

**Mute Swan *Cygnus olor***

1981-1983 survey regression on day 1 is shown on graph 140. ANOVA probability was highly significant ( $P < 0.01$ ) and the intercept was non-significant ( $P > 0.05$ ), shown in table 95. The null hypothesis was rejected in favour of the alternative hypothesis.

Graph 140

Confluence: regression of Mute Swan residuals and water stage height residuals on day 1 1981-1983

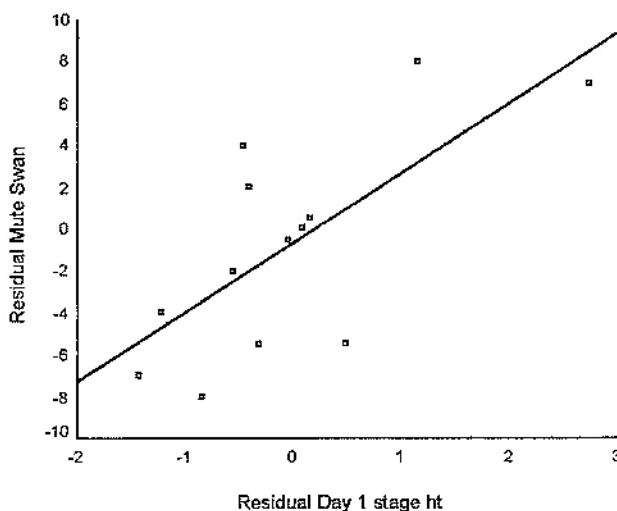


Table 95

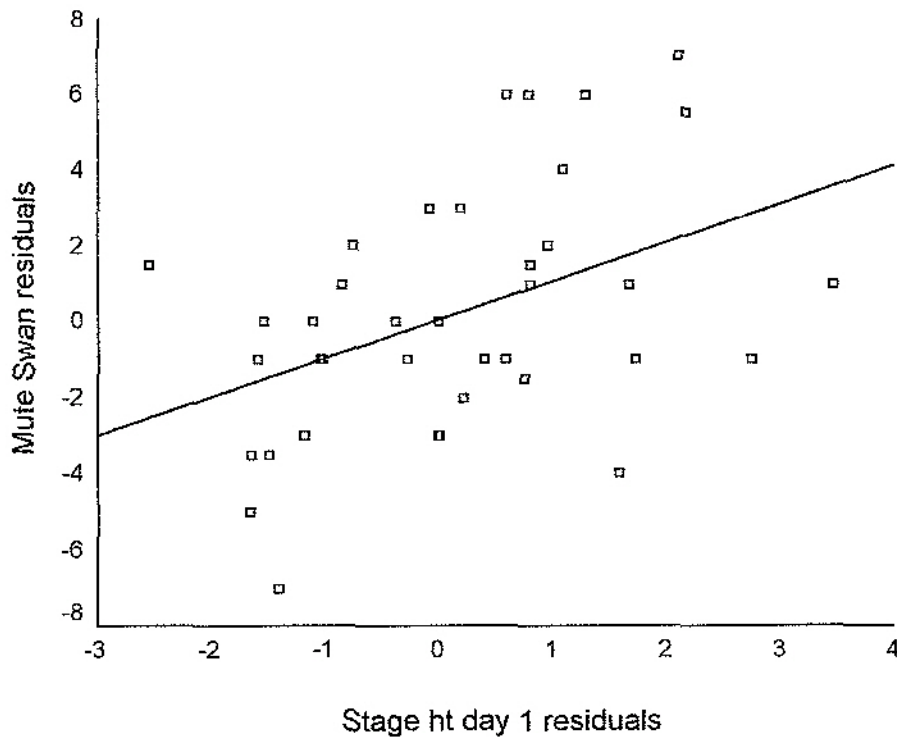
Confluence: regression results of Mute Swan residuals and water stage height residuals on day 1 1981-1983

Water stage height day	Mute Swan residual removal	AVOVA probability	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
1	none	0.007	3.33	3.286	-0.661	-0.624	0.546	0.495	H <sub>1</sub>

WeBS ANOVA probability on day 1 was close to significant, shown in table 96, and remained so on removal of atypical residual outlier 23 but when outlier 13 was also deleted probability declined to highly significant, shown on graph 141, but the intercept was non-significant and then the null hypothesis was rejected in favour of the alternative hypothesis.

Graph 141

Transect C: regression of Mute Swan residuals and water stage height residuals on day 1 WeBS



Atypical outliers 23 and 13 have been deleted

Table 96

Transect C: regression results of Mute Swan residuals and water stage height residuals on day 1 WeBS

Water stage height day	Mute Swan residual removal	AVOVA probability	Slope	t-test	Intercept	t-test	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
				the slope is zero		that the intercept is zero			
1	none	0.068	1.078	1.878	0.905	1.191	0.241	0.081	H <sub>0</sub>
1	23	0.058	0.826	1.955	0.42	0.747	0.46	0.089	H <sub>0</sub>
1	23 and 13	0.005	1.019	2.969	0.0698	0.133	895	0.188	H <sub>1</sub>

**Whooper Swan *Cygnus cygnus***

Both surveys on each term day ANOVA probability were non-significant, thus the null hypothesis was accepted in each case.

**Eurasian Wigeon *Anas penelope***

The 1981-1983 survey for each term day the probability was non-significant, therefore the null hypothesis was accepted.

WeBS day 1 regression is shown in graph 142. The ANOVA probability was very highly significant ( $P < 0.001$ ) but the intercept was non-significant, shown in table 97. The null hypothesis was rejected in favour of the alternative hypothesis.

Graph 142

Transect C: regression of Eurasian wigeon residuals and water stage height residuals on day 1 WeBS

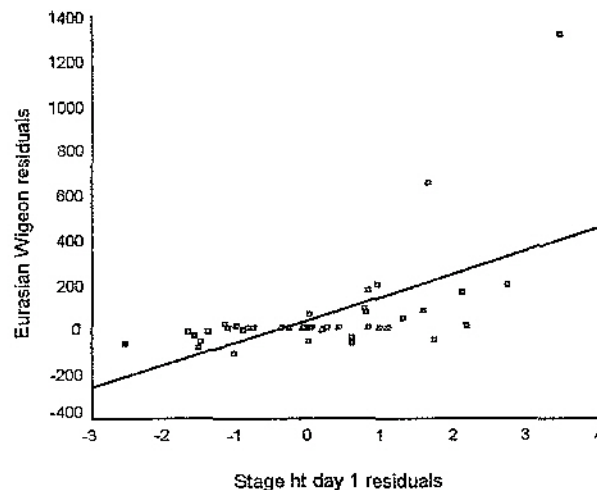




Table 97

Transect C: regression results of Eurasian wigeon residuals and water stage height residuals on day 1 WeBS

Water stage height day	Eurasian Wigeon residual removal	ANOVA probability	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
1	none	< 0.001	100.8	4.477	45.629	1.531	0.134	0.334	H <sub>1</sub>

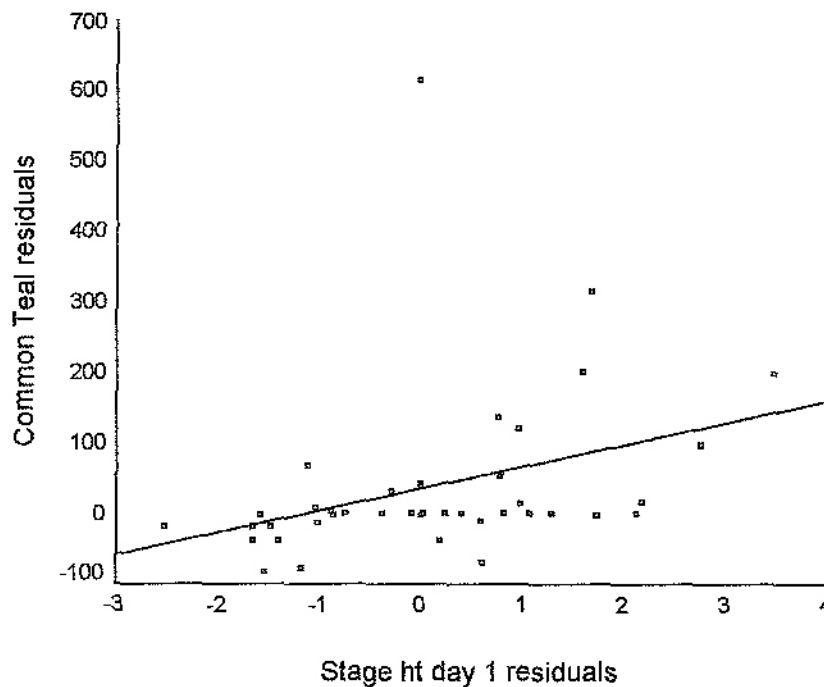
**Common Teal *Anas crecca***

The 1981-1983 survey the ANOVA probability for each term day was non-significant, thus the null hypothesis was accepted.

WeBS ANOVA probability was non-significant for each day, thus the non-hypothesis was accepted. When atypical outlier 1182 was deleted on day 1, ANOVA probability diminished to significant and the intercept was close to significant, shown in table 98. The regression is shown on graph 143.

Graph 143

Transect C: regression of Common Teal residuals and water stage height residuals on day 1 WeBS



Residual outlier 1182 has been removed.

Table 98

Transect C: regression results of Common Teal residuals and water stage height residuals on day 1 WeBS

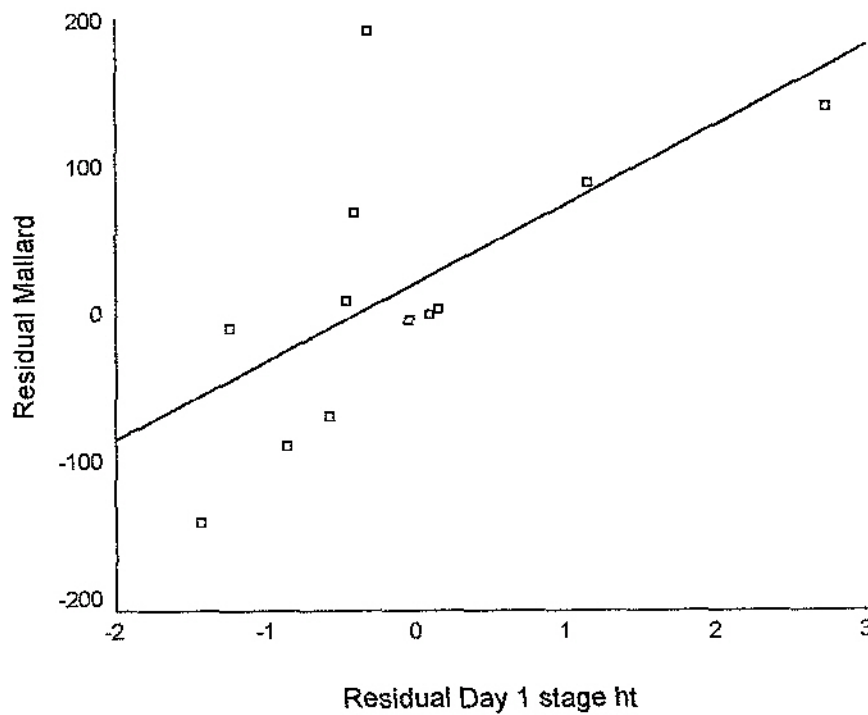
Water stage height day	Eurasian Teal residual removal	AVOVA probability	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
1	1182	0.026	31.06	2.311	33.608	1.875	0.068	0.12	H <sub>1</sub>

**Mallard *Anas platyrhynchos***

1981-1983 survey ANOVA probability for each term day was non-significant. On deletion of mallard atypical outlier 191.5 on day 1 ANOVA probability decreased to significant, shown in table 99. The regression is shown on graph 144. The null hypothesis was rejected in favour of the alternative hypothesis

Graph 144

Confluence: regression of Mallard residuals and water stage height residuals on day 1 during 1981-1983



Residual outlier 191.5 has been removed.

Table 99

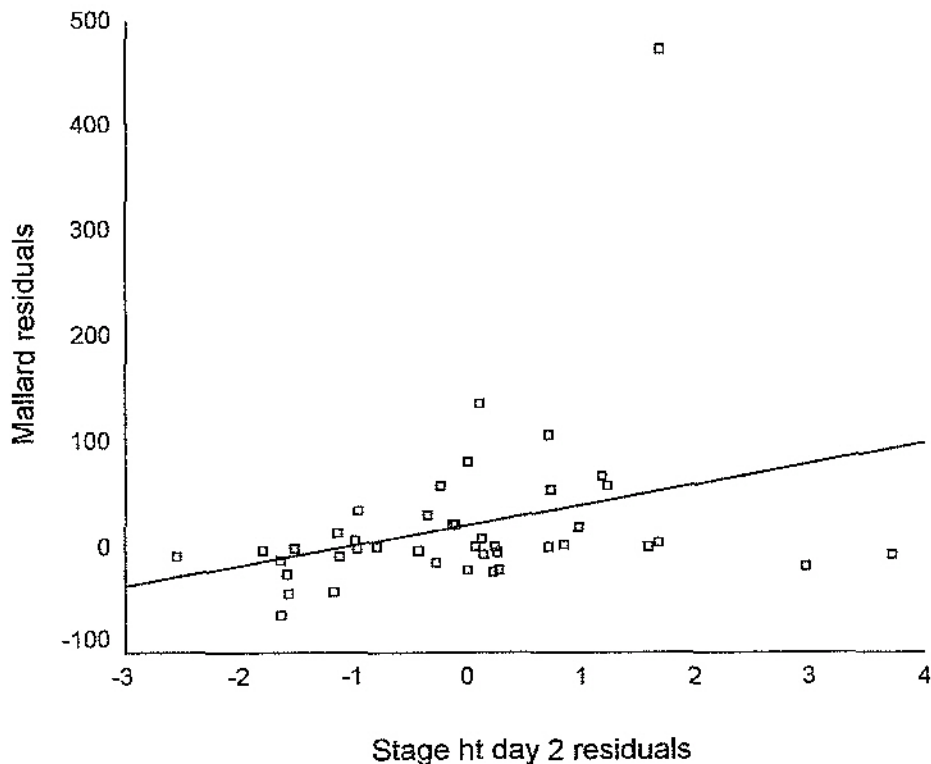
Confluence: regression results of Mallard residuals and water stage height residuals on day 1 1981-1983

Water stage height day	Mallard residual removal	ANOVA significance	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
1	191.5	0.027	53.368	2.589	21.322	0.958	0.361	0.401	H <sub>1</sub>

WeBS day 2 regression is shown on graph 145. The ANOVA probability was significant and the intercept was non-significant, shown on table 100. On day 1 deletion of mallard atypical outlier 474, the ANOVA probability declined to significant but the intercept was non-significant. The regression is shown on graph 146. The null hypothesis was rejected in favour of the alternative hypothesis in both cases.

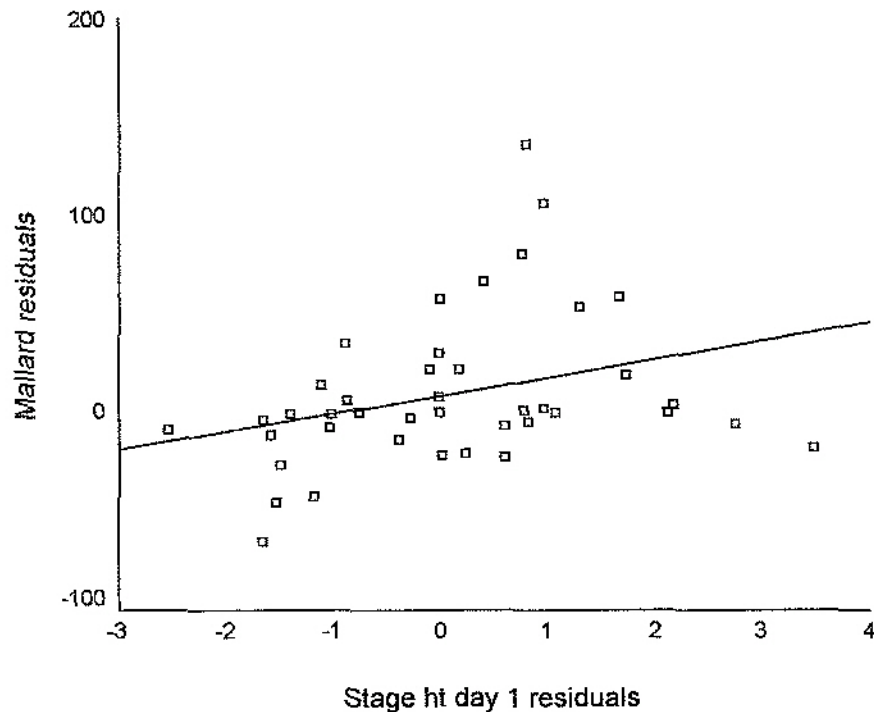
Graph 145

Transect C: regression of Mallard residuals and water stage height residuals on day 2 WeBS



Graph 146

Transect C: regression of Mallard residuals and water stage height residuals on day 1 WeBS



Residual outlier 474 has been removed.

Table 100

Transect C: regression results of Mallard residuals and water stage height residuals WeBS

Water stage height day	Mallard residual removal	AVOVA probability	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
2	none	0.05	19.34	2.019	21.354	1.76	0.086	0.092	H <sub>1</sub>
1	474	0.047	9.215	2.048	8.696	1.468	0.15	0.097	H <sub>1</sub>

**Northern Pintail *Anas acuta***

1981-1983 survey dataset consisted of nine zeros, thus regression was not computable. The null hypothesis was accepted.

WeBS day 1 regression is shown on graph 147. The ANOVA probability was very highly significant ( $P < 0.001$ ) but the intercept was non-significant, shown in table 101. The null hypothesis was rejected in favour of the alternative hypothesis.

Graph 147

Transect C: regression of Northern Pintail residuals and water stage height residuals on day 1 during WeBS

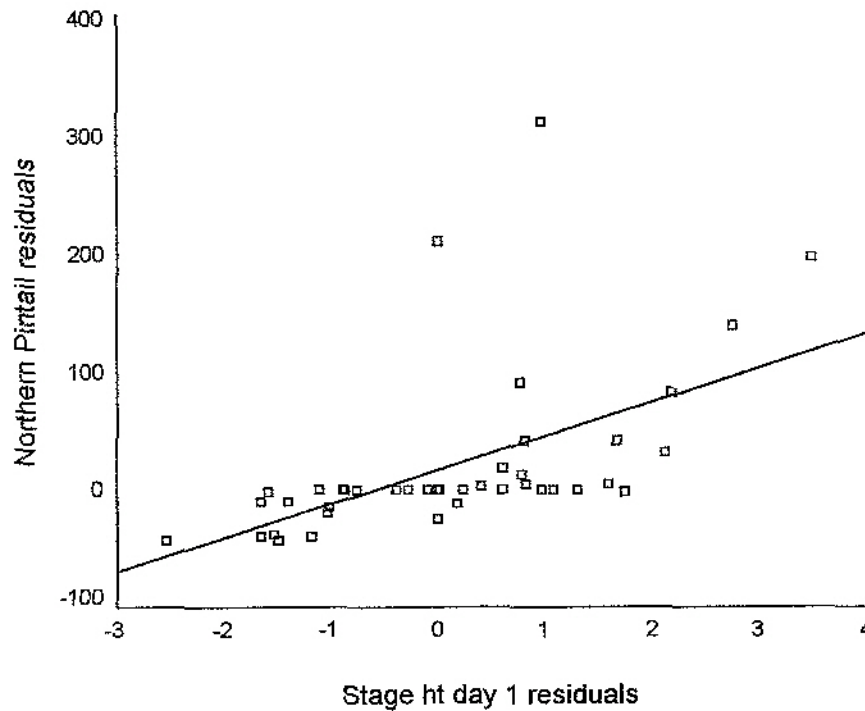


Table 101

Transect C: regression results for Northern Pintail residuals and water stage height residuals on day 1 WeBS

Water stage height day	Northern Pintail residual removal	ANOVA probability	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	$r^2$	Hypothesis favoured
1	none	< 0.001	28.87	4.04	16.954	1.793	0.081	0.29	$H_1$

**Northern Lapwing *Vanellus vanellus***

1981-1983 survey day 1 regression is shown on graph 148. The ANOVA probability was highly significant but the intercept was non-significant, shown

in table 102. The null hypothesis was rejected in favour of the alternative hypothesis.

Graph 148

Confluence: regression of Northern Lapwing residuals and water stage height residuals on day 1 1981-1983

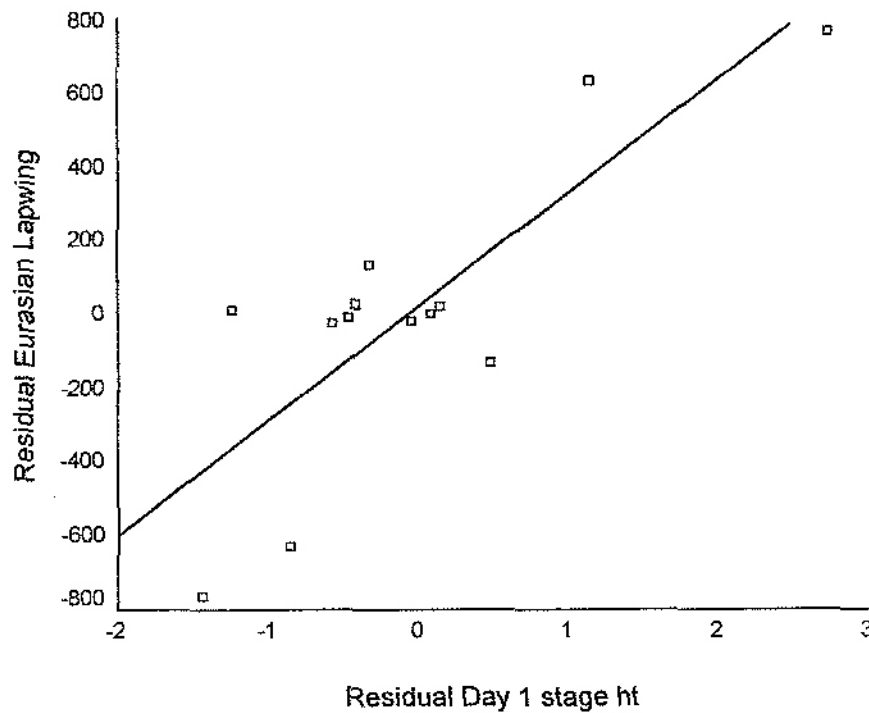


Table 102

Confluence: regression results of Northern Lapwing residuals and water stage height residuals on day 1 1981-1983

Water stage height day	Northern Lapwing residual removal	AVOVA significance	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
1	none	0.001	306.734	4.697	17.036	0.249	0.808	0.667	H <sub>1</sub>

WeBS day 1 regression is shown on graph 149. The ANOVA probability was significant as was the intercept, shown on table 103. The null hypothesis was rejected in favour of the alternative hypothesis.

Graph 149

Transect C: regression of Northern Lapwing residuals and water stage height residuals on day 1 WeBS

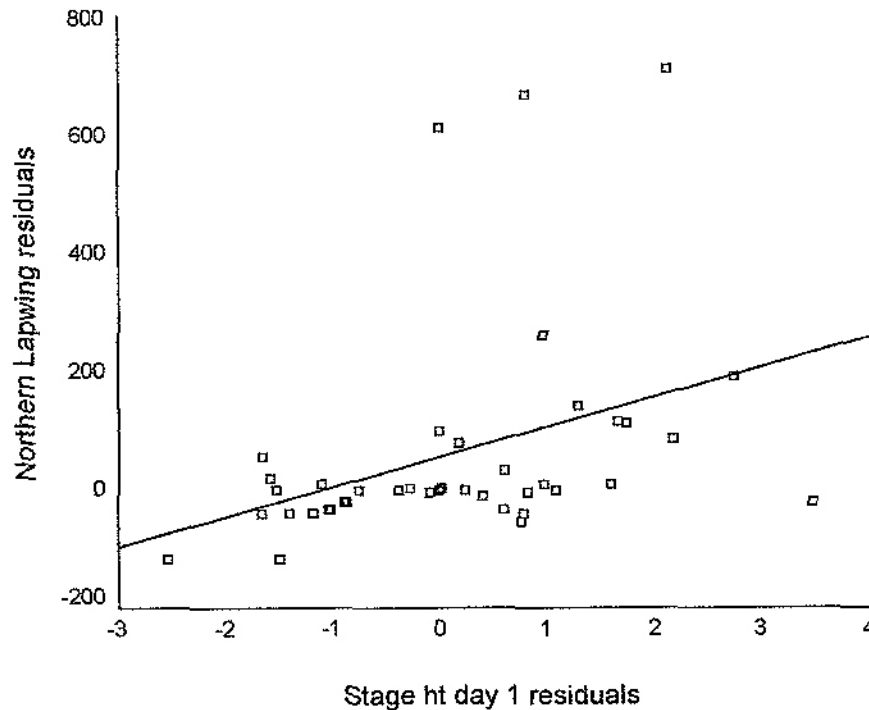


Table 103

Transect C: regression results for Northern Lapwing residuals and water stage height residuals on day 1 WeBS

Water stage height day	Northern Lapwing residual removal	ANOVA probability	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
1	none	0.016	50.98	2.519	54.632	2.04	0.048	0.137	H <sub>1</sub>

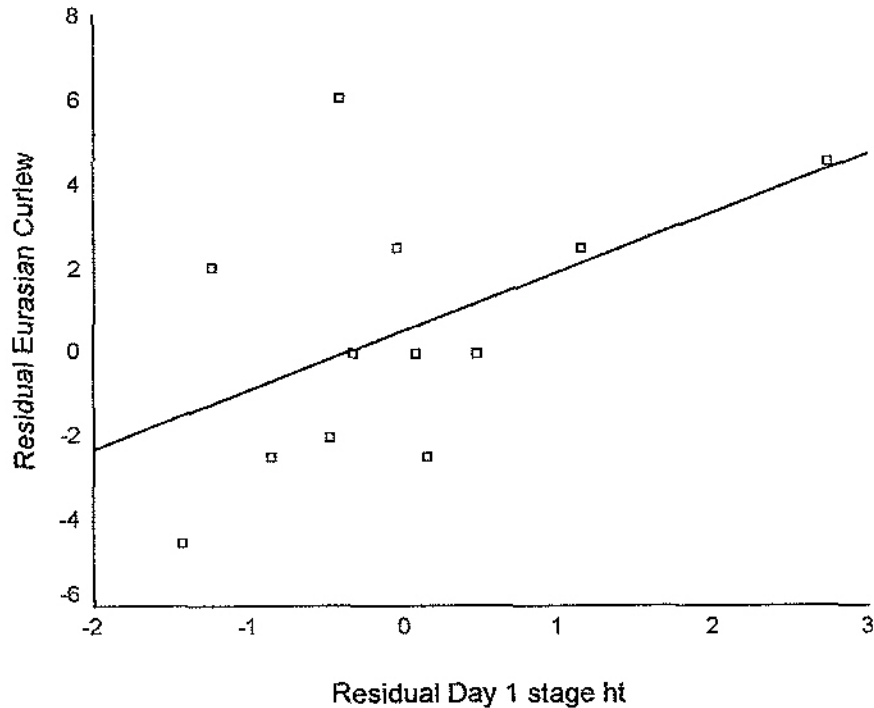
**Eurasian Curlew *Numenius arquata***

1981-1983 survey ANOVA probability was non-significant for each term day. On deletion of Eurasian curlew atypical outlier -6 on day 2, the ANOVA probability declined to significant but the intercept was non-significant, shown in table 104. The regression is shown on graph 150. The null hypothesis was rejected in favour of alternative hypothesis.



Graph 150

Transect C: regression of Eurasian Curlew residuals and water stage height residuals on day 2 1981-1983



Residual outlier -6 has been removed.

Table 104

Confluence: regression results of Eurasian Curlew residuals and water stage height residuals on day 2 1981-1983

Water stage height day	Eurasian Curlew residual removal	AVOVA significance	Slope	t-test the slope is zero	Intercept	t-test that the intercept is zero	Probability the intercept is zero	r <sup>2</sup>	Hypothesis favoured
2	-6.0	0.021	2.033	2.728	0.493	0.691	0.505	0.427	H <sub>1</sub>

WeBS ANOVA probability was non-significant on each term day, thus the null hypothesis was accepted.

**Summary**

The surveys' regression results are summarised in tables 105 and 106 and are compared in table 107. The main comparative conclusions are: (i) more species, without outlier deletion, had a significant relationship with stage

heights during WeBS than in 1981-1983; (ii) twice as many species had a non-significant relationship during 1981-1983 compared to WeBS and (iii) the 1981-1983 dataset was small, thus interpretation must be with caution. The quantity of data for WeBS allowed a better interpretation.

Table 105

Summary of Confluence regression results of species residuals and water stage height residuals 1981-1983

Species	Term day number	Residual removed	ANOVA probability	Intercept probability	Hypothesis favoured
Mute Swan	1	none	$P < 0.01$	$P > 0.05$	$H_1$
Whooper Swan	1, 2 and 3	none	$P > 0.05$	na	$H_0$
Eurasian Wigeon	1, 2 and 3	none	$P > 0.05$	na	$H_0$
Eurasian Teal	1, 2 and 3	none	$P > 0.05$	na	$H_0$
Mallard	1, 2 and 3	none	$P > 0.05$	na	$H_0$
Mallard	1	-191.5	$P < 0.05$	$P > 0.05$	$H_1$
Northern Pintail	1, 2 and 3	none	$P > 0.05$	na	$H_0$
Northern Lapwing	1	none	$P < 0.01$	$P > 0.05$	$H_1$
Eurasian Curlew	1, 2 and 3	none	$P > 0.05$	na	$H_0$
<i>Eurasian Curlew</i>	2	-6	$P < 0.05$	$P > 0.05$	$H_1$

na: not applicable

Table 106

Summary of transect C regression results of species residuals and water stage height residuals WeBS

Species	Term day number	Residual removed	ANOVA probability	Intercept significance	Hypothesis favoured
Mute Swan	1, 2 and 3	none	$P > 0.05$	na	$H_0$
Mute Swan	1	23 and 13	$P < 0.05$	$P > 0.05$	$H_1$
Whooper Swan	1, 2 and 3	none	$P > 0.05$	na	$H_0$
Eurasian Wigeon	1	none	$P < 0.001$	$P > 0.05$	$H_1$
Eurasian Teal	1, 2 and 3	none	$P > 0.05$	na	$H_0$
Eurasian Teal	1	1182.0	$P < 0.05$	$P > 0.05$	$H_1$
Mallard	1 and 3	none	$P > 0.05$	na	$H_0$
Mallard	2	none	$P < 0.05$	$P > 0.05$	$H_1$
Mallard	1	474.0	$P < 0.05$	$P > 0.05$	$H_1$
Northern Pintail	1	none	$P < 0.001$	$P > 0.05$	$H_1$
Northern Lapwing	1	none	$P < 0.05$	$P < 0.05$	$H_1$
Eurasian Curlew	1, 2 and 3	none	$P > 0.05$	na	$H_0$

na: not applicable

Table 107

Summary of the comparative results of species residuals and water stage height residuals of the 1981-1983 survey and WeBS

Subject of comparison	1981-1983 Survey			WeBS 1995-2002		
	Species	Nos of species	Nos of guilds	Species	Nos of species	Nos of guilds
P > 0.05 for days 1, 2 and 3	Whooper Swan Eurasian Wigeon Eurasian Teal Mallard Northern Pintail Eurasian Curlew	6	3	Mute Swan Whooper Swan Eurasian Teal Eurasian Curlew	4	3
Minimum P < 0.05 for one day	Mute Swan Northern Lapwing	2	2	Eurasian Wigeon Mallard Northern Pintail Northern Lapwing	4	2
Minimum P < 0.05 for one day after residual removal	Mallard Eurasian Curlew	2	2	Mute Swan Common Teal Mallard	3	2

## Chapter 15

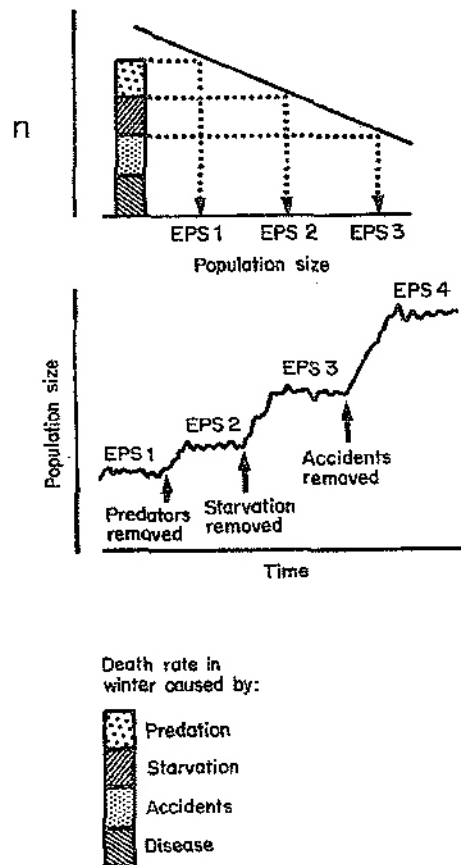
### Discussion

UK 1981-1983 and WeBS published and populations of this thesis are the same datasets but respective trends were computed differently as requirements were different.

Winter populations are theoretically affected by mortality rates that depended on action of four separate factors, predation, starvation, accidents and disease that acted additively in winter, shown in figure 1. On removal of each factor, the proportion dying declined so the equilibrium population moved from EPS1 to EPS4 at which only disease killed birds in winter (Goss-Custard 1993).

Figure 1

Factors controlling equilibrium population size in winter



(Goss-Custard 1993)

Numbers of UK sites monitored increased from 707 in 1981-1982 (Salmon 1982) to 1940 in 1994-1995 (Waters et al. 1996) and remained relatively stable until 2001 (Pollitt et al. 2003), thus WeBS datasets were more accurate and population differences were partly due to improved coverage (Jassby and Powell 1990; Mac Nally 1997). Anglers' toxic lead weights, ingested by foraging waterbirds, were prohibited from 1986 (Cranswick et al. 1999) and the 1995-1996 voluntary ban of lead shooting pellets (Cranswick et al. 1997) influenced populations.

Sources of survey bias included: (i) counts of large aggregations were estimated proportions (Cranswick et al. 1999); (ii) counts of wader flocks on estuaries were more accurate than wildfowl dispersed along coasts and inland; thus the latter datasets may not accurately reflect all relative abundances (Waters et al. 1996; Cranswick et al. 1999) and (iii) European and Russian breeding species may winter further east or west within Europe depending on weather conditions (Cranswick et al. 1999), producing inter-annual population variation. Population change was directly affected by mortality and recruitment (Pollitt et al. 2003).

Summaries of ranges for 1981-1983 and WeBS environmental variables are respectively:

- (i) 11-day term temperatures ranged above  $0^{\circ}\text{C}$  to  $-8.8^{\circ}\text{C}$  and  $0^{\circ}\text{C}$  to  $-9^{\circ}\text{C}$ ; intra-December 1981-January 1982 term temperatures declined for 23 days to  $-25.2^{\circ}\text{C}$  and over January-February 1982 for 12 days to  $-21.4^{\circ}\text{C}$ ;
- (ii) 4-day term wind velocities ranged from calm to near gale, 0-33 knots and calm to gale, 0-40 knots and
- (iii) 3-day water stage height term ranges from below bank top to high flood altitudes, 0-5.9 m and 0-5.8 m.

1981-1983 datasets are small and cautious interpretation is required (Jassby and Powell 1990). Annual population variation is described by logarithms to base 10.

Time series data analysis was based on few assumptions (James, McCulloch and Wiedenfeld 1996), including data precision and survey protocol compliance (Thomas 1996). Time series data yield was constrained by: (i) survey interval length; wide oscillations can be missed by wide intervals (Jassby and Powell 1990); (ii) omission of cycles beyond temporal scale (Thomas 1996) and lurking covariables (Barker and Sauer *in* McCulloch and Barrett 1992; Greenwood and Baillie 1991). Trend computation by subtraction of median from raw data was unlikely to produce artificial autocorrelation in variables' residuals (Jassby and Powell 1990). The median emphasizes trend (Green *in* Maddy and Brew 1995), an expression of seasonal equilibrium (Goss-Custard 1993). Causation can be detected from: (i) atypical outliers (Thomas 1996) and (ii) concomitant change with known perturbation (Jassby and Powell 1990).

Timing of migrants departure was interspecifically variable and influenced by *physiological condition and favourable weather* (Elkins 1988); subsiding air in anticyclones that divert frontal depressions to provide good visibility, advection of cold air in polar air mass, a food shortage supply signal and light winds with low drift risk probability (Sparks et al. 2002).

### **Mute Swan *Cygnus olor***

Surveys' UK autumn population trend peaks were attributable to arrival and residency of Continental immigrants in southeast England (Spray, Coleman and Coleman *in* Wernham et al. 2002) and to *herding of immatures and non-breeders at traditional sites* (Cramp et al, 1977; Ogilvie *in* Lack, Lack and Spencer 1986). The latter process caused population trend peaks in September 1981-1983 and in November during WeBS at mild temperatures. Ability to withstand low temperatures was demonstrated over December 1981-January 1982 with 23 days of severe weather to  $-25.2^{\circ}$  C when the population increased 2.5 fold but declined to zero over January-February 1982 when habitat re-froze, an energetic conflict (Kingsford and Norman 2002).



Greater abundances on transect C showed low temperature tolerance, for instance January 1997 10 days to  $-8.2^{\circ}$  C. Higher populations occurred at milder temperatures of longer duration, such as November 1998 only two days to  $-1^{\circ}$  C and conversely as indicated by absence in February 1998 five days to  $-10^{\circ}$  C, supporting the cold weather movement hypothesis (Cramp et al. 1977) due to reduction in food accessibility at lower temperatures and increase in metabolic rate (Rehfish, Insley and Swann 2003).

1981-1983 population trend peaked in light-moderate wind force trend of September and with a January sub-peak during joint highest wind force term and WeBS populations increased over September-November moderate force and conversely in January-April. In 1981-1983 greater abundances occurred during strong winds of moderate duration, such as January 1983 two days to 22-27 knots in contrast to the lower population of February 1983 one day to 28-33 knots.

During WeBS greater abundance occurred for short durations at high velocity winds, for example November 1998 one day to 28-33 knots as opposed to the lesser population of February 1995 two days to 17-21 knots, contrary to 1981-1983. Overall, greater abundances preferred slower winds for longer periods, less chill factor, for example October 2000 three days to 11-16 knots due to reduced energy expenditure (Rehfish, Insley and Swann 2003; Sparks et al. 2002).

1981-1983 Confluence population trend January sub-peak corresponded with the water stage height peak. 83% of above median abundances corresponded with flood altitudes and greater numbers occurred during high-medium floods, such as December 1982-January 1983, that provided heterogeneous foraging depths (Taft et al. 2002). Lower abundances were present in the low temperature flood events of January 1982 due to inadequate food resources and greater energy expenditure (Rehfish, Insley and Swann 2003).

WeBS transect C population trend peaked in November at low flood altitudes, a month's lag to the UK peak due to post breeding dispersal (Waters et al. 1996) and herd formation of immatures and non-breeders (Ogilvie *in* Lack, Lack and Spencer 1986). Post January population decline was attributable to adults return to minor water-breeding sites (Salmon 1983; Waters et al. 2002), diminution in flood altitudes and mortality of immatures (Spray, Coleman and Coleman *in* Wernham 2002).

67% of greater abundances corresponded with mainly medium-low flood altitudes, for example October 2000 low flood. Lesser abundances were twice as probable at non-flood altitudes, such as December 1996. Thus larger populations preferred temporary low-median flood altitudes, 2-4.9 m.

Surveys' greater median abundances preferred low-high flood altitudes (Paillison, Reeber and Marion 2002) was corroborated by 1981-1983 ANOVA highly significant results. Variable topographic altitudes resulted in heterogeneous water stage heights at higher flood altitudes that enabled populations to forage different habitats at various depths (Taft et al. 2002) to 50 cm. (Paillison, Reeber and Marion 2002) enabled by long neck and bill morphology (Colwell and Taft 2000; Kingsford and Norman 2002), for example upending to one metre, dipping to 20-45 cm. and co-existence of feeding and roosting conditions (Anderson and Smith 1999; Cramp et al. 1977). Peaks and greater abundances were often short duration (Waters et al. 1996), dispersing locally as Midland swans move short distances (Spray, Coleman and Coleman *in* Wernham et al. 2002) along the wetland continuum (Parkinson, Mac Nally and Quinn 1998). During non-flood altitudes small populations were present on the river Severn and on pools (Salmon 1983), some defending territories (Spray, Coleman and Coleman *in* Wernham 2002) and grazed Confluence pastures (Ogilvie *in* Lack, Lack and Spencer 1986) but on transect C abundant Tufted hair-grass *Deschampsia cespitosa* was unpalatable, which with continued ingestion of shot accounted for the WeBS marginal trend increase and 1981-1983 Confluence greater population but overall decline.

### **Whooper Swan *Cygnus cygnus***

Surveys' zero counts were predominant, thus infrequency (Lawton 1994), hence interpretation must be cautious. The majority of the UK population comprised the Icelandic population that winter exclusively in the British Isles and have mainly a northern Wirral-Humber distribution (Cranswick et al. 1999; Merne *in* Lack, Lack and Spencer 1986). The Scandinavian and Russian population had an eastern UK distribution (Cranswick et al. 1997).

1981-1982 severe winter, temperatures declined to  $-25.2^{\circ}$  C, deterred southern movement (Salmon 1982) due to increased energy requirement (Goss-Custard and Dit Durrell 1990). UK-Confluence population seasonal trend peaked in November and December-January respectively, the lag attributable to 1982-1983 mild autumn stopovers, consequently low population in England (Salmon 1983; Cranswick et al. 1997).

WeBS UK-transect C trend populations increased by 0.22 and declined 0.1 respectively, diminution of the latter was due to mortality and lack of recruitment to the sink population (Lawton 1994). UK-transect C seasonal population trends peaked in February, as aggregations formed at surveyed sites (Cranswick et al. 1999), and January respectively, attributable to mild autumn stopovers (Cranswick et al. 1997) and Shropshire being south of the Wirral-Humber northern limit (Rees et al. *in* Wernham et al. 2002).

Population's January peak lagged one month compared to the minimum temperature trend due to stopovers (Cranswick et al. 1997); subsequently, variables declined and the population dispersed locally (Cranswick et al. 1999). Greater abundances were low temperature tolerant, for example January 2001 seven days to  $-5.9^{\circ}$  C; higher populations of greater abundances occurred for shorter durations at lower temperatures, such as January 1995 four days to  $-9^{\circ}$  C but were absent over prolonged cold periods, such as January 1997 10 days to  $-8.2^{\circ}$  C when energy expenditure was greater and food resources were frozen (Goss-Custard and Dit Durrell 1990). 1981-1982 severe winter and 1997-1998 mild-wet winters'

populations' absence supported the ameliorating weather northern distribution theory (Pollitt et al. 2000).

1981-1983 Confluence December-January peak population trend occurred as winds increased from light to fresh, 1-21 knots. Greater abundances' tolerance extended to strong winds, 22-27 knots, as during January 1983.

WeBS transect C population trends peaked in January as winds increased from light to moderate, 1-16 knots, and declined in February as velocity increased to fresh. Greater abundances occurred at near gale velocities, 28-33 knots, for example November 1998 but the high populations of greater abundances occurred in slower winds as in January 1995 fresh winds, 17-21 knots.

Empirical evidence disclosed tolerance to higher velocities but greater populations were present during slower winds because of the reduced chill factor and less energy expenditure (Rehfish, Insley and Swann 2003; Sparks et al. 2002).

1981-1983 Confluence population trends corresponded with December-January low-high floods, 2-5 m and above. Greater abundances occurred at medium flood altitudes, 4-4.9 m, such as December 1982. Other abundances were zeros.

WeBS transect C population-water stage height trends peaked in January low flood altitudes and subsequent absence suggested local dispersal (Cranswick et al. 1999). 70% of greater abundances corresponded to flood altitudes, mainly low-medium floods, for example January 1995 low flood and occasionally during residual flooding. High floods (Isola et al.2000) and turbidity in shallow areas (Power et al. 1995) deterred foraging hence low populations or absence during such inundations, as in December 2000.

Preferred habitat was temporary low-medium floods, 2-4.9 m in heterogeneous topography that provided diverse foraging depths, exploitable



by long neck and bill morphology (Isola et al. 2003; Kingsford and Norman 2002), to one metre (Cramp et al. 1977) and secure roosting sites (Rees et al. *in* Wernham et al. 2002). Smaller abundances present at residual flooding and non-flood events support opinion of increased tendency to forage pasture and arable crops (Merne *in* Lack, Lack and Spencer 1986). Transect C sink population decline was due to mortality and lack of recruitment from the source population (Lawton 1994). Inter-generational annual occurrence (Brown, Mehlman and Stevens 1995) confirmed site fidelity (Rees et al. *in* Wernham et al. 2002).

### **Eurasian Wigeon *Anas penelope***

1981-1983 population trend peaked in March and the December sub-peak, the second coldest month, corresponded with the UK population trend. Greater abundances revealed low temperature tolerance, for example December 1982 six days to  $-6.9^{\circ}$  C; smaller abundances disclosed lower temperature tolerance of shorter duration, such as February 1983 three days to  $-8.8^{\circ}$  C. Lesser abundances decreased over December 1981-February 1982 *harsh conditions when frozen food resources and roosting sites induced cold weather movement* (Mitchell *in* Wernham et al. 2002); population synchronously increased with temperatures to March 1983 six days to  $-4.1^{\circ}$  C (Lawton 1994) as habitat thawed, thus population tracked food supplies (Goss-Custard and Dit Durrell 1990).

WeBS population trend increased over October-March as new arrivals aggregated with the residual population, indicative of site carrying capacity (Goss-Custard and Dit Durrell 1990). Population-temperature trends were opposite during January-March because: (i) a proportion of the population remained during most months on pools and selectively grazed pastures resulting in spring dietary improvement (Mayhew and Houston 1999); (ii) western and northern movements of *Scandinavian and Icelandic immigrants* respectively (Mitchell *in* Wernham et al. 2002) and (iii) surveys' February-March trend increase suggest return migration by northwest England population (Cranswick et al. 1997).

Greater abundances disclosed low temperature toleration, for example December 1998 nine days to  $-7.6^{\circ}$  C; higher populations of greater abundances withstood lower temperatures of shorter duration, for instance December 1999 four days to  $-9.8^{\circ}$  C. Relatively mild temperature preference was demonstrated by population increase during October-December 2000 three days to  $-3^{\circ}$  C because of reduced energy expenditure (Goss-Custard and Dit Durrell 1990) and foraging and roosting resources were available (Owen *in* Lack 1986). Contrastingly, December 1996-January 1997 16 days to  $-8.2^{\circ}$  C, frozen habitat induced a cold weather movement (Mitchell *in* Wernham et al. 2002) due to greater energy requirement (Rehfishch, Insley and Swann 2003).

High numbers over the surveys' durations indicated inter-generational return (Brown, Mehlman and Stevens 1995) and site fidelity (Mitchell *in* Wernham et al. 2002).

1981-1983 Confluence December population trend sub-peak lagged one month to the wind trend peak of November. Both variables declined in January-February and rose to seasonal March peaks. Greater and lesser abundances corresponded with higher and lower wind velocities respectively, for example March 1982 one day to near gale force, 28-33 knots, and March 1983 two days to moderate force, 11-16 knots. Greater abundance-stronger wind association indicated wind assisted flight, an energy conservation strategy (Sparks et al. 2002).

WeBS October-February population-wind force trends correspondingly increased to wind force fresh, 17-21 knots, except for the December decline, indicative of flight wind assistance. March-April population diminution lagged one-month wind force decline, suggesting temporal factor migration response rather than wind assistance. Greater abundances revealed high wind velocity tolerance, for example December 1999 two days to near gale force, 28-33 knots. Higher populations of greater abundances occurred at lower velocities, for instance December 2000 one day at moderate force, 11-16 knots.

Surveys' empirical evidence was opposite: in 1981-1983 greater abundances occurred in sheltered locations (Rehfishch, Insley and Swann 2003) to near gale force, thus enabling extended foraging time required by herbivorous species due to relative indigestibility of fibrous vegetation (Kingsford and Norman 2002), but during WeBS higher populations preferred open areas for predation detection (Colwell and Taft 2002) at lower velocities, reduced wind chill factor hence lower metabolic requirement (Rehfishch, Insley and Swann 2003); stronger winds constrained foraging and comfort activities (Ntiamao-Baidu et al. 1998); the former may be due to the small dataset. During neither survey did storm force winds occur to test the association under harsher conditions.

1981-1983 Confluence population trend peaked in March, a non-flood trend month, when birds foraged pastures adjacent to pools (Owen *in* Lack, Lack and Spencer 1986). Residual populations attracted passage birds to form aggregations for opportunistic social feeding (Paillison, Reeber and Marion 2002). 60% of greater abundances corresponded to flood events, such as November 1982-January 1983 low-high floods when heterogeneous topography enabled foraging in shallows (Colwell and Taft 2000); smaller populations-reduced wetland area association (Taft et al. 2002) occurred during non-flood events on residual flooding from the preceding month, as during February-January 1982. Energy expenditure increase (Taft et al. 2002) by shooting disturbance (Cranswick et al. 1999) was the probable cause of the majority of 80% of lesser abundances at mainly low flood altitudes, such as December 1982, the exception was the January 1982 high flood in severe weather when shooting was banned. Higher populations of March 1982 and 1983 were at non-flood altitudes and probably foraged wet grassland (Owen *in* Lack, Lack and Spencer 1986) enabled by short bill and leg morphology (Colwell and Taft 2000) and roosted on pools and the river.

WeBS transect C-water stage height seasonal trends closely mirrored the 1981-1983 patterns, except the flood trends were low altitudes, 2-3.9 m. 81% of greater abundances corresponded to flood altitudes (Owen *in* Lack, Lack and Spencer 1986), the balance during non-flood events grazed and roosted



on pools and the river. Small abundance-wetland area negative correlation was twice as probable at non-flood altitudes, such as January 1996; in flood events, as in November 1999 low flood, shooting disturbance was the likely cause of population decline (Musgrove et al. 2001) and sub-optimal use (Rehfishch, Insley and Swann 2003).

March population trend peak, at non-flood altitudes in the closed shooting season, lagged the UK peak three months, which suggested secure occupation of pools (Cranswick et al. 1997) and on residual flooding a few centimetres deep to forage and roost (Cranswick et al. 1997); late season improved herbage quality suited foraging wigeon (Mayhew and Houston 1999). The Ribble-Mersey-Dee Estuaries were the UK high population region (Pollitt 2003; Salmon 1982) and was probably the major source of the return migration. WeBS very highly significant ANOVA probability supported the greater abundance species-flood altitude relationship. Closely related Eurasian wigeon and Eurasian teal shared similar herbivorous diets but the former demonstrated greater behavioural foraging flexibility (Safran et al. 1997) in deeper water due to longer neck, leg and bill morphology (Colwell and Taft 2000).

#### **Eurasian Teal *Anas crecca***

1981-1983 Confluence seasonal population-temperature index seasonal trends showed broad correspondence and peaked in March. Greater abundances demonstrated low temperature tolerance, for example February 1983 three days to  $-8.8^{\circ}\text{C}$ ; higher populations of greater abundances occurred at higher temperatures, such as March 1983 population of 446 three days to  $-4.9^{\circ}\text{C}$ , thus ameliorating conditions were preferred (Pollitt et al. 2003) due to less energy expenditure (Rehfishch, Insley and Swann 2003). Prolonged harsh conditions, induced cold weather displacement (Pollitt et al. 2003), for example lesser abundances declined from 54 to 15 during December 1981-January 1982 at temperatures to  $-25.2^{\circ}\text{C}$  but increased to 122 in the February 1982 window of milder weather; high mobility enabled rapid response to changing perturbations conditions (Ogilvie in Wernham et al. 2002) to track food availability (Goss-Custard and Dit Durrell 1990).

WeBS population-temperature index seasonal trends peaked February compared to the UK's December. Greater abundances demonstrated low temperature tolerance, for example February 1996 five days to  $-10^{\circ}$  C but over severe conditions of January 1997, 10 days to  $-8.2^{\circ}$  C the population declined to zero. Greater populations occurred at relatively mild temperatures, such as December 2000 three days to  $-3^{\circ}$  C, thus preferred milder conditions. Sequential greater abundances, as over October-December 2000 0-3 days to  $-3^{\circ}$  C, indicated higher temperature preference because of reduced energy expenditure, increased food accessibility (Goss-Custard and Ditt Durrell 1990) and habitat suitability (Brown, Mehlman and Stevens 1995).

Seasonal population trends: (i) March 1981-1983 peak was due to dispersal of the northwest England population (Salmon 1983) and females from the south (Ogilvie *in* Lack, Lack and Spencer 1986); (ii) February peak was attributed to arrival of the western influx of the Scandinavian-Russian population; (iii) WeBS north western England population spring diminution (Pollitt et al. 2003) mirrored transect C's trend population compared to the greater 1981-1983 population and (iv) intermittent influxes aggregated with monthly residual populations. Late winter population peaks characterized seasonality. High mobility enabled frequent synchronous abundance-local perturbation variations (Lawton 1994), cold and mild temperatures (Ogilvie *in* Wernham et al. 2002; Pollitt et al. 2003). Late season trend decline and lower abundances supported the post February non-return of populations' theory (Ogilvie *in* Wernham et al. 2002) *in* WeBS but not during 1981-1983.

1981-1983 seasonal population trend December sub-peak lagged the November joint highest wind force trend, indicative of wind assisted migration (Sparks et al. 2002). Greater abundances correlated with strong wind forces of brief duration, for example November 1982 two days to near gale force, but abundance was reduced in March 1982 over three days of strong-near gale force velocities when sheltered habitat was sought. March 1983 higher population of greater abundances occurred during two days of moderate winds. Thus winds to near gale force were tolerated for two days but over

longer periods populations diminished (Ogilvie *in* Wernham et al. 2002) due to increased energy budget requirement and diminished food accessibility (Rehfishch, Insley and Swann 2003).

WeBS transect C November sub-peak corresponded with autumnal stronger winds; the pattern was repeated over December-February to February peaks, evidence of wind assisted passage (Sparks et al. 2002). Greater abundances corresponded with short duration higher velocities, for instance November 1998 one day to near gale force, and were often continuous for some months, such as October 1999-March 2000 one day per month maximum to gale force, suggesting relatively stable population (Waters et al. 1998) and herbivores were less affected by wind than insectivores (Colwell and Taft 2000), such as lapwing. Often larger populations were associated with lower velocities, such as January 1995 population of 1,200 one day to fresh winds. Sequential greater abundance decline during longer episodes of forceful winds was indicative of tolerance limitation (Ogilvie *in* Lack, Lack and Spencer 1986), as over February-March 1996 three days of strong winds population 700-34 decline due to chill factor and resulting increased energy requirement (Goss-Custard and Dit Durrell 1990). Teal, a high mobility species, carry small fat reserves and react quickly to temperature and wind change (Goss-Custard and Dit Durrell 1990) to sustain energy demands (Kingsford and Norman 2002).

1981-1983 October-March seasonal population overall trend increase during the November-February flood trend phase testified that the flooded heterogeneous topography with diverse shallow foraging depths was preferred habitat (Colwell and Taft 2000). March population peak, a non-flood term, was preceded by November-February flood terms; the population foraged wet grassland and roosted on pools and in dense vegetation (Cramp et al. 1977), notably tufted hair-grass *Deschampsia cespitosa*.

67% of greater abundances corresponded with flood altitudes, as during November 1982-February 1983 low-high flood altitudes; on recession turbidity diminished and vegetation was deposited, a food resource, (Power et al.

1995); the 33% balance at non-flood altitudes, the preceding term was often a flood event, such as February-March 1983. Sequential lesser abundances during November 1981-February 1982 flood events were partly caused by December 1981-January 1982 population decline due to frozen habitat but numbers increased in the February 1982 thaw, supporting the rapid site return hypothesis (Ogilvie *in* Wernham et al. 2002) as food accessibility increased (Goss-Custard and Dit Durrell 1990).

WeBS population trends show that immigrants arrived with the onset of November flooding that continued to February but populations decreased over December-January, probably due to hunting disturbance (Ogilvie *in* Wernham et al. 2002) and peaked in February, closed shooting season and on dispersal of the Mersey-Dee-Ribble Estuaries population (Pollitt et al. 2003) and lagged the January water stage height low flood peak. 78% of greater abundances occurred during flood altitudes and 50% were sequential, for example October 1999-March 2000 and October-December 2000 at predominantly low floods that short neck morphology permitted surface and bottom feeding (Colwell and Taft 2000); a proportion of abundances at non-flood events were preceded by a flood incident term, for instance November-December 1998 medium-low flood. Lesser abundances were more than twice as probable during non-flood altitudes, for example January 2001, due to wetland area reduction (Paillisson, Reeber and Marion 2002) and consequential food supply diminution (Goss-Custard and Dit Durrell 1990).

Extensive, eutrophic flooding attracted populations (Cramp et al. 1977; Ogilvie *in* Lack, Lack and Spencer 1986) that fed in shallowly flooded pastures (Ogilvie *in* Wernham et al. 2002) of clear water (Power et al. 1995) and roosted on pools and in taller vegetation (Cramp et al. 1977) during non-flood altitudes. Closely related Blue winged-teal *Anas discors* preferred under 10 cm depth of open water (Islola et al. 2000) but 5-25 cm depth on flooded grassland (Taft et al. 2002). Density was positively correlated with open water, topographic variation and population increased with area (Goss-Custard and Dit Durrell 1990). Foraging depth was correlated with culmen (Isola et al. 2000) and neck and leg lengths (Colwell and Taft 2000). WeBS



significant probability supported the greater abundance-flood altitude relationship.

### **Mallard *Anas platyrhynchos***

The northwest England and north Wales population was the UK's most important (Pollitt et al. 2003) holding 9%-14% of the UK's monthly 1981-1982 population (Salmon 1982).

1981-1983 Confluence seasonal population-temperature trends peaked in December and March respectively. Westward migration during declining temperatures caused the December population peak, the UK's peak lagged one month. Greater abundances revealed low temperature tolerance, for example February 1983 three days to  $-8.8^{\circ}$  C but the January 1983 population was greater and temperature above  $0^{\circ}$  C, thus milder temperature preference. The December 1981-January 1982 229-37 population decline demonstrated intolerance to prolonged severe low temperatures and the resultant residual population had high site fidelity, some were locally reared and released birds (Mitchell, King and Cook in Wernham et al. 2002).

WeBS population-temperature seasonal trends peaked in November, the UK's lagged one month, and December respectively. Subsequent declines were partly due to first year birds' high mortality and shooting (Waters et al. 1996). Greater abundances disclosed low temperature tolerance, for instance February 1996 five days to  $-10^{\circ}$  C. Higher populations of greater abundances were more frequent with milder weather, such as February 2000 one day to  $-0.6^{\circ}$  C, thus higher temperature preference due to greater food availability and reduced energy expenditure (Goss-Custard and Dit Durrell 1990).

1981-1983 Confluence December population peak lagged increasing wind velocity of October-November. Greater abundances disclosed tolerance to higher wind velocities of short duration, for example January 1983 two days to force strong, 22-27 knots, and probably aggregated in sheltered locations (Rehfish, Insley and Swann 2003).

WeBS transect C November population trend peak and February sub-peak were associated with preceding periods of increasing wind velocities and subsequent corresponding population-wind force decline that suggested wind assisted migrations (Sparks et al. 2002). November and February high populations were respectively westward and return migrations from the high northwest England concentration (Cranswick et al. 1997; Pollitt et al. 2003).

Greater abundances revealed tolerance to strong winds, such as February 2000 two days to force strong, 22-27 knots. Conversely, higher populations were associated with less forceful winds of shorter duration, for example January 1995 one day to force fresh, 17-21 knots. The October 1999 500 high population during four days at fresh-moderate winds, 11-21 knots indicated aggregation of local flocks in sheltered locations to minimize energy expenditure and to increase accessibility (Rehfish, Insley and Swann 2003).

1981-1983 Confluence population trend December peak corresponded with increased low flood altitudes; population declined from December as flood altitudes rose to high flood levels, because of preferred foraging depth area reduction (Taft et al. 2002) and turbidity (Power et al. 1995). 83% of greater abundances sequentially corresponded with low flood altitudes of October-November 1981 and low-high floods during December-February 1983; remaining 17% during March 1983, a non-flood term, received residual flooding and vegetation deposition, a food resource (Power et al. 1995), from the February 1983 high flood. Mid-winter lower abundances occurred during low-high flood altitudes, such as the prolonged freezing conditions of December 1981-January 1982, when food resources were unavailable (Goss-Custard and Dit Durrell 1990) and November 1982 low floods, probably resulting from shooting disturbance (Mitchell, King and Cook in Wernham et al. 2002).

In contrast to 1981-1983, WeBS transect C population trends displayed a bimodal distribution. Low September-October population trend comprised sedentary birds (Mitchell, King and Cook in Wernham et al. 2002); November-February greater populations were associated with low floods (Salmon 1983).

Western movement of immigrants, attracted by flocking (Brown, Mehlman and Stevens 1995 and flooding (Salmon 1983), resulted in the November peak. February sub-peak occurred during the dispersal of the Dee-Martin Mere-Morcambe Bay population and during receding low flood altitudes (Pollitt et al. 2002) when vegetation, food supplies, were deposited (Paillison, Reeber and Marion 2002). 78% of greater abundances corresponded with flood altitudes, such as October 1999 low flood; remaining 22% at non-flood altitudes were usually smaller populations, for instance December 1996 population of 24, an indication of the sedentary population size and restricted food resources (Paillison, Reeber and Marion 2002).

Greater populations preferred low floods, (Salmon 1982; Mitchell, King and Cook *in* Wernham et al. 2002) 2-3.9 m deep, clear (Power et al. 1995), open water (Colwell and Taft 2000) and in heterogeneous topography of diverse habitats (Taft et al. 2002). Short neck and leg morphology constrained foraging depth to 13-25 cm but less precisely compared to teal because of larger size (Colwell and Taft 2000) and omnivorous diet (Cramp et al. 1977), thus greater feeding ecology flexibility (Safran et al. 1997). Fast floodwater discharge rate and population declines were synchronous (Lawton 1994; Taft et al. 2002) and population size increased with low flooded altitude area (Paillison, Reeber and Marion 2002), contrary to the findings of Colwell and Taft (2000), because of respective food supply diminution and increase (Paillison, Reeber and Marion 2002). Surveys' significant ANOVA probabilities supported the greater abundance-flood altitude relationship.

Aggregation of immigrants with local flocks occurred under preferred conditions (Salmon *in* Lack, Lack and Spencer 1986). Post mid-winter population diminution was caused by first year birds' high mortality, dispersal to breeding sites (Waters et al. 1996) and shooting (Salmon *in* Lack, Lack and Spencer 1986).

#### **Northern Pintail *Anas acuta***

1981-1983 high proportion of zeros in transects' datasets was symptomatic of small abundance and infrequency (Lawton 1994), for example absent in



December 1981-January 1982 freezing conditions to avoid starvation (Goss-Custard and Dit Durrell 1990). Lower population abundances demonstrated low temperature tolerance, for example February 1983 three days to  $-8.8^{\circ}\text{C}$  but greater populations occurred for longer durations at higher temperatures, such as March 1982 six days at  $-4.1^{\circ}\text{C}$ .

WeBS transect C and the Northwest England population decreases were synchronous, for example the river Mersey population declined from 59% to 2.4% of the UK population over 1981-2001 (Salmon 1982; Pollitt et al. 2003).

Transect C post 1997 zeros reduction supports theory of increased abundance and frequency (Lawton 1994). In contrast to 1981-1983, WeBS had a bimodal seasonal population trend distribution: November sub-peak was due to southern movement of the Icelandic population (Cranswick et al. 1999) that corresponded with the October-November temperature decline. Transect C population peaked in January, western movement of the Scandinavian-Russian population (Cranswick et al. 1999; Pollitt et al. 2000), that lagged one month the temperature decline.

Greater abundances displayed short term low temperature endurance, for example February 1996 five days to  $-10^{\circ}\text{C}$ ; greater frequencies occurred at relatively mild temperatures, for example the November 2000 population of 320, surpassing qualifying level of national importance (Pollitt et al. 2003), two days to  $-2.7^{\circ}\text{C}$  and for November-December 2000 three days to  $-3^{\circ}\text{C}$ .

Seasonal population double peaks, autumn and winter, were unusual because of different arrival dates of Icelandic and continental populations (Ogilvie *in* Wernham et al. 2002). Populations preferred ameliorating weather close to  $0^{\circ}\text{C}$  (Ogilvie *in* Wernham et al. 2002) to facilitate foraging and roosting on open water (Colwell and Taft 2002) and reduced energy requirement (Goss-Custard and Dit Durrell 1990).

1981-1983 Confluence population trend February arrival occurred as wind velocity diminished but both correspondingly increased to the March

population peak. Median abundances revealed equal probability of occurrence during higher and lower wind velocities, such as February 1983, one day to near gale force, and February 1982 three days to moderate gale force.

WeBS transect C November and January population trend sub-peak and peak corresponded with autumnal and winter wind force increases respectively. Post January, the variables were opposite. Thus movements were possibly wind aided. Greater abundances disclosed high velocity tolerance, for instance December 1999 320 population for two days to near gale force, 28-33 knots. Smaller populations tended to occur at lower velocities, such as March 1996 three days to force fresh, 17-21 knots. Populations aggregated (Ogilvie *in* Wernham et al. 2002) in protected areas to minimize energy expenditure (Rehfishch, Insley and Swann 2003) during stronger winds (Goss-Custard and Dit Durrell 1990).

Frequent population fluctuations were attributable to high mobility (Cranswick et al. 1999) in response to wind force variation and resulted in inter-site movements (Ogilvie *in* Wernham et al. 2002). WeBS post January higher population trends suggested dispersal of the northwest England-north Wales population to exploit inland sites (Pollitt et al. 2003). Inter-generational annual occurrence (Brown, Mehلمان and Stevens 1995) indicated lowland preference (Pollitt et al. 2003) and site fidelity.

1981-1983 Confluence population-water stage height seasonal trends peaked in March and January respectively. 75% of median abundances occurred during non-flood altitudes and were on open, shallow pools suited to foraging (Colwell and Taft 2000) and predator detection (Brown, Mehلمان and Stevens 1995; Goss-Custard and Dit Durrell 1990).

WeBS transect C November sub-peak corresponded with autumnal increasing water stage heights to the commencement of November low floods and dynamically corresponded to January peaks.

Greater abundances corresponded to lower flood altitudes, such as February 1996 and low-medium flood of November 2000. Lesser abundances were associated with the January 1998 high flood due to greater turbidity (Power et al. 1995) and neck length morphological foraging constraint (Colwell and Taft 2000). Shallowly flooded heterogeneous topography provided diverse habitats (Taft et al. 2002) to preferred foraging depths of 10-20 cm (Isola et al. 2000) and to 5-25 cm on flooded grassland (Taft et al. 2002), indicating feeding ecology flexibility (Safran et al. 1997). Populations increased with flooded area, such as November 2000, contrary to the findings of Colwell and Taft (2000); greater area reduced intraspecific competition (Goss-Custard and Ditt Durrell 1990). The WeBS ANOVA highly significant probability supported the greater abundance-flood altitude relationship.

#### **Northern Lapwing *Vanellus vanellus***

1981-1983 UK trend data was only available for December-February annually. Overall autumnal temperature diminution induced cold weather western movements (Pollitt et al. 2003) and along the river Severn flyway to traditional Shropshire wintering sites (Wright 1983) producing a December population peak and low temperature sub-peak (Brown, Mehlman and Stevens 1995). Greater abundances disclosed short-term low temperature tolerance, such as December 1982 six days to  $-6.9^{\circ}$  C, on preferred pasture foraging sites (Fuller in Lack, Lack and Spencer 1986). Brief periods of relatively ameliorating temperatures, for instance January 1983 when all days were over  $0^{\circ}$  C, populations were dispersed over primary and secondary sites due to intraspecific competition (Goss-Custard and Ditt Durrell 1990; Rehfish, Insley and Swann 2003). Population rose during the December 1981-January 1982 severe conditions but declined to zero over January-February 1982 as feeding areas re-froze and invertebrate prey were inaccessible and metabolic rate increased (Rehfish, Insley and Swann 2003), reverse correspondence to the UK trend was caused by cold weather movement to coasts; nationally many lapwing died (Salmon 1982).

With declining temperatures transect C autumnal population trends increased to a November sub-peak; temperatures declined to December, habitat froze,

invertebrate activity diminished (Rehfishch, Insley and Swann 2003), visual feeding was prevented (Ntiamao-Baidu et al. 1998) and this produced cold weather movement to the coast (Cranswick et al. 1999). Adult survival was correlated to temperature (Peach, Thompson and Coulson 1994; Appleton *in* Wernham et al. 2002). January transect-UK population peaks lagged one month to minimum temperature as western movements of immigrants aggregated with local flocks (Pollitt et al. 2000), an indication of site carrying capacity (Goss-Custard 1993).

Greater abundances demonstrated short term low temperature tolerance, for example February 1996 five days to  $-10^{\circ}$  C; populations were more frequent, often larger and more widely distributed, due to intraspecific competition as adults and dominants were aware of better foraging sites (Rehfishch, Insley and Swann 2003), under ameliorating conditions, such as January 1998 when all term days were above  $0^{\circ}$  C, hence greater activity of prey (Goss-Custard and Dit Durrell 1990).

Regular winter occurrence supported the site fidelity theory. Regular movements were high mobility responses to temperature variation (Goss-Custard and Dit Durrell 1990; Peach, Thompson and Coulson 1994) and consequential opportunistic social feeding (Fuller *in* Lack, Lack and Spencer 1986).

Confluence seasonal population grew over the autumn to peak in December, a western movement of immigrants flocked with residents as wind forces increased to November. The December-February population was relatively stable and subsequently declined on emigration commencement as wind strength rose.

Greater abundances revealed brief duration, high wind tolerance, for example January 1983 two days to force strong. The abundance was equally frequent for shorter periods of stronger winds as during February 1983 one day to near gale force, and longer periods of slower winds, March 1983 two days to



moderate force. Populations were more frequent for short duration, one-two days, to wind force fresh.

WeBS transect C November population trend sub-peak attainment was for the same reasons as the 1981-1983 trend maximum during autumnal wind force increase. January peak corresponded with rising wind force, wind assisted movement (Sparks et al. 2002). Both surveys' populations departed from February for breeding grounds (Appleton *in* Wernham et al. 2002). Greater abundances disclosed tolerance to short-term high velocities, for instance November 1998 one day to near gale force. Larger populations of greater abundances were more frequent at slower velocities, such as December 1997 one day to moderate force and sequentially, for example January-February 1995 to fresh force, because of reduced chill factor and reduced energy expenditure and increased prey accessibility (Goss-Custard and Dit Durrell 1990).

1981-1983 Confluence seasonal population trends autumnal increase corresponded with rising water stage heights over October-January. The population peaked in the December low flood that provided soft substrate suitable for foraging (Ntiamoa-Baidu et al. 1998); population declined consequent to the January high flood because deep water reduced foraging habitat area, constrained by leg length (Colwell and Taft 2000) and prey reduction (Goss-Custard and Dit Durrell 1990); different benthic invertebrate species inhabit different depths (Safran et al. 1997). Population-water stage height January-February decline to low flood altitudes coincided with commencement of prompt emigration (Appleton *in* Wernham et al. 2002). Populations were responsive to perturbations (Pollitt et al. 2003), for example February 1982 absence due to frozen residual flooding and inaccessible prey (Rehfish, Insley and Swann 2003).

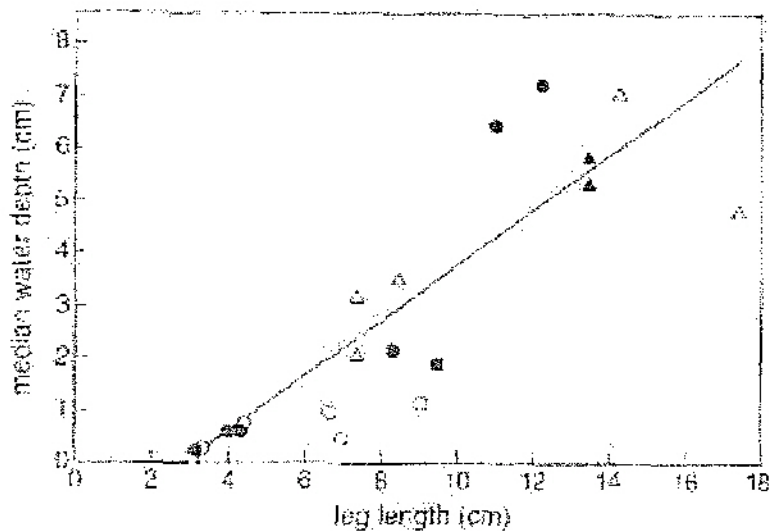
83% of greater abundances corresponded with flood altitudes, for instance November 1982-February 1983 low-high flood altitudes when prey was flushed from vegetation (Ntiamoa-Baidu et al. 1998); smaller populations, probably less experienced birds (Rehfish, Insley and Swann 2003), occurred

during mainly frozen, low floods, such as November-December 1981 and at non-flood events, for example February-March 1982.

WeBS transect C variables had corresponding bimodal distributions with November and January sub-peak and peak, corresponded with UK trend, respectively because immigrants' aggregated with residents (Niemuth and Solberg 2003). 57% of the 68% of greater abundances occurred during medium-low flood altitudes, such as January 1995, as soft substrate is the preferred foraging habitat (Ntiamoa-Baidu et al. 1998); smaller populations were present at non-flood events, for example March 1999, except 170 in January 1996; absence was most probable during non-flood events, for instance October 1996-February 1997.

Preferred habitat was shallowly flooded grassland (Fuller *in* Lack, Lack and Spencer 1986) that released invertebrate prey (Ntiamoa-Baidu et al. 1998). Species of the same taxonomic guild (Brown, Mehlman and Stevens 1995) and similar morphology, for example Killdeer *Charadrius alexandrinus* and Black-bellied plover *Pluvialis squatarola*, preferred flooded grassland water depth under 15 cm (Taft et al. 2002), which correlated to leg length (Colwell and Taft 2000; Ntiamoa-Baidu et al. 1998), shown on figure 2, an eco-morphological pattern (Taft et al. 2002), and visual feeders, such as Grey plover *Pluvialis squatarola*, to 6 cm (Ntiamoa-Baidu et al. 1998). Lesser abundances occurred during deeper floods, due to habitat and food supply reductions (Power et al. 1995) when opportunistic foraging (Fuller *in* Lack, Lack and Spencer 1986) occurred along the water's edge (Colwell and Taft 2000) due to leg length and tactile, visual and auditory foraging constraints (Cramp et al. 1983). During non-flood events traditional grassland sites were foraged for invertebrate prey (Fuller *in* Lack, Lack and Spencer 1986). Surveys' significant ANOVA probabilities supported the greater abundance-flood altitude relationship.

Figure 2  
Water depth as a function of leg length



Water depths selected by foraging waders as a function of exposed leg length in different species (Ntiamoa-Baidu et al. 1998).

#### **Eurasian Curlew *Numenius arquata***

Copious zeros in transects' datasets between September-January showed small abundance and infrequency (Lawton 1994). 1981-1983 UK trend data was only available for December-February annually.

UK-Confluence seasonal populations peaked in February. Seasonal population-temperature peaked in March on return migration from coastal wintering sites (Salmon 1983). Greater abundances demonstrated short term low temperature tolerance, for example February 1983 three days to  $-8.8^{\circ}\text{C}$ ; but were at greater frequencies and at relatively milder temperatures, such as March 1983 three days to  $-4.9^{\circ}\text{C}$  but lesser abundances were during longer periods of frozen conditions that prevented probe and tactile foraging (Cramp et al. 1983; Ntiamoa-Baidu et al. 1998), such as March 1982 six days to  $-4.1^{\circ}\text{C}$ , when food supplies, such as worms, (Bainbridge *in* Wernham et al. 2002) were inaccessible. (Rehfish, Insley and Swann 2003).



WeBS UK-transect C seasonal population trends, compared over December-February window, peaked in February and overall on transect C in March, when there was saturated substrate consequent to winter flooding. The latter peak was due to emigration of west coast concentrations and UK residents return to natal areas (Bainbridge *in* Wernham et al. 2002).

Transect C populations peaked in March and sub-peaked in February, as temperatures seasonally rose. Greater abundances demonstrated short term low temperature tolerance, for example February 1996 five days to  $-10^{\circ}$  C; *more frequent and often larger populations of greater abundance occurred at higher temperatures, such as March 1997 40 population at two days to  $-3.3^{\circ}$  C, as prey mobility increased and energy expenditure declined (Goss-Custard and Dit Durrell 1990).*

The UK population winters mainly on the western English coasts (Bainbridge *in* Wernham et al. 2002), *an indication of high food abundance (Goss-Custard and Dit Durrell 1990); Morecambe Bay- Dee Estuary population comprised 19.4% of the 1999-2000 UK population (Musgrove et al. 2001). UK seasonal population temporal and spatially asymmetrical distributions masked local inland distributions (Cranwick et al. 1997) where males were more probable (Bainbridge *in* Lack, Lack and Spencer 1986), especially on wet grassland during milder weather. Earthworms and invertebrates were inaccessible during freezing temperatures (Rehfish, Insley and Swann 2003) when cold weather movements ensued (Bainbridge *in* Wernham et al. 2002), such as February-March 1999, due to increased energy requirement (Rehfish, Insley and Swann 2003). Post August inland passage was rare and site fidelity high with little movement. There was a post January return to breeding sites (Bainbridge *in* Wernham et al. 2002).*

Confluence seasonal population-wind forces increased to February-March with a spring population peak. Small populations tolerated forceful winds, for instance November 1982 two days to gale force, high chill factor and diminished prey accessibility (Goss-Custard and Dit Durrell 1990), conversely, higher populations were associated with lower velocities, such as March 1983

two days to moderate force, hence increased prey accessibility and decreased metabolic rate (Rehfisch, Insley and Swann 2003), or shorter duration and stronger winds, such as February 1983 one day to near gale force.

In the WeBS December-February window, population-wind force peaks were in February and December respectively with the overall population peak in March. Greater abundances disclosed population tolerance of moderate wind forces, for example February 1996 three days to force strong, because of prey availability and reduced metabolic rate (Rehfisch, Insley and Swann 2003). Smaller populations occurred at weaker forces, for example February 1998 two days to force fresh, or briefer periods at greater velocity, as during March 1999 one day to force strong.

Surveys' greater abundances demonstrated tolerance to higher velocities but *in reverse correspondence*; the broad tendency was for slower winds during which populations were greater in 1981-1983 and smaller in WeBS, a reflection on the UK and transect C population declines. Coastal distribution (*Bainbridge in Wernham et al. 2002*) resulted in September-January absence inland.

1981-1983 Confluence population-water stage height seasonal trends peaked in March and January respectively. 60% of greater abundances occurred during low-high flood altitudes, for example February 1983 high-low flood; of the remaining 40% at non-flood altitudes, half were preceded by flood event terms, soft substrate in cold months facilitated tactile foraging (*Ntiamoa-Baidu et al. 1998*), for instance February-March 1983.

WeBS transect C population-water stage height seasonal trends peaked in March and January respectively. Greater abundances were between January-April of which half had larger populations at low flood altitudes. Long leg and bill morphology enabled wading to 10 cm (*Ntiamoa-Baidu et al. 1998*), for example the March 1995 124 population at low flood altitudes compared to the balance at non-flood events, such as March 1997 40 population as harder

substrate had fewer accessible prey (Rehfish, Insley and Swann 2003). Flood incident preference was demonstrated by February-March 1999 low flood-non-flood 50-24 population decline. Different zones of flooded heterogeneous topography was inhabited by different benthic invertebrate prey, thus flood land provided a wide food resource spectrum (Safran et al. 1997)

Infrequency over September-January demonstrated transitory site usage (Taft et al. 2002) and improbability of post August return (Bainbridge *in* Wernham et al. 2002). Post January population return was from the Morecambe Bay-Dee-Ribble Estuaries population (Musgrove et al. 2001), some to natal sites (Pollitt et al. 2000). Variable population dynamics demonstrated flexible behaviour in response to the ephemerality of the floodplain (Taft et al. 2002).

Saturated substrate was necessary for bill probing (Cramp et al. 1983). For species with similar morphology, such as Greater and Lesser yellowlegs *Tringa melanoleuca* and *Tringa flavipes* and Long-billed and Short-billed dowitchers *Limnodromus scolopaceus* and *Limnodromus griseus* there was a negative correlation between presence and water depth (Colwell and Taft 2000); for these species and Long-billed curlew *Numenius americanus* under 15 cm water was the optimal average depth (Taft et al. 2002) but 10 cm for Eurasian curlew in Ghana (Ntiamao-Baidu et al. 1998) determined by tarsus length (Colwell and Taft 2000). Saturated pasture was preferred habitat where favoured prey of earthworms was abundant (Bainbridge *in* Wernham et al. 2002). Extensive dense sward of tufted hair-grass deterred bill penetration, secondary habitat (Goss-Custard and Dit Durrell 1990). A multi-wetland complex of alternatively flooded sub-sites for food supply replenishment would attract greater numbers (Taft et al. 2002) of Eurasian curlew.

Individuals demonstrate intraspecific tolerance variation to extremes environmental perturbations, foraging depths being a conspicuous example (Colwell and Taft 2002).

## Chapter 16 Conclusion

Environmental perturbation extremes in relation to greater abundance occurrence are compared to access tolerance range, shown on tables 108 to 110. Perturbations in north temperate winters are stressful to birds due to high metabolic requirements and limited food resources that affect survival (Rehfish, Insley and Swann 2003). Waterbirds respond to perturbations (Power et al. 1995) to minimize starvation risk (Goss-Custard and Dit Durrell 1990).

### Temperature

Temperature ranges are shown on table 108.

Table 108

Species greater abundances and temperature range

Species	Temperature Range			
	1981-1983 Range		WeBS Range	
	Temp ° C Minimum	Temp ° C Maximum	Temp ° C Minimum	Temp ° C Maximum
Mute Swan	(3) -8.8	(2) -1.4	(10) -8.2	(0) +0
Whooper Swan	(6) -6.9	(0) +0	(4) -9	(2) -1
Eurasian Wigeon	(6) -6.9	(0) +0	(9) -7.6	(0) +0
Eurasian Teal	(3) -8.8	(0) +0	(5) -10	(0) +0
Mallard	(3) -8.8	(0) +0	(5) -10	(0) +0
Northern Pintail	(3) -8.8	(2) -1.8	(5) -10	(0) +0
Northern Lapwing	(3) -8.8	(0) +0	(5) -10	(0) +0
Eurasian Curlew	(3) -8.8	(0) =0	(5) -10	(1) -0.6

(number): number of days below 0° C during which the lowest was temperature recorded

Greater abundances generally tolerated low temperatures of short duration but smaller species with low fat reserves were more mobile than larger



species (Lawton 1994), due to short term larger metabolic requirements, for example over January-February 1995 population of Eurasian teal declined when Mute swan increased. Over prolonged periods of freezing temperatures populations diminished, such as Mute swan and Northern lapwing in December 1981-February 1982. Temperature rise to approximately 0° C was associated with higher populations but markedly above 0° C distributions were less clumped due to intra and interspecific competition as food accessibility increased further (Goss-Custard and Dit Durrell 1990), adults and dominants defended better foraging sites (Rehfishch, Insley and Swann 2003).

### Wind Force

Wind force tolerance ranges are shown in table 109

Table 109  
Species greater abundances and wind force range

Species	Wind Force Range							
	1981-1983 Range				WeBS Range			
	Minimum		Maximum		Minimum		Maximum	
	Wind Index	Force knots	Wind Index	Force knots	Wind Index	Force knots	Wind Index	Force knots
Mute Swan	2 (2)	11-16	5 (1)	28-33	2 (1)	11-16	5 (1)	28-33
Whooper Swan	3 (2)	17-21	4 (2)	22-27	2 (4)	11-16	6 (1)	34-40
Eurasian Wigeon	3 (2)	17-21	5 (2)	28-33	2 (2)	11-16	6 (1)	34-40
Eurasian Teal	2 (2)	11-16	5 (2)	28-33	1 (3)	0	6 (1)	34-40
Mallard	2 (2)	11-16	5 (1)	28-33	2 (2)	11-16	5 (1)	28-33
Northern Pintail	2 (2)	11-16	5 (1)	28-33	2 (1)	11-16	5 (1)	28-33
Northern Lapwing	2 (2)	11-16	5 (1)	28-33	2 (2)	11-16	5 (1)	28-33
Eurasian Curlew	2 (2)	11-16	5 (1)	28-33	2 (2)	11-16	4 (3)	22-27

(number): number of days of above median wind index force

Greater wind force increased wind chill factor resulting in prey accessibility decline, thus energy intake rate was reduced (Rehfishch, Insley and Swann 2003). Greater abundances tolerated higher wind velocities for brief periods but larger populations were more frequent for longer periods at lower forces, for example Eurasian wigeon during January 1998 compared to February 1995 and Northern lapwing in January 1998 compared to January 1995 respectively due to reduced energy expenditure and increased food accessibility at slower forces (Rehfishch, Insley and Swann 2003). During nominal forces intra and interspecific competition correspondingly increased with food accessibility, for example Eurasian teal in January-February 2000.

### Water Stage Heights

Table 110 shows water stage heights tolerance ranges.

Table 110

Species greater abundances and water stage heights

Species	Water Stage Height Range							
	1981-1983 Range				WeBS Range			
	Minimum		Maximum		Minimum		Maximum	
	Class	Ht m	Class	Ht m	Class	Ht m	Class	Ht m
Mute Swan	bbt	–	hf	5 m	bbt	–	hf	5 m
Whooper Swan	lf	2 - 3.9	hf	5 m	bbt	–	hf	5 m
Eurasian Wigeon	bbt	–	hf	5 m	bbt	–	hf	5 m
Eurasian Teal	bbt	–	hf	5 m	bbt	–	hf	5 m
Mallard	bbt	–	hf	5 m	bbt	–	hf	5 m
Northern Pintail	lf	2 - 3.9	hf	5 m	lf	2 - 3.9	hf	5 m
Northern Lapwing	bbt	–	hf	5 m	bbt	–	hf	5 m
Eurasian Curlew	bbt	–	hf	5 m	bbt	–	lf	2 - 3.9

bbt: below bank top, non-flood event; lf: low flood; hf: high flood

Population trends increased correspondingly through the autumn with water stage heights, except Eurasian curlew. Populations demonstrated tolerance from below bank top to high flood inundations, except Northern pintail.

Flooded heterogeneous topography provided diverse depths and habitats that were interspecifically foraged (Colwell and Taft 2000; Taft et al. 2002). Ephemeral flooding increased intensity of use and prey populations (Parkinson, Mac Nally and Quinn 2002). Rivers connected a mosaic of wetlands (Haig, Mehlman and Oring 1998; Parkinson Mac Nally and Quinn 2002), habitats for residual abundances (Paattison, Reeber and Marion 2002). Interaction of perturbations affected populations, for example freezing conditions arrested foraging in December 1999 medium-high flood, thus low populations of all species except Northern pintail, and wind stirring water's surface during January 1998 high flood to force strong, 22-27 knots, confined populations to sheltered locations.

### **Other Perturbations**

It is possible that lurking perturbations were present and influential but not considered (Botsford and Brittnacher in McCullough and Barrett 1992; Greenwood and Baillie 1991), for example snow covered food resources in January-February 1982 that caused Eurasian wigeon Confluence population decline; adverse effects of rainfall on Eurasian lapwing survival rates (Peach, Thompson and Coulson 1994).

### **Threats**

Habitat threats include increase in arable area and further drainage operations to increase discharge rates. Likely consequence of anthropogenic climate change and associated milder winter temperatures will result in migrants travelling shorter distances, hence smaller UK and local populations (Pounds and Puschendorf 2004; Thomas et al. 2004). The Environment Agency is considering establishment of wash lands in the locality to minimize urban flooding (Gouldstone pers. comm. 2002), which would increase habitat area for wintering and breeding waterbirds.

### **Future Research**

As variability increases overtime (Lawton 1994), future research should consist of greater monitoring frequency of populations and perturbations to deduce fine-grained preferred conditions. Multiple regression analysis should be computed to reveal sequence of influence of perturbations.



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## Appendix 1

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