

# Weather to disperse? Evidence that climatic conditions influence vertebrate dispersal

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## Summary

1. Dispersal is regarded as critical to the stability of existing populations and the spread of invading species, but empirical data on the effect of travelling conditions during the transfer phase are rare. We present evidence that both timing and distance of ex-natal dispersal in buzzards (*Buteo buteo*) are strongly affected by weather.

2. Dispersal was recorded more often when the wind changed to a more southerly direction from the more common westerly winds, and when minimum temperatures were lower. The effect of wind direction was greatest in the winter and minimum temperature was most important in the autumn. Poor weather did not appear to initiate dispersal.

3. Dispersal distance was most strongly correlated with maximum temperature during dispersal and wind direction in the following 5-day period. Combined with the sex of the buzzard these three variables accounted for 60% of the variation in dispersal distance.

4. These results are important for conservationists who manage species recovery programs and wildlife managers who model biological invasions.

*Key-words:* buzzard, dispersal, raptor, weather.

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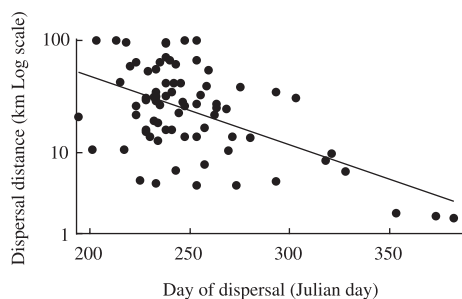
## Introduction

Biologists are often asked to predict how fast alien species will invade and how species of conservation concern will adapt to changing environments. In both cases, dispersal is a key consideration (Clobert *et al.* 2001; Bullock, Kenward & Hails 2002), and a need for models of dispersal is increasingly apparent (Sutherland & Watkinson 2001). However, relevant empirical data are hard to obtain (Marsh & Jones 1988; Kareiva & Wennergren 1995; Wennergren, Ruckelshaus, & Kareiva 1995; Lima & Zollner 1996; Zollner & Lima 1999; Macdonald & Johnson 2001), which constrains the progress of dispersal models (Turchin 1998). In a summary of studies on the three phases of dispersal (leaving, transfer and settling), Andreassen, Stenseth & Ims (2002) noted that empirical data on behaviour during the transfer phase is almost absent in the vertebrate literature, especially in an ecological context, due to the methodological and logistical problems associated with following dispersing animals.

A factor that may influence the transfer phase of dispersal is weather. It has long been recognized that weather affects seeds and invertebrates during dispersal (e.g. Johnson 1969; van der Pijl 1982). It has also been clear to ornithologists since the early 1900s that migrant birds appeared in certain places in certain weather conditions. It took the technology of radar for these observations to be assessed more objectively, but since then much research has shown that weather affects migration (e.g. Hentzelman 1975; Richardson 1978; Elkins 1983; Sparks *et al.* 2002). Therefore, it is reasonable to hypothesize that weather affects ex-natal dispersal in birds, but empirical data are rare except for the evidence that wind direction altered dispersal direction for Spanish imperial eagles (*Aquila adalberti* Brehm) (Ferrer 1993a).

We found that radio-tagged buzzards (*Buteo buteo* Linnaeus) are more likely to disperse away from their natal nest in their first autumn rather than winter, and birds that dispersed in autumn moved further than those dispersing in winter (Walls & Kenward 1998; Kenward, Walls & Hodder 2001a; Fig. 1). Dispersal distance was related to brood size and habitat around the nest, but over half the variation in dispersal distance remained unexplained (Kenward *et al.* 2001a). To

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**Fig. 1.** Ex-natal dispersal distances of buzzards radio-tagged in Dorset, UK, plotted against time of year (as in Kenward *et al.* 2001a).

explain the observation that early dispersers travelled furthest, there are three possible hypotheses: (i) distant autumn dispersers were genetic morphs that differed from short-distance winter dispersers; (ii) birds less competent at foraging tended to leave early and then also travelled far before finding suitable conditions for settling; and (iii) weather conditions favouring prolonged flight in the autumn resulted in longer dispersal distances. Very different techniques (perhaps including mathematical modelling) would be required to address the different hypotheses, each of which describes a different mechanism explaining the variation in distance. Here we present strong empirical evidence to support the third hypothesis, that weather affects the timing and distance of dispersal, although we can neither establish nor discount additional influences of variation in genetics or foraging ability. In this process we provide insights into the leaving and, more unusually, the transfer phase of dispersal.

### Materials and methods

All fledgling buzzards found within a 120-km<sup>2</sup> strip of Dorset, southern England (centred at 2°30' E, 50°42' N) were radio-tagged in the years 1990–92. Of these, 74 fledglings were fitted with a 30-g backpack using a Teflon ribbon harness (Kenward *et al.* 2001b) and another 16 with tail-mounted radio-tags (Biotrack Ltd, Dorset, UK). Buzzards were classed as male if their tarsus width was below 6 mm, otherwise female (Walls & Kenward 1995). Two locations were recorded per week until the end of September, when the tracking frequency was reduced to once per week in 1990–91 and once per fortnight in 1992. A Landrover fitted with a five-element Yagi antenna was used to record the locations of buzzards by triangulation from within 1–2 km of the buzzard. The location accuracy was therefore generally within 100 m, a very small distance when compared to the distance buzzards dispersed.

Fifty-five percent of radio-tagged buzzards dispersed more than 1 km from their natal nest (median 15 km) by mid-winter (Walls & Kenward 1998). Those that dispersed did not wander, but settled in a median minimum convex polygon of 1.2 km<sup>2</sup> (Walls *et al.* 1999) until the following spring. Although some juveniles

made excursions of over 40 km from their settled areas during the following summer, the median movement of 38 buzzards that changed their activity centres by more than 1 km between the first winter and the following winter was only 2.9 km; moreover, buzzards that bred moved their centre of activity a median 0.9 km from where they were settled the previous winter (Kenward *et al.* 2001a). Therefore, the distance buzzards bred from their origin, and hence their colonization ability, was heavily dependent on dispersal in the first six months.

We measured the dispersal distance between the natal nest and the buzzard's location in December, when movements of settled buzzards were minimal, or to its carcass location if it died beforehand. Three buzzards not found during the winter, but which returned briefly the following spring, were attributed dispersal distances of 100 km, the surrounding area having been searched thoroughly up to that distance (Walls & Kenward 1998). On returning, the buzzards did not stay long (often less than 1 week). Apart from these brief philopatric movements, migration was virtually non-existent: only one radio-tagged buzzard had regular movements of 5 km between separate summer and winter areas.

The earliest dispersal occurred on 20 July (Julian day 201). As the date of dispersal for 48 buzzards could not be estimated to less than 5 days, each year was divided into 33 5-day periods until the end of December. Dispersal was investigated in relation to weather during the 5-day period centred on the estimated dispersal date and during the preceding 5-day period, during which the weather could have induced dispersal by affecting feeding opportunities. There were 99 possible pairs of 5-day periods during the 3 years, although sample sizes varied slightly because weather variables were not all available for every period (e.g. Tables 4 and 5 differ by 1 d.f. when wind direction is included because it was not available on one dispersal occasion).

As each bird left, the number and the proportion of birds available to disperse declined, at the same time as there were seasonal trends in weather, such as a decline in temperature. To minimize dependence of results on mutual correlations with time, analyses were based on change in weather between adjacent pairs of 5-day periods (during which similar numbers of birds were available) and on whether or not any dispersal occurred in a period (i.e. not on numbers or proportions of dispersers) in two ways. 'Change-at-dispersal' analyses compared each period containing dispersal with the period immediately before by applying Mann–Whitney *U*-tests. Secondly, 'all-periods-change' regression analyses used (weather in period<sub>(t)</sub> – weather in period<sub>(t-1)</sub>) for all periods in a binary logistic regression with presence or absence of dispersal as the binary response variable. This approach removed all correlation between weather variables and Julian date ( $P > 0.2$ ). Finally, we separated periods with and without dispersal in the autumn (defined as days 201–273, i.e. until 30 September) from

those in winter (days 274–365, i.e. until 31 December). Previous analyses had demonstrated differences in frequency and distance of dispersal between but not within these periods, with marked between-season differences in how dispersal related to habitat and social conditions (Kenward *et al.* 2001a), which suggested that response to weather might also differ between autumn and winter.

Analyses of dispersal distances were based on weather in 5-day periods during and after dispersal, on the basis that bad weather after dispersal may prevent further movement, whereas good weather may encourage it. As with the dispersal timing, the distance was correlated with date: distance declined as the year progressed (Walls & Kenward 1995). Therefore, dispersal date was included in the regression models to examine residual covariance. Further investigation of temporal correlation between weather variables and distance involved testing whether distance correlated as well with weather two periods after dispersal as with weather during the period of dispersal. Finally, we divided the data into autumn and winter periods (before and after the 1st October), to test whether relationships between dispersal distance and weather for the autumn might predict dispersal distances in winter. A cross-validation, using a random 20% of cases (Tabachnick & Fidell 2001) tested for any residual dependence of the results on the division into seasons.

Dispersal dates and distances were calculated using Ranges V (Kenward & Hodder 1996). Statistical analyses were performed using Minitab 13 (Minitab Inc., State College, PA, USA). The weather data were supplied by British Atmospheric Data Centre and included minimum and maximum daytime temperatures, rainfall, visibility and wind direction at midday, because these were most likely to have affected flight (Elkins 1983). Data were from the Winfrith weather station (8752, 4 km west of the study area), which gave the most complete weather record of three nearby sites, with Poole (4 km east) and Swanage (10 km east) also being more coastal. Weather records from all 3 stations were highly correlated (Pearson's correlation,  $r > 0.95$ ). In any case, dispersing buzzards were exposed to weather up to 100 km from the area.

Distributions of all continuous variables were tested for normality and inspected for heteroscedasticity. Dispersal distances were normal after a  $\log_{10}$  transformation. Temperatures were normal when squared and wind direction could be normalized by an arcsine transformation of the bearing divided by 360 degrees. There were many days when there was no precipitation or no wind, which prevented normalization of rainfall and wind-strength data. The sex of the buzzard was included as a factor in the regression models, because female buzzards dispersed significantly further than males (Walls & Kenward 1995). Results were not unduly influenced by ordinal variables that lacked normality, because only a (weak) relationship with sex was observed in the final models.

## Results

### TIMING OF DISPERSAL

The only weather variable that changed significantly between dispersal periods and the previous 5 days was the wind direction at midday. Winds tended to veer from westerly in the preceding 5 days to southerly during the 5 days in which dispersal occurred (Table 1).

In all-periods-change analyses (Table 2) the best predictor of dispersal was change in wind direction (concordance = 70%). However, minimum temperature showed a marginally significant effect, and increased the predictability slightly in a multivariate model (concordance = 74%). Thus, in both analysis approaches, wind direction was the most important weather variable associated with timing of dispersal. In fact, the raw wind direction data were no more temporally correlated ( $r = -0.14$ ,  $P = 0.23$ ) than the difference in wind direction between periods ( $r = -0.05$ ,  $P = 0.68$ ), and a logistic regression based solely on wind direction in 5-day periods with or without dispersal gave a similar result to the change-at-dispersal analysis ( $G = 8.95$ ,  $P = 0.003$ ).

A plot of change in wind direction between periods against time of year shows that very few of the 29 dispersal periods occur above the regression line of non-dispersal periods (Fig. 2). There is also a very noticeable divergence between the regression lines of changes at dispersal and non-dispersal, such that winds had swung more south-easterly in the winter dispersal periods ( $r = -0.49$ ,  $P = 0.007$ ), whereas the trend was not so obvious or significant for periods when no dispersal was recorded ( $r = 0.15$ ,  $P = 0.311$ ). This is best explained by looking at each season in turn.

### Seasonal differences

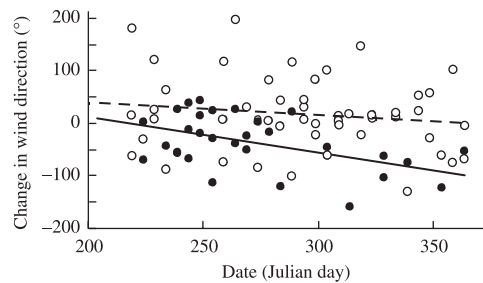
In winter, winds were predominantly south-easterly during periods of dispersal (median = 153°), rather than westerly in periods without dispersal (median = 242°) (Mann–Whitney  $U$ :  $W = 135$ ,  $n = 46$ ,  $P = 0.008$ ), but no differences were found for the autumn (Mann–Whitney  $U$ :  $W = 324$ ,  $n = 39$ ,  $P = 0.122$ ). Separating into seasons also showed that the minimum temperature, marginally significant in the previous analysis, was

**Table 1.** Weather conditions during the 31 periods of 5 days when buzzards were recorded dispersing compared to the conditions in the period before, using Mann–Whitney  $U$ -tests. Significant  $P$  values shown in bold

	Before	During	$P$
Rainfall (mm)	4.6	7.4	0.96
Maximum daily temp. (°C)	18.1	17.8	0.76
Minimum daily temp. (°C)	11.0	9.6	0.13
Wind direction (° true)	234	196	<b>0.03</b>
Wind speed (knots)	6.8	6.8	0.79
Visibility (m)	12000	10480	0.24
Average daily temp. (°C)	15.8	15.4	0.49

**Table 2.** Binary logistic regressions, using change in weather variables between all 99 paired 5-day periods as predictors of dispersal of radio-tagged buzzards in the second period. Significant *P* values shown in bold

Changed weather variable	<i>G</i>	<i>P</i>	Best model		
			<i>z</i>	<i>G</i>	<i>P</i>
Rainfall	0.055	0.815			
Maximum daily temp.	0.522	0.470			
Minimum daily temp.	3.931	0.058	MinT	-1.95	
Wind direction	11.87	<b>0.001</b>	WinDir	-2.94	16.078
Wind speed	0.061	0.805			
Average daily temp.	0.325	0.569			

**Fig. 2.** The change in wind direction between adjacent periods plotted against time of year, comparing the periods when dispersal occurred (●) and when no dispersal was recorded (○). Regression lines are for pairs of periods with dispersal (solid line) and without dispersal (dashed line).

highly significant in the autumn (Mann–Whitney *U*:  $W = 385$ ,  $n = 48$ ,  $P = 0.008$ ), and not significant in the winter (Mann–Whitney *U*:  $W = 254$ ,  $n = 54$ ,  $P = 0.648$ ). Thus, the importance of individual weather variables differed between seasons.

#### Dispersal distance

Dispersal distances correlated most strongly with maximum temperature in the period that buzzards dispersed (Table 3); buzzards dispersed further during warmer weather. In 5-day periods immediately following dispersal, a correlation with wind direction was also highly significant; buzzards dispersed further when the wind was from a more westerly direction. Dispersal distance correlated significantly but less strongly with date and was weakly related to sex. Correlations were less significant with minimum temperature.

**Table 3.** Correlation coefficients of dispersal distance with date, sex and weather in the five days during which buzzards dispersed and in the subsequent 5-day period. Significant *P* values shown in bold.

<i>n</i> = 48	<i>r</i>	<i>P</i>	<i>R</i>	<i>P</i>
Date	-0.464	<b>0.001</b>		
Sex	0.437	<b>0.002</b>		
Period during dispersal			Period after dispersal	
Rainfall	0.503	0.503	Rainfall	-0.109
Maximum daily temp.	0.635	<b>0.000</b>	Maximum daily temp.	0.564
Minimum daily temp.	0.347	<b>0.016</b>	Minimum daily temp.	0.367
Wind direction	0.206	0.164	Wind direction	0.512
Wind speed	0.125	0.403	Wind speed	0.111
Visibility	0.241	0.100	Visibility	0.225

For multiple regression, date was the only transformed variable that did not fit assumptions that residuals are normal, linear and homoscedastic because two particularly late dispersers resulted in a heteroscedastic distribution. With these late dispersals excluded, all necessary regression assumptions were met. As temperature correlated strongly with date ( $r = -0.781$ ,  $P < 0.001$ ) date was included in the analyses. Interaction terms were also tested, but were never more significant than their constituent variables.

In multiple regression analyses, date was never significant when maximum temperature was included as a factor and was only significant when combined in a bivariate regression with wind direction (Table 4b). Exclusion of a buzzard that dispersed furthest and left during the hottest period (Fig. 3) only reduced the explanation of maximum temperature, wind direction and sex from 60% to 57% (cf. Table 4e).

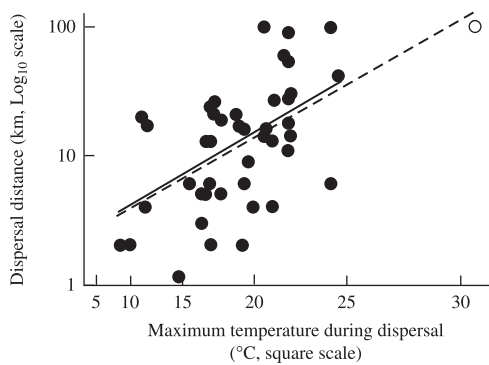
The partial regression coefficient for maximum temperature alone remained highly significant after adjusting for date ( $t = 3.79$ ,  $P < 0.001$ ) and still explained 25% of the variation in dispersal distance, compared to 35% before adjustment. In contrast, the partial regression coefficient for date after adjusting for maximum temperature was not significant ( $t = 0.64$ ,  $P = 0.526$ ). When wind direction was partialled out, again temperature explained 34% of the variation ( $t = 0.501$ ,  $P < 0.001$ ).

#### Seasonal differences

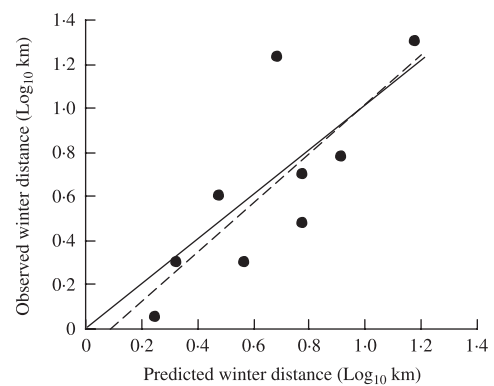
Despite the lack of correlation between distances and date in autumn ( $r = -0.035$ ,  $P = 0.837$ ), similar correlations with weather were obtained for this season

**Table 4.** Multiple regression relationships of weather variables with distances buzzards dispersed from the nest in their first autumn or winter. Date was included in (a), (c) and (d) to show absence of its effect after inclusion of temperature

<i>n</i> = 46	<i>t</i>	<i>P</i>	d.f.	<i>R</i> <sup>2</sup>	<i>P</i>
(a)					
Date	0.63	0.531			
Maximum temperature during	3.75	0.001	44	35.8	0.001
(b)					
Date	-2.38	0.022			
Wind direction after	3.11	0.003	42	32.8	0.000
(c)					
Date	0.92	0.363			
Maximum temperature during	3.58	0.001			
Wind direction after	3.24	0.002	41	48.9	0.000
(d)					
Date	1.14	0.259			
Maximum temperature during	3.44	0.001			
Wind direction after	4.01	0.000			
Sex	3.53	0.001	40	60.6	0.000
(e)					
Maximum temperature during	3.77	0.001			
Wind direction after	3.87	0.000			
Sex	3.48	0.001	41	59.7	0.000



**Fig. 3.** Regression of distance that buzzards dispersed against maximum temperature in the 5-day period of dispersal. The two lines show regression with a potential outlier (○) included (dashed) or excluded (solid).



**Fig. 4.** Buzzard ex-natal dispersal distances during winter plotted against distances predicted from wind direction, temperature and sex in the autumn. Solid line shows 1 : 1 ratio if predictions were accurate and the dashed line shows the regression of observed vs. predicted.

alone (Table 5). Maximum temperature remained best correlated with distance travelled ( $r = 0.51$ ,  $P = 0.001$ ). Wind direction in the period after dispersal was correlated as before, but less strongly ( $r = 0.36$ ,  $P = 0.031$ ). Correlation of distance with maximum temperature diminished if the period of measurement was delayed by 5 days ( $r = 0.375$ ,  $P = 0.022$ ), and vanished if the following period was used ( $r = 0.25$ ,  $P = 0.136$ ). None of the other weather variables had significant correlations with weather two periods after dispersal.

Date was never significant in a multiple regression, and again maximum temperature remained the most important weather variable for the autumn season. Wind direction was important after including maximum temperature and sex (Table 5). So, despite removing the influence of date in every way possible, maximum temperature in the period of leaving and wind direction

in the 5 days following were strongly correlated with dispersal distance.

Of the 46 dispersal events, 37 were in autumn and nine in winter. Using a regression equation based on the 37 autumn distances alone, the nine winter dispersal distances were predicted from the autumn weather conditions and buzzard's sex. The strength of prediction was indicated by the correlation of predicted winter distances from the autumn data, and the observed winter values ( $r = 0.807$ ,  $P < 0.01$ ) (Fig. 4). To test whether this result, with an arbitrary separation date, differed from any prediction drawn from the data set, the correlation was also estimated for prediction from 37 randomly selected dispersal events from both seasons and used to predict the remaining 9 dispersal distances, with 500 iterations. The resulting distribution of correlation coefficients was arcsine transformed to obtain

**Table 5.** Multiple regression analyses of dispersal distance against weather and date for those radio-tagged buzzards that left in the autumn

<i>n</i> = 37	<i>t</i>	<i>P</i>	d.f.	<i>R</i> <sup>2</sup>	<i>P</i>
(a)					
Date	1.37	0.179			
Maximum temperature during	3.80	0.001	35	29.9	0.002
(b)					
Date	-0.06	0.953			
Wind direction after	2.39	0.023	33	15.5	0.101
(c)					
Date	1.79	0.083			
Maximum temperature during	3.74	0.001			
Wind direction after	2.52	0.017	32	41.2	0.001
(d)					
Date	1.64	0.112			
Maximum temperature during	3.22	0.003			
Wind direction after	2.93	0.006			
Sex	2.44	0.020	31	50.7	0.000
(e)					
Maximum temperature during	2.71	0.011			
Wind direction after	2.67	0.012			
Sex	2.58	0.015	32	46.5	0.000

a mean  $r = 0.790$  (SD = 0.218). The close fit of observed and predicted values drawn at random confirms the lack of any residual effect of date.

## Discussion

The results support the hypothesis that weather affects dispersal in buzzards. This appears to be the first empirical demonstration of weather affecting dispersal distance in a non-migratory vertebrate. The evidence is only correlative, as it is impossible to manipulate the weather experimentally and impractical to provoke buzzards to disperse under particular weather conditions. Nevertheless, the evidence is compelling.

### WHAT AFFECTED TIMING OF DISPERSAL?

Bad weather instigates migration (Elkins 1983) and causes forced temporary moves, 'irruptive dispersal' (Gessaman & Worthen 1982) as part of an 'emergency life history stage' (Jacobs 1996). Recent studies have demonstrated a plausible mechanism explaining how weather-induced stress could force migratory behaviour through changes in the hormone corticosterone (Wingfield & Ramenofsky 1997). None of our analyses found evidence that bad weather preceded the ex-natal dispersal of buzzards. Minimum temperature in autumn was significantly lower during periods of dispersal, but although the median rainfall was higher, it was not significantly so. The lower minimum temperature may merely have been associated with good weather in high-pressure systems.

Tendency to disperse was also related to habitat and presence of siblings (Kenward *et al.* 2001a), so perhaps food supply, social behaviour or genetics influenced the decision to disperse, which was then instigated by

*opportunity* during better weather rather than being *driven* by bad weather. This would not be surprising, as these dispersal movements concern leaving the parental territory rather than cross-continent dispersal to an area of better weather. Similar cases have been observed for Spanish imperial eagles, that did not leave when the wind was blowing towards the sea (Ferrer 1993a), and Damaraland mole-rats (*Cryptomys damarensis* Ogilby), whose dispersal was restricted to periods following good rainfall, when burrowing through sandy soils is facilitated (Molteno & Bennett 2002).

### WHAT AFFECTED DISPERSAL DISTANCE?

Dispersal distances correlated with temperature and wind direction, indicating that good weather appeared to favour longer dispersal distances. Buzzards are adapted for soaring, with classic low wing loading and long primaries with deep U-shaped slots that prevent stalling at low speed (Elkins 1983). Thermals, as used by soaring buzzards, rely on differential ground temperatures and are most abundant on warmer days with less wind to disturb their formation. Thus the results agreed with expectations from flight dynamics. Although it is impossible to control the weather for an experiment, a possible test could be to track the same species at different latitudes, where temperature and seasons vary. For example, in warmer climates we would expect the autumn dispersal period to be extended and it would be interesting to see if buzzards also dispersed further. However, it is very difficult to know that like is being compared with like, because in other habitats birds are likely to be adapted for differing local foraging pressures.

The breakdown into seasons was based on prior analyses that demonstrated associations between

dispersal and different factors in autumn and winter periods. The separation removed within-season dependence of distance on date (Kenward *et al.* 2001a) but the date itself was arbitrary. In this paper, dividing into autumn and winter did not result in any different weather variable correlations than those from the undivided analyses, but it added detail. For example, variation in distance related strongly to the variable temperatures during the autumn but during the winter, when temperatures varied little, wind direction was more important. Moreover, the winter dispersal distances could be predicted reasonably well from the autumn data set, despite there being very little overlap in temperature between the two seasons.

As with the timing of dispersal, distance is likely to depend on factors other than weather as indicated by the 'priming' of distant buzzard dispersal by poor habitat (Kenward *et al.* 2001a). Ferrer (1993b) has also shown how dispersal movements are correlated with urea levels in the blood of Spanish imperial eagles, which indicated a nutritional component to the timing of dispersal. However, in that case he concluded that the better nourished dispersed earlier and went further.

Our analyses concentrate on dispersal during the first autumn and winter, even though buzzards can delay ex-natal dispersal and those that have dispersed can make additional extra-natal movements (Kenward *et al.* 2001a). However, we also know that these later movements are short (Walls & Kenward 1998). The speed of modelled invasions is extremely sensitive to the influence of the individuals that disperse furthest (Kot, Lewis & van den Driessche 1996), so the initial long-distance movements are the most important when considering the adaptability of animals to changing environments or their invasive ability. In fact we are extremely fortunate to have extreme movements well documented, as these distances are the most difficult to determine in the field with any degree of accuracy (Bullock & Clarke 2000).

## Conclusion

Evidence that over half the variation in dispersal distance could be attributed to weather and sex is important in many ways. In practice, knowing something of how weather affects dispersal could be helpful when trying to re-introduce a species, e.g. sometimes it is beneficial for the released animals not to disperse too far, so it is better to release them when the weather does not favour long distance dispersal. Also, those building colonization models should account for the weather and consider how global warming may alter invasion rates, as it appears to be affecting the timing of migration (Sparks *et al.* 2002). Alternatively, complex colonization models based on the exact position of individuals and habitats may not be necessary because the weather may enforce a pattern that is more easily mimicked by a simpler diffusion model. For example, Stephens *et al.* (2002) found that individual-based

population models performed worse than simpler group-based matrix models at predicting basic population dynamics, although behaviour-based models were necessary to predict transient density-dependent effects. Studies like ours would be practical in many species for addressing the paucity of empirical data on the transition phase of dispersal, as identified by Andreassen *et al.* (2002).

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