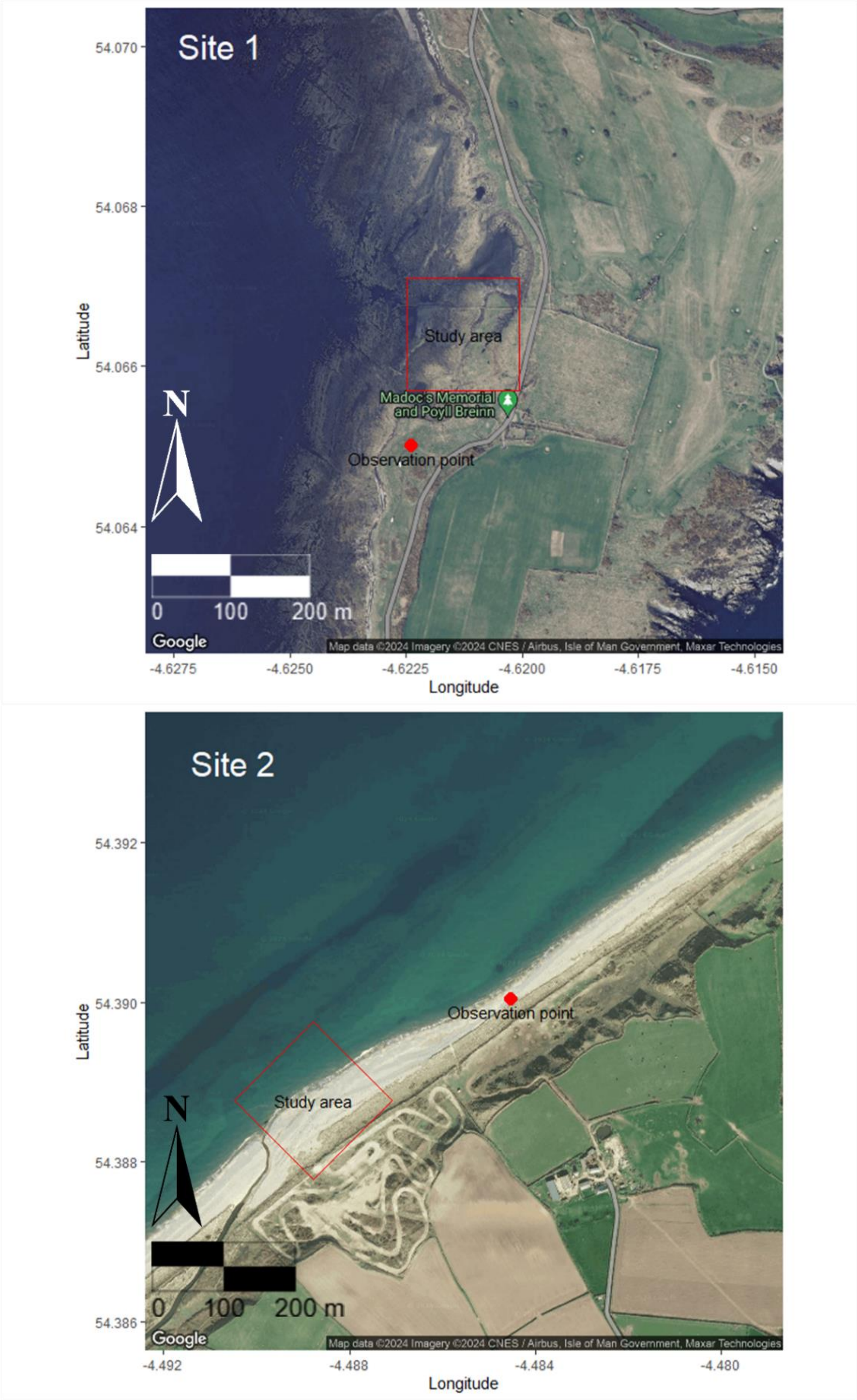

Figure 2. Satellite images for Langness (site 1) and Blue Point (site 2), showing the study areas where the Curlew roosts were located. The red spot shows the position of the observation point used for all data collection. The red box outlines the study site where Curlews were positioned.

Data collection

The study involved 20 individual site visits, each occurring on a different day (Blue Point: n = 8 and Langness: n = 12) with a mean of 13.9 (± 4.3 SD) observations of individual Curlew per visit. For the collection of individual behaviour data, a different bird was selected for each observation, which was possible on most occasions as the birds frequently remained in the same place throughout the session. When this was not possible due to small group sizes, multiple observations were taken from the same bird, which occurred during 6 sessions. As the birds were not individually identifiable in the field, we cannot eliminate the possibility that the same individuals might have been observed more than once but on different days. Behavioural data were taken using a Leica 20-40x 60 mm scope on a Manfrotto 055 tripod for a period of 2 minutes, during which the behaviour was recorded at 5 second intervals. Behaviours were categorised into look, preen, roost, flight, other, and out of sight (Table 1). Group data were collected using a scan method with a tally counter to ensure birds were only counted once, and the number of birds in the group performing each behaviour (Table 1) was also recorded. Group data were recorded in alternation with individual behaviour recordings during the site visit, with a mean of 13.7 (± 4.7 SD) scan observations per session, and a 5-minute period between observations.

Table 1. Behaviour categories for individual and group level behaviour records.

Behaviour	**Description**
Look	Beak up and parallel to the ground
Preen	Rubbing head on its back or preening feathers
Roost	Beak tucked under wing
Flight	Both legs are off the ground
Other	Includes any other behaviour, may be walking, pecking, feeding, calling etc
Out of sight (OOS)	Bird is no longer visible

Potential anthropogenic disturbances that occurred during the 2-minute individual observation were also recorded at the 5 second intervals, and were categorised into vehicle, person, dog, or other. All potential disturbance types were recorded, for example a dog with people would be recorded as such, however the number of each type was not recorded. The maximum threshold distance for when a disturbance would be recorded as a disturbance event was constrained by the size of the sites, meaning that any potential disturbance that became visible to the observer was within the lower flight initiation distance of the Curlews as determined by Goodship & Furness (2022) of 188m.

For the analysis of environmental variables on the Curlew populations over multiple winter periods, the annual peak count data for Curlews recorded between October and March on the Isle of Man were extracted from the 2022/2023 Wetland Bird Survey report (Woodward *et al*., 2024), covering the period from 1998/1999 to 2022/23. The Wetland Bird Survey (WeBS) is a monitoring scheme for non-breeding waterbirds in the UK and is funded and delivered by the British Trust for Ornithology, the Royal Society for the Protection of Birds, and the Joint Nature Conservation Committee, in association with the Wildfowl and Wetlands Trust. It includes monthly counts at defined sites at high tide between September and March, on dates synchronised across the country, as well as additional low tide counts at key locations. Volunteers survey the same site throughout the year using a 'look-see' methodology and record the number of all waterbird species present (BTO, 2017). Of the 24 sites included in the counts on the Isle of Man, 4 WEBs sites that are geographically adjacent and include the area of site 1 were used for analysis, to provide a more consistent peak count. These data did not include three periods between 1997/98 to 2004/04, 2006/07 to 2007/08, and 2010/11 to 2014/15 where counts were not taken. The peak count of the four sites for each year with available data was then used for analysis.

Weather data were supplied by the Isle of Man Meteorological Office and covered the data collection period, and the historical period between October and March from 1998 to 2023. These data included the mean daily temperature during the 24 h period between 09:00 am on one day to the next in degrees centigrade, the mean daily windspeed in knots, and the maximum gust speed in knots. These variables were used in the analysis of vigilance behaviours and were used to produce four measurements of temperature to be included as variables when analysing the historical population size: minimum mean daily temperature, overall mean daily temperature, days below LCT (5 degrees C), and days below 0 degrees C (Table 2). For further details and definitions of the variables collected, see Table 2.

Table 2. Description of variables used in the analysis of Curlew behaviour.

Variable name	Description
Session	The day on which the data collection occurred; an alternative measurement to date.
Group size	Number of Curlews present at one time within the data collection area.
Peak count	The largest group size recorded at the site on a given day.
Individual behaviour	The behaviour performed by one individual over a 120 second observation period, with behaviour type recorded at 5 second intervals. Where possible, each bird was recorded for one data observation period during that visit, unless flock size was below 13.
Group behaviour	Number of Curlews within the group performing each behaviour type at the same time when counted using a scanning count method, allowing each bird to be counted only once.
Vigilance frequency	The number of times an individual began performing the 'Look' behaviour in a 120 second observation period.
Vigilance duration	The number of seconds within a 120 second observation period that the individual spent performing 'Look' behaviour.
Disturbance	A potential anthropogenic disturbance including cars, people, dogs, or other anthropogenic entity entering the study area during the 120 second behavioural observation period.
Wind speed	The mean wind speed between 9 am and 9 am the following day.
Temperature	The mean ambient temperature between 9 am and 9 am the following day.
Temperature below LCT	A binary value identifying whether the temperature was below the lower critical temperature of 5 degrees.
Minimum mean daily temperature	The minimum mean daily temperature of each winter period from October to March of the following year.
Overall mean daily temperature	The mean temperature taken across the winter period of each year.

Days below LCT	The number of days with mean daily temperature of 5 °C or below from each winter period October to March.
Days below 0 degrees C	The number of days with mean daily temperature of 0 °C or below, from the same period.

Statistical analysis

Variables affecting individual vigilance in Curlews

All analyses were carried out using R, version 4.3.3 (R Core Team 2024). Generalized linear mixed effect models (GLMMs) using the function ‘glmmTMB’ from the R package ‘glmmTMB’ (Brooks *et al*., 2017) were used to analyse the relationship between the vigilance behaviour of individual Curlews, anthropogenic disturbances and environmental variables. Poisson models were used, with the site and session fitted as nested random terms to control for the non-independence of repeated measures. Vigilance frequency was used as the response variable, and disturbance, wind speed, peak count, and temperature below LCT were included as fixed effects in the initial model (Table 2). The date on which the data collection occurred was converted to a session number. The group size variable refers to the number of Curlews present at one time within the data collection area, while the peak count variable is the largest group size recorded at the site in that session (Table 2).

Prior to model selection, collinearity between explanatory variables was checked following Zuur *et al*. (2009), assessing collinearity visually and calculating variance inflation factors (VIFs). All variables were included in the model as pairwise correlations were weak ($r \le 0.5$ for all pairings), and no VIFs were > 3. A backwards stepwise deletion method was then used to refine the initial model, where model terms were removed in order of increasing test statistic value if the likelihood tests used to test significance did not indicate significant variation, removing the variables sequentially. This was then repeated until the minimal model was obtained, at which point each removed term was put back into the minimal model to ensure significant variables had not been dropped, and to extract the level of non-significance using an analysis of variance ‘ANOVA’ against the minimal model. This process was then repeated using vigilance duration as the response variable, with all the explanatory variables remaining the same. The ‘SimulateResiduals’ function from dHARMA (Hartig, 2022) allowed for a visual assessment of model fit and provided values for the inbuilt tests of model fit in this package.

Variables affecting group vigilance in Curlews

The relationship between anthropogenic and environmental disturbances and vigilance behaviour of groups of Curlews was analysed using hurdle models with the function ‘glmmTMB’ from the R package ‘glmmTMB’ (Brooks *et al*., 2017). Binomial and truncated Poisson models were used, with the session and site fitted as nested random terms to control for the non-independence of repeated measures. A hurdle model was used for this analysis due to the large proportion of zero counts in the data. It models the probability of a zero value, whether the behaviour occurred or not, separately from the probability of the non-zero values, in this case; how many birds exhibited the behaviour. The number of birds within the group performing vigilance was used as the response variable, and it was converted to a binary value for the binomial model to indicate whether there was vigilance in the group. Temperature and group size were included as fixed effects in the initial model. A backwards stepwise deletion method was again used to refine the model, following the same process outlined above.

Effect of temperature on the Curlews wintering population

For this analysis, general linear models (GLMs) were used to analyse temperature variables versus yearly peak count of Curlews. Due to the small size of the data set, each measure of temperature was analysed separately (Table 2). Yearly peak count of Curlews was used as the response variable, and the temperature variable as the independent variable, with a Gaussian distribution. The ‘SimulateResiduals’ function from dHARMA (Hartig, 2022) again allowed for a visual assessment of model fit and provided values for the inbuilt tests of model fit. As each model contained one term, the level of non-significance was then extracted from the model statistics.

Results

Variables affecting individual level vigilance in Curlews

During the data collection period, we recorded 278 observation periods of 120 s of individual behaviour summing to 556 minutes of observation. Curlews spent the largest percentage of their time performing roosting or vigilance behaviours (Fig. 3). Less than 10% of total observation time was spent in flight, preening, or performing other behaviours such as foraging. Curlews were observed taking flight on 14 separate occasions across the 278 individual behaviour observations, at a rate of 1 recording of flight every 0.05 observations, or 1.5 recordings of flight per hour. Individual Curlews were recorded as out of sight of the observer on 11 occasions.

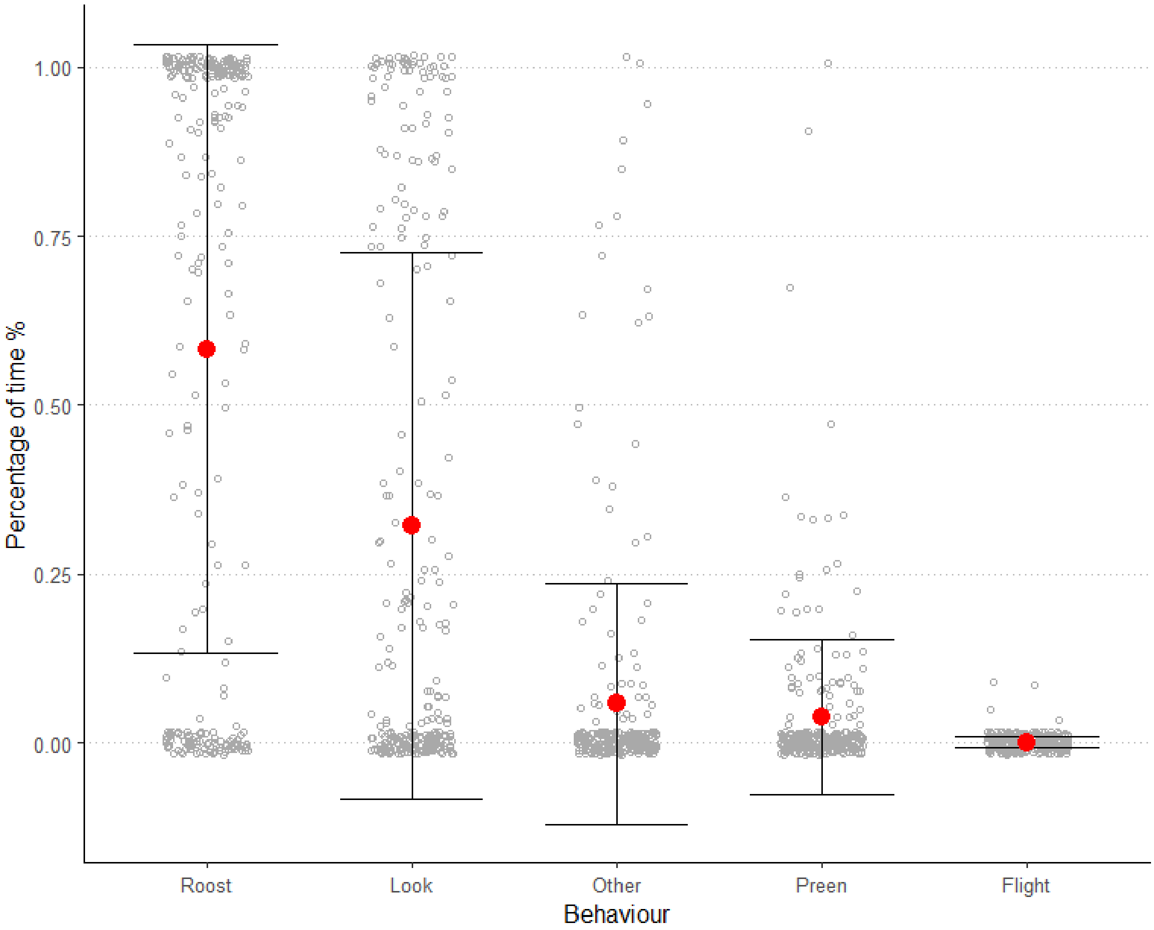

Figure 3. Mean percentage of time individual Curlews spent performing behaviours at winter roost sites during 120 second observation periods. Red point shows mean, and whiskers show standard deviation of the mean. Data collected from two sites combined, across n = 21 data collection sessions, and totalled n = 278 observation periods.

The frequency of vigilance behaviours in individual Curlews increased significantly with the peak count of Curlews on that day (Fig. 5a) and decreased with temperatures below their LCT (Table 3, Fig. 4a). Wind speed (Fig. 6a) and potential anthropogenic disturbances (Fig. 7a) were not found to be significantly correlated with vigilance frequency (Table 3). The duration of vigilance behaviour in individuals was also negatively correlated with temperatures below LCT (Fig. 4b) and positively correlated with peak count (Fig. 5b), however vigilance duration was also found to increase with mean wind speed (Table 3, Fig. 6b). There was no significant correlation between vigilance duration and anthropogenic disturbance (Table 3, Fig. 7b).

Table 3. A GLMM of vigilance frequency and vigilance duration by Curlews at winter roost sites. *Values below the 0.05 significance threshold are shown in bold.

Response	**Fixed effects**	**Estimate ± SE**	**Chi^2**	**p***
Vigilance frequency	Intercept	-0.20 ± 0.27		
	Temperature < LCT	-0.15 ± 0.07	8.97	**0.003**
	Peak Count	0.19 ± 0.06	4.85	**0.03**
	Mean wind speed	0.01 ± 0.30	0.01	0.94
	Disturbance	-0.20 ± 0.15	2.28	0.13
Vigilance duration	Intercept	3.32 ± 0.35		
	Temperature < LCT	-0.55 ± 0.35	9.86	**0.001**
	Peak Count	0.01 ± 0.01	9.30	**0.002**
	Mean wind speed	0.05 ± 0.01	9.99	**0.002**
	Disturbance	-0.30 ± 0.16	3.39	0.07

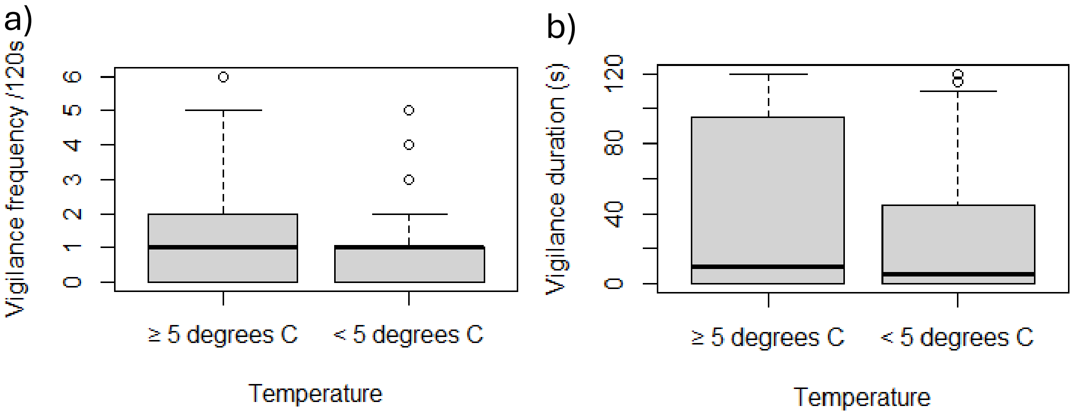

Figure 4. a) The frequency of vigilance behaviours of individual Curlews at roost sites per 120 s at temperatures at and above 5 °C and temperatures below 5 °C and b) the duration of vigilance behaviours of individual Curlews at roost sites for the same categories. The thicker line indicates the median value, and the whisker bar indicates the upper interquartile value.

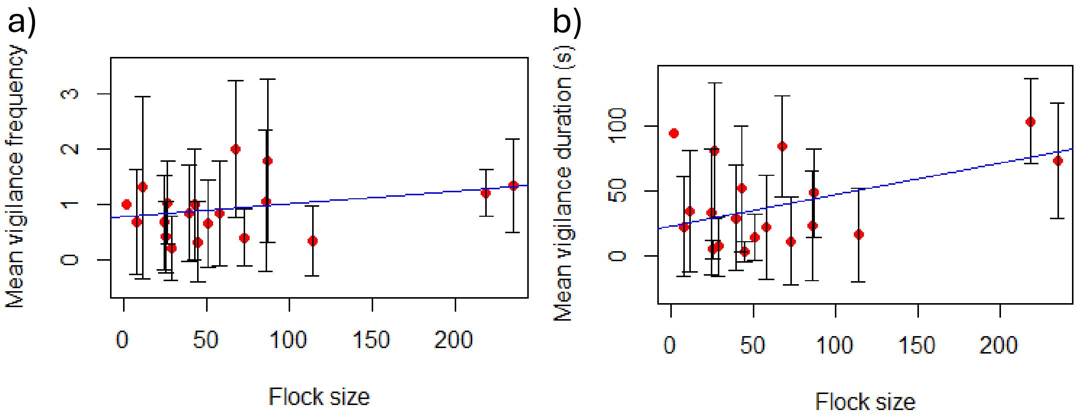

Figure 5. a) The mean frequency of vigilance behaviours of individual Curlews at roost sites as a function of peak flock size and b) the mean duration of vigilance behaviours of individual Curlews at roost sites as a function of peak flock size. Error bars indicate the standard deviation.

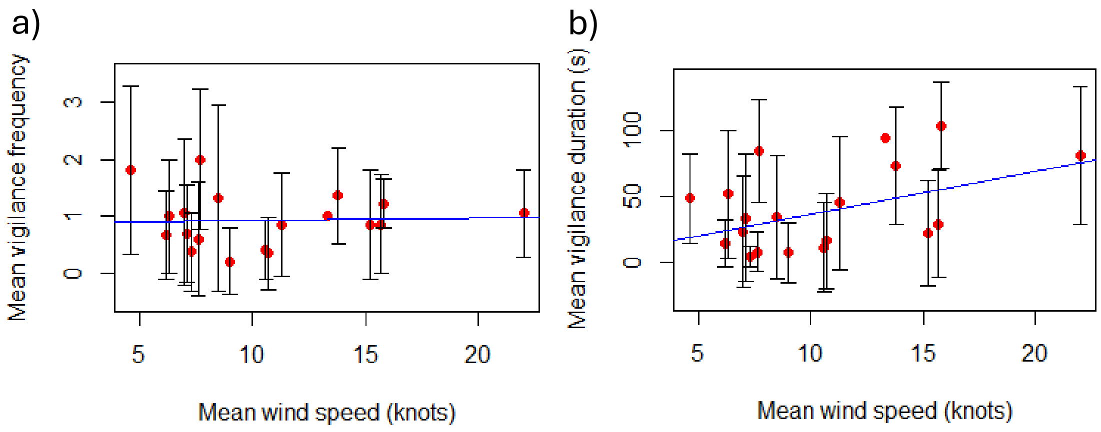

Figure 6. a) The mean frequency of vigilance behaviours of individual Curlews at roost sites as a function of mean daily wind speed and b) the mean duration of vigilance behaviours of individual Curlews at roost sites as a function of mean daily wind speed. Error bars indicate the standard deviation.

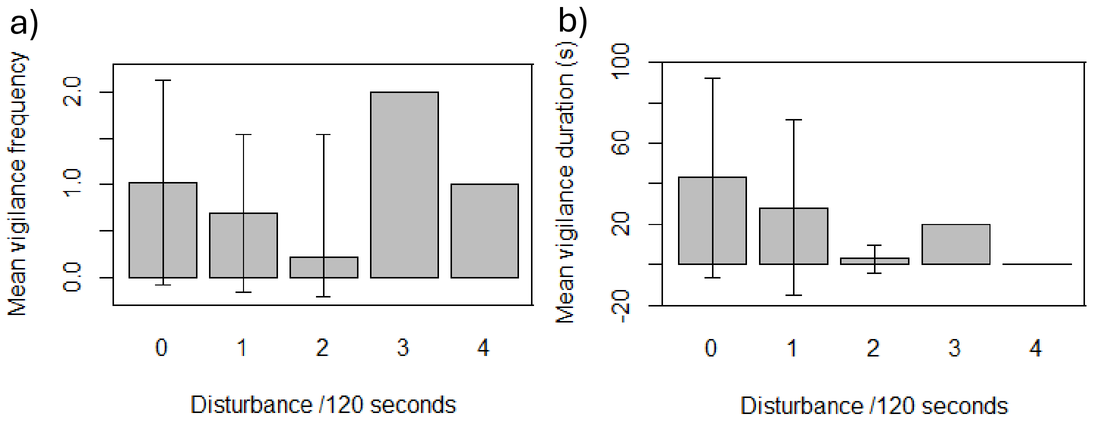

Figure 7. a) The mean frequency of vigilance behaviours of individual Curlews at roost sites as a function of the frequency of potential anthropogenic disturbances and b) the mean duration of vigilance behaviours of individual Curlews at roost sites as a function of the frequency of potential anthropogenic disturbances. Error bars indicate the standard deviation.

The most frequent source of anthropogenic disturbance was vehicles, and individual Curlews were observed changing their behaviour to vigilance behaviours during the period when they were exposed to this disturbance (Table 4). This change in vigilance behaviour was not recorded for any of the other anthropogenic disturbance sources

(Table 4). The number of times that Curlew performed vigilance behaviours during potentially disturbance events was also highest for vehicles, however, Curlews were not observed taking flight on any occasions when exposed to potential disturbances (Table 4).

Table 4. The total number of observed potential anthropogenic disturbance and response behaviours by individual Curlews. Began vigilance refers to the number of events when individual Curlews changing their behaviour from another behavioural category to vigilance behaviour during the time when they were directly exposed to the potential disturbance.

Disturbance type	Potential disturbances	Began vigilance	Vigilance	Flight
Vehicle	56	4	12	0
Person	14	0	3	0
Dog	3	0	0	0
Other	8	0	2	0

Variables affecting group level vigilance in Curlews

Group size (Fig. 8a) and temperature (Fig. 8b) were not found to be correlated with the presence of vigilance behaviour within the Curlew flock, and temperature did not affect the number of Curlews performing vigilance when at least one Curlew was performing vigilance (Table 5, Fig. 8d). However, group size did positively correlate with the number of Curlews performing vigilance when vigilance was recorded in the group (Table 5, Fig. 8c).

Table 5. Results of a hurdle model describing the number of Curlews within a group performing vigilance behaviours at the same time with mean daily temperature and group size. The binomial model uses binary values to show presence or absence of vigilance within the group, and the positive count model omits zero values, to show correlation of variables with vigilance when vigilance is present within the flock. *Values below the 0.05 significance threshold are shown in bold.

Model	**Fixed effects**	**Estimate ± SE**	**X^2**	**p***
Binomial model	Intercept	1.00 ± 1.60		
	Group size	0.02 ± 0.01	2.86	0.09
	Temperature	0.17 ± 0.23	0.68	0.41
Positive count model	Intercept	0.40 ± 0.54		
	Group size	0.01 ± 0.01	1320.3	**<0.001**
	Temperature	0.17 ± 0.09	3.734	0.18

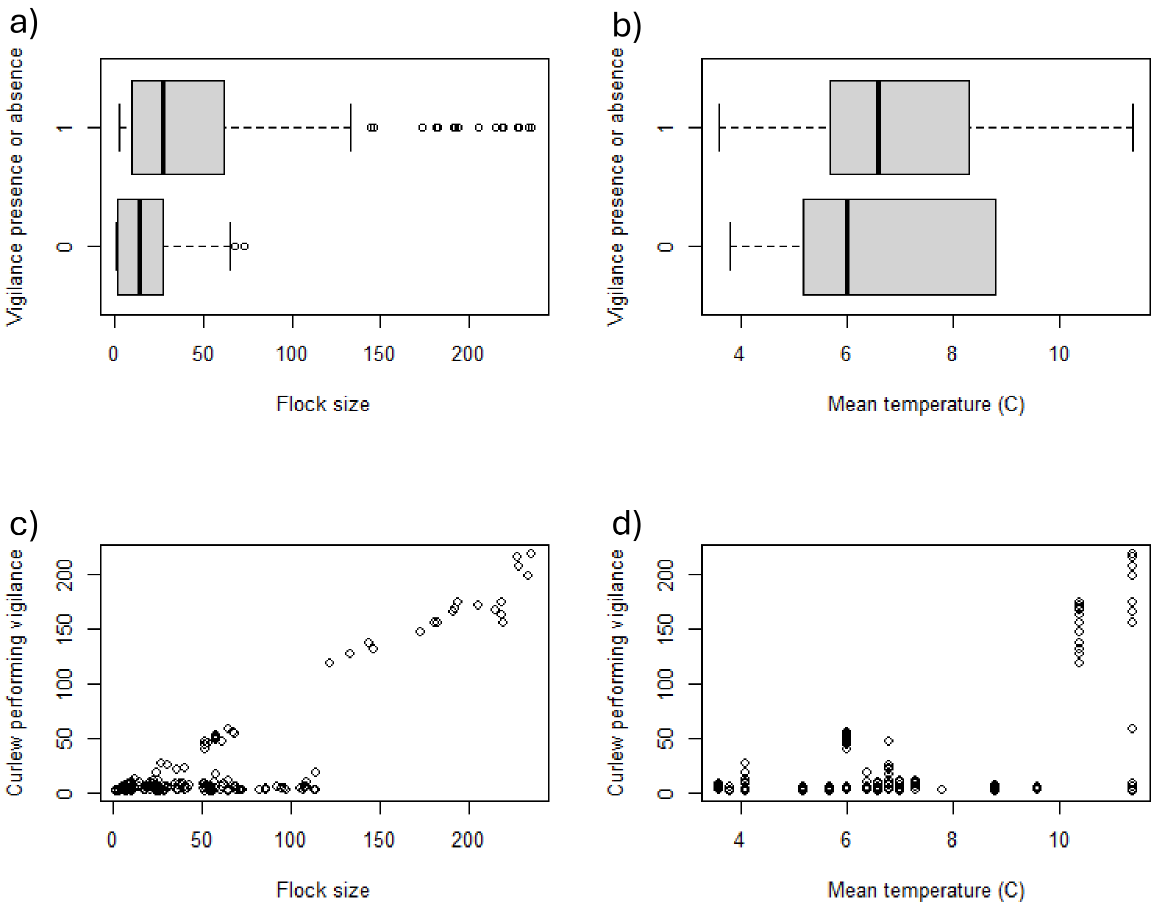

Figure 8. a) the presence or absence of vigilance behaviours in a flock of Curlews in relation to flock size and b) the presence or absence of vigilance behaviours in a flock of Curlews in relation to mean environmental temperature. The thicker line indicates the median value, and the whisker bars indicate the lower and upper interquartile value. c) the number of Curlews performing vigilance when at least one individual was performing vigilance as a function of flock size and d) the number of Curlews performing vigilance when at least one individual was performing vigilance as a function of mean temperature.

Effect of temperature on the Curlews wintering population

Temporal changes in winter Curlews group size were not found to be correlated to environmental temperature, as there was no statistically significant change in group size for any of the temperature measures (Table 6).

Table 6. Results of GLMs describing correlation of temperature with yearly peak count of Curlews at winter roost sites. *Values below the 0.05 significance threshold are shown in bold.

Fixed effect	Estimate ± SE	t	p*
Intercept	182.03 ± 49.03		
Minimum mean daily temperature	26.71 ± 24.87	1.07	0.308
Intercept	266.713 ± 538.619		
Overall mean daily temperature	-6.28 ± 67.56	-0.09	0.928
Intercept	281.398 ± 114.071		
Temperature ≤ 5 degrees	-1.41 ± 2.35	-0.60	0.561
Intercept	234.34 ± 43.46		
Temperature ≤ 0 degrees	-16.23 ± 19.94	-0.81	0.434

Discussion

We have shown that vigilance behaviour of Curlews at winter roost sites increased with peak count of flock size and decreased when ambient temperatures were below the Curlew's lower critical temperature (LCT); the ambient temperature below which increased energy expenditure by the organism is required for survival. Wind speed was positively correlated with vigilance duration, but was not correlated with vigilance frequency behaviour, and group level vigilance was positively correlated with group size. However, anthropogenic disturbance could not be linked to behavioural changes of Curlews in this study.

The Curlews spent less than 10% of their time at the roost sites preening, in flight, and performing other behaviours including feeding, walking, and vocalising. For much of their time at the sites, the Curlews were roosting or performing vigilance, with little time spent foraging. This is likely either due to a low availability of food because of the rocky shoreline at the study sites, with little vegetation or substrate to probe, or because they had consumed enough food in the previous hours at their low tide foraging habitat or at nearby grassland. This is supported by Fitzpatrick & Bouchez's (1998) findings of increased foraging behaviours of Curlews during the periods between high tides. Similar patterns of behaviour were recorded in Avocet *Recurvirostra avosetta* (Hotker, 1999) and in mixed wader flocks in Kenya, which for the first 1-2 hours following high tide spent most of their time resting at the roost site, with the rest of this time spent preening, stretching, or feeding at the roost (Fasola & Biddau, 1997). As all data were collected during the period of high tide, the Curlews' regular foraging areas on the lower shore were not available during the observation period.

On days with a mean daily temperature at or below the LCT of Curlews, the observed birds showed a decrease in vigilance frequency, and when they did perform vigilance behaviours, they did so for a shorter duration than days with an ambient temperature above LCT. This supports the hypothesis that a decrease in ambient temperature below LCT would negatively affect vigilance, because of the added pressures of low temperatures on fitness. To maintain internal body temperature in conditions below LCT, birds must increase metabolic rate to maintain thermoregulation. This results in a trade-off of non-essential antipredation behaviours, including vigilance, in favour of increasing energy intake by foraging and/or conserving energy by roosting when food is unavailable at high tide (Kersten & Piersma, 1987; Pravosudov & Grubb, 1995). Similar behaviours were observed in Tufted Titmice *Baeolophus bicolor*, where vigilance behaviour when foraging was positively correlated with ambient temperature (Pravosudov & Grubb, 1995). In addition, body mass was also positively correlated with vigilance, further supporting our hypothesis that birds decrease vigilance behaviours in order to increase energy intake, as birds with lower body mass are likely to have fewer energy reserves and will do this as a response to colder temperatures (Pravosudov & Grubb, 1995).

The group peak count was positively correlated with vigilance frequency and vigilance duration in individual Curlews, and with the number of Curlews within the group performing vigilance at the same time. These findings do not support the hypothesis of a decrease in vigilance behaviours with increasing group size and contrast with previous studies on Curlew group size-vigilance effects that measured behaviour in non-roosting periods (Zhang *et al.,* 2021). The findings are, however, consistent with research on vigilance behaviour of other avian species when roosting. Vigilance in roosting gulls did not decline with increasing group size, but instead neighbour vigilance levels were the determining factor (Beauchamp, 2009). Similar behaviour was also recorded in Oystercatchers, where vigilance behaviours reduced with increasing flock size, however, it increased when neighbours were also vigilant (McBlain *et al*., 2020). Distance to the nearest neighbour has also been found to be associated with an increase in vigilance behaviours (Novcic & Vidovic, 2021). Vigilance at roost sites for flocking birds such as Curlews may also be impacted by position in the flock, a measure that was not included in the study. Black-tailed Godwits *Limosa limosa* showed higher rates of vigilance behaviours when positioned at the edge of a flock in comparison to birds located centrally (Dominguez, 2002). Similar findings were found for Scaled Doves *Columbina squammata* (Dias, 2006), Brown-headed Cowbirds *Molothrus ater* (Fernandez-Juricic & Beauchamp, 2008), Black-necked Cranes *Grus nigrocollis* (Kuang *et al*., 2014), and Semipalmated Plovers *Calidris pusilla* (Beauchamp, 2010). To resolve these differences in findings, future work on Curlews at roost sites should also consider neighbour behaviour, particularly vigilance, as well as the number of neighbours and their position within the flock. These variables may also relate to the extent of impact of environmental disturbances on individuals, and to what extent they perceive anthropogenic disturbances.

The effect of higher wind speed on vigilance resulted in an increase to the duration of vigilance behaviours but did not alter the frequency with which vigilance was performed. This limited effect of wind speed may be because the Curlews' behaviour was not recorded at high wind speeds due to issues with observer safety and recording equipment. Previous studies found that vigilance in Oystercatchers increases with wind speed (McBlain *et al*., 2020). Similarly, Hilton *et al*., (1999) found that Redshanks *Tringa totanus*, another coastal winter wader species, altered their foraging behaviour in high winds, which was posited to be due to perceived threat of predation. Wind speed also contributes to increased energy expenditure as it increases rate of heat loss, however, the choice by the Redshank to feed in an area more exposed to the wind but less likely to be predated suggests a high perceived risk of predation in higher wind speeds (Hilton *et al.,* 1999). Our finding of increased vigilance duration in higher winds may suggest a similar increased perception of threat of predation by Curlew. Future studies on Curlew vigilance may benefit from data collection methods that allow for windier conditions, as well as the recording of wind direction. Wind speed should also be considered when analysing response rate to potential disturbances, as well as the frequency of predation in these conditions.

Despite the results showing significant correlations between ambient temperature and group size on vigilance, these variables did not account for a large portion of the variance in vigilance behaviours in individuals, and variance in the number of birds performing vigilance within the flock, when vigilance was present. This is particularly evident in the graphing of the positive count model, which might suggest a difference in the importance of flock size and mean temperature at low counts of vigilance in the flock as compared to higher counts of vigilance. Beauchamp (2008) showed this to be a common issue across studies of group size effects on vigilance, and that while studies generally support the decline in vigilance because of group size, a large portion of the variation in vigilance behaviours in this study could not be explained by group size (Taraborelli, 2007; Olson *et al.,* 2015; Hammer *et al*., 2023). This suggests that while group size and temperature does impact vigilance, there are potentially other factors not measured in this study that heavily alter vigilance behaviours. These may be external such as position in the flock as previously discussed, other measures of temperature such as minimum daily temperature or temperature fluctuations or may in fact be a result of high levels of individual variation between Curlew in the flock. Further research is required to determine how much, if at all, that individual variation accounts for vigilance behaviour in Curlew. This would require individuals to be distinguishable to allow for repeated measures, in which case a mark such as a colour ring could be used. Individual variation may also impact their sensitivity to anthropogenic disturbance and environmental factors. The Hurdle model used for the analysis may also have restricted the exploration of group size vigilance dynamics, by constraining it to two groups: absence and presence of vigilance. Future analysis may consider further division of the presence group, to determine whether there is a group size threshold at which factors such as flock size or mean temperature may have a greater impact on vigilance behaviours.

This study did not find a significant correlation between vigilance and anthropogenic disturbances, and is in contrast to some previous findings which evidence the disruptive nature of anthropogenic activities on Curlews and other wading birds (Kirby *et al.,* 1993; Fitzpatrick & Bouchez, 1998; Burton *et al.,* 2002b; Collop *et al*., 2016; Larson *et al*., 2019; Linssen *et al*., 2019; Kolk *et al.,* 2020; McBlain *et al.,* 2020; Dertien *et al*., 2021; Goodship & Furness, 2022). This may however be a result of insufficient variation in the data, in relation to distance from potential disturbance, as well as disturbance frequency, and disturbance type. In Kirby *et al*.'s (1993) study of roost disturbances, the most frequent disturbance was walkers and dogs, and most disturbances to Curlews resulted in flight to another roost on the site, but other waders frequently left the site entirely. While Kirby *et al.* (1993) were able to demonstrate a correlation between potential disturbance agents and disturbance responses – in this case just flight – they did not include measures of vigilance behaviours in the study. Fitzpatrick & Bouchez (1998) found that the behaviours of Curlews and other waders changed when exposed to potential disturbances; vigilance behaviour, measured as scan rate, was positively correlated with human activity, as was prey capture rates. The Curlews most frequent response to disturbance was to fly away altogether, however they were also recorded stopping foraging, walking away, and flying elsewhere on the beach. In these previous studies on Curlews, walkers and dogs were the most frequent source of anthropogenic disturbance, whereas in our findings, vehicles were the most frequent potential disturbance. This may have impacted the level of response from the Curlews to the potential disturbance; however, of the 14 events of walkers entering the study site, there was no observed change in behaviour by the Curlews. Stolen (2003) found that vehicle disturbance was linked to disturbance behaviours in other wading bird species Snowy Egret *Egretta thula* and Great Egret *Ardea alba*, and that smaller the distance from the disturbance, the greater the probability that the birds would take flight. While the distance from vehicles at our study sites was considered within the flight initiation distance for Curlew at roost sites based on previous studies (Goodship & Furness, 2022), the distance of the vehicles from the Curlews may have in fact been great enough to not prompt anti-predation behaviours.

These findings may be in keeping with disturbance studies of other bird species including wading birds that found evidence of habituation or desensitization toward anthropogenic disturbances, (Stolen, 2003; Bisson *et al*., 2011; Vincze *et al*., 2016; Cook *et al.,* 2017). To determine whether this habituation is occurring in Curlew populations, the data would benefit from further samples at more sites, and a greater range of disturbance rates and habitat types at these sites, to increase the variation in the data. To further this, the inclusion of experimental disturbance as a variable would provide clarity through the controlled exposure to disturbance at these sites, as previously used by Collop *et al*. (2016) to measure the flight initiation distance, flight time, and energy expenditure of experimentally disturbed Curlews.

The study did not show a relationship between temporal variation in maximum flock size and measures of ambient temperature, unlike previous studies that found changes in flock size in wading birds correlated negatively with temperature, likely due to the fluctuations in food source as a result of lower temperatures (Yalden & Pearce-Higgins, 1997; Pearce-Higgins *et al*., 2010; Cook *et al.,* 2021; Woodward *et al*., 2022). We cannot determine from these findings whether temperature does impact the Curlew flock size, as the consecutive records for the full study period from 1998-2024 were not available, and therefore data may not fully represent actual variation in the data. While this method of data collection is effective at scale when using a high number of sites (Cook *et al*., 2021), this was not effective for understanding temporal variation because of environmental temperature at one location.

Conclusion

The findings of this study suggest that the vigilance behaviours of Curlews at winter roost sites are impacted by weather, with decreased vigilance behaviours at temperatures below LCT, but with increased vigilance duration with higher wind speeds. Curlew vigilance was also correlated with group size; however, the observed effects of group size oppose the many eyes hypothesis. Instead, the increase in vigilance with group size is in keeping with intra-specific dynamics previously recognised in other avian species, of increased vigilance with group size and the impact of neighbour behaviour on roost activity. While anthropogenic disturbance was not found to alter vigilance behaviour at individual or group level, this may have been affected by the type of disturbance or habituation to the disturbance by the Curlews and does not follow the current research consensus on the impact of anthropogenic disturbance to wading birds. Long-term population data did support the hypothesis that extreme weather conditions would result in population decline, however, the available data set was small, so further investigation is needed. Future work on Curlew vigilance at roosts should investigate further the impact of neighbour birds, position in the flock, and behaviour in extreme weather conditions.

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