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Weather conditions and conspecific density influence survival of overwintering Dunlin *Calidris alpina* in North Wales

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Capsule Inter-annual survival rates of juvenile Dunlin *Calidris alpina* increased with wet weather conditions but decreased with the density of conspecifics in winter, ranging from 0.34 to 0.62 in the best model. Adult inter-annual survival remained high and constant at 0.72.
Aims To estimate inter-annual survival rates of both adult and juvenile Dunlin in North Wales. To quantify the effects on survival rates of weather conditions and conspecific density.
Methods Cormack–Jolly–Seber models in Program MARK were used to analyse 21 years of ringing data (1990–2011) from Traeth Lafan, North Wales. Models were constructed using a two age-class structure. The influence of a range of weather conditions and WeBS census data on survival were examined.
Results Adult survival was best modelled at a constant rate of 0.72 (se 0.008) across the 21 years. Juvenile survival rates were found to vary most strongly with total rainfall (mm) during the season and the number of conspecifics present. Survival rates varied from 0.34 (se 0.06) to 0.62 (se 0.09), with higher survival in years with high rainfall and low numbers of birds.
Conclusion Survival rates of juvenile Dunlin are affected by both weather and density of conspecifics. These results have implications for the future of Dunlin in the UK when considering both climate change and habitat loss.

Declines in many migratory bird species have increased the demand to create accurate models of their life histories, in order to identify the factors affecting their populations (Warnock *et al.* 1997, Green 1999, Robinson *et al.* 2005, 2007, Duriez *et al.* 2009, Schaub & Royle 2014). Long-term and large-scale monitoring and data collection that allows the estimation of key parameters, such as population size, breeding productivity and survival rates (Clobert & Lebreton 1991, Pienkowski 1991, Lebreton *et al.* 1992), will improve the understanding of the demography of given species and define their requirements to help target conservation efforts (Pienkowski 1991, Sandercock 2003, Stroud *et al.* 2006).

Wading birds are characterized by their site fidelity and extensive seasonal migrations (Piersma & Baker 2000, Meltofte *et al.* 2007, Piersma 2007). These factors make them particularly vulnerable to changes in climate and habitat (Nethersole-Thompson & Nethersole-Thompson 1986, Atkinson 2003, Meltofte *et al.* 2007). Understanding changes in population trends of wader species should continue to be a high priority given that many species have been in decline for a number of years (Stroud *et al.* 2006, Holt *et al.* 2012). Adult survival is high in many species (Evans 1991, Yalden & Pearce-Higgins 1997, Piersma & Baker 2000, Schwartzer *et al.* 2012) but productivity low (Meltofte *et al.* 2007), therefore threats to adult survival can have particularly large impacts on the population size. Juvenile survival has been found to be lower and more variable (Kus *et al.* 1984, Johnson *et al.* 2001, Conroy *et al.* 2002), with recruitment strongly linked to temperature on high-latitude breeding grounds (Beale *et al.* 2006).

Wading birds spend a significant proportion of their lives on their wintering grounds, with most mortality likely to occur there (Evans 1991). It is widely acknowledged that severe weather events can have detrimental consequences on wading bird populations (Evans 1991, Yalden & Pearce-Higgins 1997, Conroy

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et al. 2002, Clark 2004, Altwegg *et al.* 2006) and these effects have been studied in depth in several species (Dugan *et al.* 1981, Peach *et al.* 1994, Insley *et al.* 1997, Burton *et al.* 2006, Duriez *et al.* 2009). For example, Common Redshank *Tringa totanus* and Dunlin *Calidris alpina* have been shown to be susceptible to periods of cold winter weather, when mortality increases significantly (Clark 2004).

The effects of density dependence on survival of waders are less well studied, but Durrell *et al.* (2000) and Whitfield (2003) found density-dependent survival in Oystercatchers *Haematopus ostralegus* and Redshank, respectively. Survival in other groups of species, including passerines and waterbirds, has also been observed to vary with population density on both the breeding and wintering grounds (Frederiksen and Bregnballe 2000, Lok *et al.* 2013, Norman & Peach 2013). Competition for resources is likely to be the most important factor behind this density-dependent variation, particularly between less experienced foraging juveniles and more efficient adults; interaction with weather and predation have also been observed (Durell *et al.* 2000, Frederiksen & Bregnballe 2000, Whitfield 2003, Tavecchia *et al.* 2007).

Dunlin are one of the UK's most numerous wintering wading birds and although they are classified by Birdlife International on a European scale as 'Least Concern', in the UK they have experienced a severe, yet slow, decline of more than 50% of the population during the last 20 years (Robinson *et al.* 2007, Eaton *et al.* 2009, Birdlife International 2012, Holt *et al.* 2012). Climate change and habitat loss are speculated to have caused an increase in mortality, as well as a shift in distribution, with many birds choosing to remain on moulting grounds in the Wadden Sea (Pienkowski 1991, Rehfisch *et al.* 2004, Maclean *et al.* 2008, Birdlife International 2012, Holt *et al.* 2012, Summers *et al.* 2012). Their favoured wintering habitats are broad, coastal, intertidal mudflats, close to adequate roosts (Dias *et al.* 2006), which are rich in their preferred foods such as polychaete worms and small crustaceans (Cramp & Simmons 1983). They display extremely high site fidelity, with Dias *et al.* (2006) finding that 99% of Dunlin captured and marked were re-sighted again only on the roost where they were first caught.

In this study, we set out to produce a robust estimate of Dunlin survival rates in the western UK. We examined the effects of different weather conditions and conspecific density on the survival of both adult and juvenile Dunlin from a substantial data set, in a geographic area with no previously published estimate. It is hoped that these estimates will add considerably to our understanding of the causes of changes in the survival of this and other wader species, particularly with regard to any density-dependent effects which have not been well studied, and that comparisons between sites and species can be made in the future, with the aim of improving conservation research and management policy.

MATERIALS AND METHODS

The study area was located on the coast of North Wales, surrounding the Menai Straits and Traeth Lafan/Lavan Sands (53°15′18″N, 04°02′31″W). Under UK legislation, the Menai Straits is designated as a Site of Special Scientific Interest (SSSI; Joint Nature Conservation Committee 2013) and separates the island of Anglesey from mainland Wales. Traeth Lafan (approximately 2700 ha) within the Menai Straits is protected under domestic and European legislation, due to the expanse of mud and sand flats which host nationally important numbers of wintering Oystercatchers (Countryside Council for Wales 2008). It also supports substantial numbers of Dunlin, Curlew *Numenius arquata*, Turnstone *Arenaria interpres* and Redshank. Dunlin have been captured by cannon netting in this area since the 1970s, but the data in this study are taken from between 1990 and 2011. This period was chosen for the continuity of the data set, with the period prior to 1990 being subject to large gaps between catches, along with additional ageing problems, both affecting the accuracy of the analysis. Dunlin were captured and ringed at two locations: Bangor Harbour (53°14′N, 04°08′W) and Beaumaris (53°27′N, 04°09′W). The data were pooled and treated as one site, due to their close proximity (approximately 4 km apart) and because preliminary analysis of recapture data indicated interchange of birds between the two sites each year. It also allowed for even time intervals between capture occasions in the models, as in several years the birds roosted at just one site. The winter season was defined as November and December of a given year, with January and February of the following year; multiple catches in a season were pooled, resulting in one sample per year. The data collected consist of live recaptures only, giving a unique metal ring number and age of the bird, which was defined on plumage characteristics in the field as either juvenile – within their first year – or adult. A total of 7565 adult and juvenile birds were ringed over the study period and 1197 recaptured (Table 1).

Table 1. Summary of Dunlin *Calidris alpina* ringing data collected at Beaumaris and Bangor Harbour between 1990 and 2011 ($N = 7565$).

Year	Trapping events[a]	Mean capture date[b]	Total birds caught (new and recaptured)	% Juveniles captured	% Birds recaptured (both adults and juveniles)
1990	3	11/12/1990	809	49.8	0.0
1991	2	24/12/1991	634	44.2	5.8
1992	2	23/01/1993	706	20.3	14.9
1993	1	31/12/1993	590	41.0	3.9
1994	2	18/01/1995	341	32.3	20.2
1995	1	10/12/1995	173	49.1	24.3
1996	2	25/12/1996	670	39.4	12.4
1997	3	11/12/1997	119	70.6	6.7
1998	1	20/02/1999	153	32.7	24.8
1999	1	23/01/2000	524	31.1	15.6
2000	1	27/01/2001	384	31.0	21.4
2001	1	03/02/2002	162	80.9	4.9
2002	2	15/12/2002	444	32.7	18.9
2003	2	31/01/2004	277	37.9	21.7
2004	2	04/01/2005	575	36.3	15.5
2005	1	04/12/2005	46	34.8	19.6
2006	2	06/12/2006	237	19.0	19.0
2007	1	09/12/2007	225	33.3	21.3
2008	2	06/12/2008	278	27.3	18.3
2009	1	14/02/2010	514	33.5	19.3
2010	1	05/12/2010	234	16.7	34.6
2011	1	10/12/2011	427	47.8	12.6

[a]Number of cannon netting events where Dunlin were caught at Beaumaris and Bangor Harbour.
[b]Mean capture date is calculated where there is more than one capture event in the winter season.

Weather data for the study site were extracted from the Meteorological Office Integrated Data Archive System (MIDAS) at the British Atmospheric Data Centre (BADC). The period over which weather conditions were observed was November to February, to cover the winter season spent on Traeth Lafan by the Dunlin. The data are taken from one station, Valley, Anglesey, approximately 32 km west of the study site. This station's extensive data set enabled all years of capture to be analysed, as well as providing daily measurements, so that duration of weather conditions could be calculated. Highly correlated weather variables were excluded from the analysis. The weather variables used were: (1) the longest number of consecutive days where grass minimum temperature was below 0°C, which represented the duration of frost periods; (2) total number of days where grass minimum temperature was below 0°C (total number of frost days) and (3) total rainfall in the season (mm). To account for the potential effect of density dependence on survival, the analysis included the seasonal highest count of Dunlin at Traeth Lafan from the Wetland Bird Survey (WeBS).

Program MARK (White & Burnham 1999) was used to build Cormack–Jolly–Seber (CJS) models. The basic assumptions of these models are that all individuals have the same chance of surviving and the same chance of remaining in the population to be recaptured (White & Burnham 1999). Violations of the assumptions of the model can arise from differences in survival between age classes, emigration, and irregular catch sizes and intervals. Here, a two age-class model allowed survival and recapture probabilities to differ between age groups (those 'marked as young' and 'marked as adults'). The global model, which consisted of time-dependent survival and recapture in both age classes achieved a variance inflation factor ($\hat{c}$) of 1.01, which is close to the ideal value of 1 (White & Burnham 1999) and indicates virtually no over-dispersion of the data. Goodness-of-fit tests were also carried out, using RELEASE within MARK, assessing the data according to the assumptions of the CJS model, particularly those of equal chance of survival and equal chance of recapture (Robinson *et al.* 2007); the results of these tests were not statistically significant ($\chi^2 = 194$, $P = 0.42$), indicating good fit of the data.

Parameters in the global model were then reduced to find the most parsimonious model. Ten models were created and run, representing annually varying time-dependent survival rate, fixed survival rate, a linear trend in survival rate and with added covariates. Five candidate models without covariates were created initially (models 1–5); the most appropriate of these was then run with the covariates identified (models 6–10). The covariates were tested singly and those with the best results were tested together, to identify any interactions. Models were chosen using the Akaike's Information Criterion (AIC) value, which balances the amount of deviation within the model and the number of parameters: a difference of 2 or more between AIC values gives some support for a difference between the models; a difference of 7 or more is evidence of very strong support for a significant difference between models (White & Burnham 1999). Whilst fewer parameters (i.e. a more parsimonious model) can be seen as better, these can be representative of biologically unlikely situations and so a cautious approach has been taken in the interpretation and comparison of models.

RESULTS

The model results (Table 2) display a clear difference between models with additional covariates and models that contain only time dependence. There is a difference of seven AIC units between model 2 (time-dependence in juvenile survival and fixed adult survival with no covariates) and model 6, the lowest ranking added covariate model. The top-ranked models possess relatively similar AIC values, but a difference of two AIC units separates the top two models, indicating preferential support for the model with the covariate interaction, rather than that with the single rainfall covariate. Models 8, 4, 9, 5 and 6 are separated by three AIC units, indicating that the models have similar support of the data and that the ability of each of the effects to predict survival is comparable (White & Burnham 1999). Annual estimates of juvenile survival from the top-ranked model (model 10) are presented in Fig. 1, alongside time series of the two covariates.

Recapture rates

Eight of the ten models created contain varying recapture rates between adults and juveniles (Table 2). Models 2 (with varying recapture rates) and 3 (with recapture rates modelled to be the same between adults and juveniles) differ by five AIC units, lending significant support to the model where recapture rates vary between the age classes. Recapture rates (from model 10) are low (adult recapture rate 0.01 (se 0.004) to 0.19 (se 0.02); juvenile recapture rate 0.01 (se 0.006) to 0.19 (se 0.04) and are similar from year to year.

Survival rates

The highest ranking candidate model without covariates was the model representing constant adult survival but varying juvenile survival (model 2, Table 2), with a change of 19 AIC units (model 1). An age effect on survival is therefore clearly demonstrated, indicating high, stable survival in adults and lower, more variable survival in juveniles. Six of the top eight models (models 2 and 6–10; Table 2) predict constant adult survival, with highly consistent estimates ranging only from 0.717 (se 0.008) to 0.72 in the best model (se 0.008). Model 2 was, therefore, chosen to be the most appropriate model with which to investigate effects of weather and bird numbers.

Covariates

All covariates were tested separately and the strongest single predictor of juvenile Dunlin survival was the total rainfall during the winter (model 7, Table 2). Survival rates from this model varied from 0.41 (se 0.06) to 0.59 (se 0.09) with a strong positive relationship between the juvenile survival estimates and the total rainfall during the winter months.

The WeBS count variable was also a high-ranking model (model 8, Table 2), less than one AIC unit higher than model 7. This model showed a clear negative relationship between juvenile survival and the highest number of birds in the estuary (Fig. 2), with the highest rate of survival (0.54, se 0.07) recorded with the lowest number of birds counted (600). Duration of frost periods decreased juvenile survival but not substantially (model 6, Table 2), with a 1–2% change in survival with one or two extra days of frost. The highest number of consecutive frost days was 18 and produced a juvenile survival rate of 0.44 (se 0.08).

To test for any interaction of total rainfall and highest population size, model 10 was tested with both covariates together. This model had an AIC 2 units

Table 2. Summary of CJS models produced in Program MARK to estimate survival and recapture rates of adult and juvenile Dunlin from 1990–2010.

Model	Variables	AICc	Delta AICc	AICc Weight	Model Likelihood	Par	Dev.
10	ϕ {Ad (constant) + Juv (WeBS*rainfall) P {age.t}	10494.64	0.00	0.46	1.00	47	1099.99
7	ϕ {Ad (constant) + Juv (rainfall)} P {age.t}	10496.85	2.22	0.15	0.33	45	1106.25
8	ϕ {Ad (constant) + Juv (WeBS)} P {age.t}	10497.43	2.80	0.11	0.25	45	1106.83
4	ϕ {Ad (constant) + Juv (constant)} P {age.t}	10497.98	3.34	0.09	0.19	44	1109.40
9	ϕ {Ad (WeBS) + Juv (WeBS)} P {age.t}	10498.02	3.39	0.08	0.18	46	1105.40
5	ϕ {Ad (T) + Juv (T)} P {age.t}	10498.65	4.01	0.06	0.13	46	1106.02
6	ϕ {Ad (constant) + Juv (frost)} P {age.t}	10499.68	5.04	0.04	0.08	45	1109.08
2	ϕ {Ad (constant) + Juv (t)} P {age.t}	10507.95	13.31	0.00	0.00	64	1078.84
3	ϕ {Ad (constant) + Juv (t)} P {t}	10512.04	17.40	0.00	0.00	43	1125.48
1	ϕ {age.t} P {age.t})	10526.85	32.21	0.00	0.00	83	1059.05

Models are listed by AIC, but numbered in order of creation, with both Delta AIC (ΔAIC) and AIC weight given as measures of difference between the models; Dev. – Model deviance. Models are age-specific (A, adult – second winter and older; Juv, juvenile – first winter only) for both survival (ϕ) and recapture (P) rates. Survival is either modelled as time dependent (t), fixed survival rate (constant), linear trend (T) or with an external covariate: rainfall – the total amount of rainfall in each season (November to February inclusive) in mm; WeBS – maximum count of Dunlin in each winter (November to February inclusive) from the Wetland Bird Survey; frost – duration of the longest number of consecutive days of frost in each season (November to February inclusive).

lower than that of the model with total rainfall alone (Table 2), showing some support for it being better than the one-covariate model. Juvenile survival rates varied from 0.34 (se 0.06) to 0.62 (se 0.09). The relationships between the variables within the model are displayed in Fig. 2; the WeBS numbers and total rainfall are visible as strong negative and strong positive indicators, respectively, with total rainfall fitting slightly better to the data.

DISCUSSION

Our study builds upon earlier work on survival rates in Dunlin (Warnock *et al.* 1997, Insley *et al.* 1997, Robinson *et al.* 2007), by presenting robust estimates from a large sample of a population with a single race and low transience, leading to an improved understanding of the demography of this species. The decline in Dunlin observed in the UK is a product of two separate circumstances; first, an increase in mortality through pressures such as habitat loss and climate change (Birdlife International 2012) and, second, a shift in core distribution, with a larger number of birds remaining on continental Europe over winter (Rehfisch *et al.* 2004, Maclean *et al.* 2008). Our study shows that adult Dunlin had consistently high annual survival, but that juvenile survival was depressed in winters with relatively low rainfall. This effect was compensated to some extent, by a negative effect of density on survival.

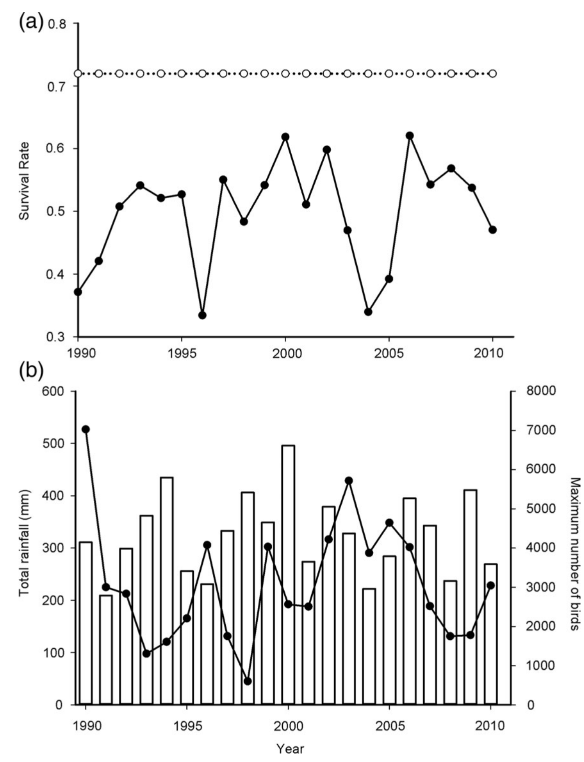

Figure 1. (a) Survival rate estimates for adult (clear circles, n = 4654) and juvenile Dunlin (filled squares, n = 2941) with standard errors from model 10 in Table 1; (b) Time series of the density of Dunlin on Traeth Lafan (maximum number of Dunlin counted in the estuary from the Wetland Bird Survey (WeBS) in each winter season, November to February inclusive; represented by black circles ●) and of total rainfall over the winter season (November to February inclusive, mm; vertical bars).

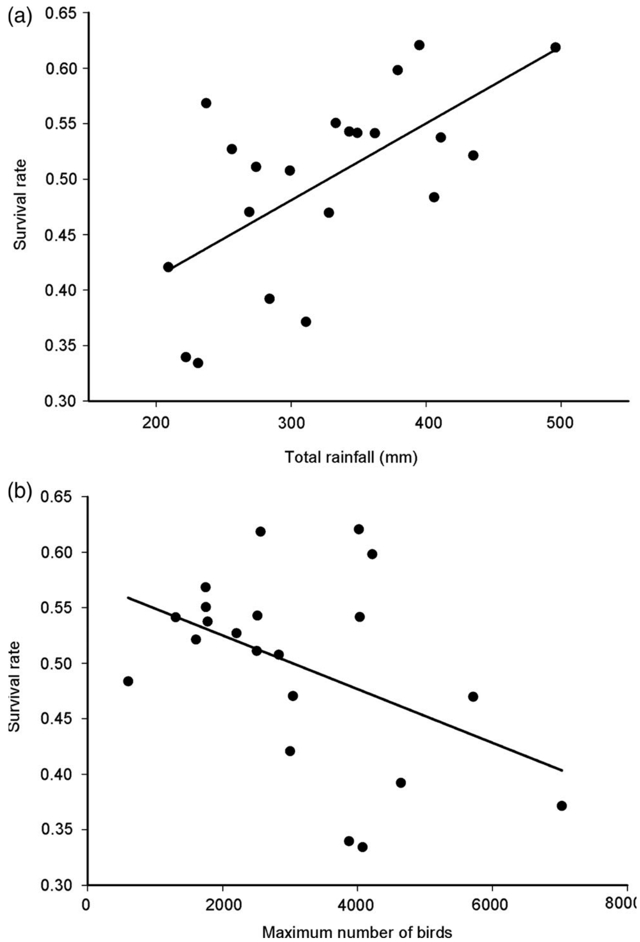

Figure 2. (a) Relationship between the annual survival of juvenile Dunlin and the total rainfall in the estuary in mm ($R^2 = 0.4$, $P < 0.01$); (b) Relationship between annual juvenile survival and the number of birds in Traeth Lafan taken from WeBs data ($R^2 = 0.2$, $P < 0.05$). Estimates are taken from model 10 in Table 1.

Effect of rainfall on survival

Of particular interest from the results of this study is the strong positive effect of total rainfall on rates of survival in juvenile Dunlin; an effect on waders that has not been reported in the majority of studies. Insley *et al.* (1997) found a non-linear relationship between Redshank survival and rainfall; survival was highest with average amounts of rainfall. In our study, there was a clear positive linear relationship with rainfall, with survival being highest during the wettest winters. Higher survival in years with more rain may imply milder conditions, with less energy expended by the birds. Rain is also thought to be a cue for the birds to start accumulating mass, in preparation for severe weather (Kelly *et al.* 2002). The highest amount of rainfall in one season (winter 2000/01) was 496 mm, around 165 mm higher than the average for the area. This is quite substantial, yet survival in this winter was the highest, at 0.59 (±0.09). Kelly *et al.* (2002) examined the effect of rainstorms on body mass and energy expenditure of Dunlin. Birds kept in captivity, whose feeding was restricted, lost body mass on days with rainfall. Those without restrictions actually gained weight, despite the apparent increased maintenance costs of rain. This suggests that if foraging remains uncompromised, the birds should gain weight, which will aid their survival. In a study of national data, Rehfisch *et al.* (2004) found an increase in Dunlin on areas of the coast where mean rainfall has also increased. Although this was not mirrored in other species of wader apart from Lapwing *Vanellus vanellus*, it does show that increased rainfall can be a positive characteristic of an area in which Dunlin winter.

Density of conspecifics

An effect of density on juvenile survival was also identified. Dunlin are highly gregarious, particularly during winter, but this appears to come at some cost since juvenile survival decreased with increasing population size. Count sizes of Dunlin as part of the Wetland Bird Survey have indicated a decline in Traeth Lafan since the 1970s. The average maximum count decreased most significantly during the late 1970s with some stabilization since 2000. The impacts of density-dependent processes have been shown, both during the breeding season and overwinter, of Sand martins *Riparia riparia* (Norman & Peach 2013), Eurasian Dippers *Cinclus cinclus* (Saether *et al.* 2000) and Eurasian Spoonbills *Platalea leucorodia leucorodia* (Lok *et al.* 2013), indicating that competition for prey resources can be an important factor in regulating survival. The negative effects of increased conspecific density seen in this study imply that reduction in appropriate habitat and roost sites through disturbance and coastal squeeze could decrease survival of juvenile birds.

Interaction of weather and density effects

An interaction between the two primary factors affecting juvenile Dunlin is demonstrated in this study, with the two-covariate model explaining more of the variation in juvenile survival than the other models. There are some unexpected results from the model interactions, for example, between 1997 and 1998 a decrease of

1152 birds was noted (maximum count), but rainfall increased from 333 to 406 mm. A decrease in the number of birds should be expected to increase survival, as should the increase in rainfall, however, a decrease in survival from 0.55 (se 0.07) to 0.48 (se 0.1) was recorded. This may suggest that perhaps this year was a particularly poor year, given the very low maximum count of 600 birds. It is clear from the above example that these two variables do not explain everything and that other factors, both in and away from the wintering area, exerted an influence.

Severe cold weather effects

Information from previous studies strongly indicates that temperature and frozen ground conditions remain important factors for increasing mortality. Wader mortality has been shown to substantially increase during periods of very cold weather (Dugan *et al.* 1981, Davidson & Evans 1982, Davidson & Clark 1985, Clark 2004, 2009). The freezing temperatures affect the birds directly, by increasing metabolic stress (Dugan *et al.* 1981, McCulloch & Clark 1992, Thompson & Hale 1993, Burton & Evans 1997, Warnock *et al.* 1997, Kelly *et al.* 2002) and indirectly, by affecting the behaviour of their prey (Goss-Custard 1969, Davidson 1981), as well as occasionally freezing the surface of the upper tidal mudflats (Thompson & Hale 1993).

The relationship presented here between duration of frost and juvenile Dunlin survival is weakly negative, with longer periods of frost resulting in higher mortality. However, we suggest that the effect of cold weather on mortality can be mitigated if the rest of winter is characterized by high rainfall and mild temperatures. The winter of 2000 contained 10 consecutive days of frost but it also contained 496 mm of rainfall, the highest amount and produced the highest rate of survival, supporting this idea. Additionally, Traeth Lafan is a mild site with an average minimum temperature in January of 3°C, which is unlikely to cause such severe frost that it would inhibit the feeding of the birds. Here, the weak relationship between juvenile survival and duration of periods of frost is also presumably a result of the mild conditions. McCulloch & Clark (1992) found that Dunlin selected estuaries with higher minimum temperatures, as well as more westerly sites. Clark (2004) found increased mortality rates with severe freezing weather, but primarily on the east coast of the UK, particularly on the Wash. This increase in mortality was not nearly as strong on the west coast, even in smaller birds such as Dunlin.

Future climate change and population stability

Global climate change is having profound influences on multiple natural habitats, with species such as wading birds that migrate long distances between habitats, at particular risk. This study allows us to speculate about the consequences of future climatic change for Dunlin, by helping us to assess whether the proportion of juveniles and their rate of survival is adequate to replenish the birds lost from the adult population each year. The mean proportion of juveniles in our catches was 37%, while the mean survival rate for juveniles in this study is 0.47 (±0.05), compared with the mean adult survival rate of 0.72 (±0.008). These figures give a slight shortfall of 1% in the number of recruits to the population in the following season. At its lowest rate of 0.34 (±0.06), juvenile survival is not high enough to sustain the population, with only 71% of the requirement met. At its highest of 0.62 (±0.09), juvenile recruits would meet 121% of the requirement. Therefore the expected rise in temperatures and increase in precipitation may hold positive benefits for wintering Dunlin (Rehfisch *et al.* 2004), but a change in weather patterns leading to larger amounts of rain falling in shorter periods and a wider climatic variance including more severe storm events (Conway 1998, Solomon *et al.* 2007), could potentially be detrimental, as has been predicted in the European Shag *Phalacrocorax aristotelis* (Frederiksen *et al.* 2008). Identifying the effects of various climatic variables and of varying population density can facilitate management decisions; for example, preserving undisturbed sites as refuges in periods of severe weather and ensuring that valuable habitat is not lost at key species' sites (Raitkainen *et al.* 2008). If current declines in Dunlin populations are more strongly linked to a shift in the population with climate change, then these declines may continue, with more waders spending the whole winter period in continental Europe, rather than continuing migration to the UK (Rehfisch *et al.* 2004, Maclean *et al.* 2008, Holt *et al.* 2012). As climate change progresses, it will be important to continue studies and analyses such as these, as well as full population models, preferably across multiple sites where sufficient data exists, to try to further understand annual variation in survival of wintering populations.

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