6 FORAGING BEHAVIOUR AND ACTIVITY PATTERNS

6.1 INTRODUCTION

In Chapter 4, the effects on habitat selection of seasonality (possibly linked to breeding constraints) were discussed, *e.g.* the generalised migration from cliffs to arable (late summer) to pasture (winter) and returning to the cliffs in spring. In the preceding chapter (5.4), it was stressed that the highest possible net energy gain (energy gained less the energy required to find and capture it) for birds is achieved by choosing prey with a high nutritive value, large size and/or low handling time, additionally, birds feeding young have to maximize the amount of food obtained within the constraints of maintaining their own condition (Richford 1978). They should, in short, forage so as to maximize return per unit time (Royama 1970). This question of foraging economics is clearly of paramount importance.

In Cornwall, during a precursor to the main study, it was found that the Choughs involved spent the vast majority of their active day in foraging and associated activities (*i.e.* vigilance and moving between foraging areas). The two birds studied were active for >98% of the day, and actively foraged with head down for >60% (Meyer 1990, see Appendix IV). With associated activities included, the amount of time spent foraging accounted for up to 80% of active time. If individuals need to spend such a great proportion of their time searching for food, the maintenance of habitat quality must *ipso facto* be extremely important: any degradation would affect foraging efficiency and, with so little disposable spare time, presumably also their condition and survival prospects.

Even within the limited scope and short duration of the early study, it was possible to demonstrate significant differences in efficiency between the two main biotopes used (agricultural fields and the cliffscape) (*ibid.*). In the main study of foraging behaviour, comparable methods were used to compare efficiency and other behaviours between study areas, which, in turn, could be compared to the Cornish investigation.

The foraging efficiency of Choughs has been examined in the past by measuring the number of pecks and swallows against time or number of paces in different habitats. Bullock (1980) showed that the birds which moved about within habitats most were the least successful foragers, and he was able to relate this to different age-classes of heath and different seasons, establishing that feeding efficiency was highest in burnt heather (30 pecks or 15s per swallow), a fact he attributed to the larger proportion of bare earth (see Section 4.3.3a). It is to be expected that winter utilised habitats (stubble fields etc), because they involve surface-gleaning and bulk intake (a greater proportion of carbohydrates), will be the most productive in terms of quantity per unit time but not neccesarily in terms of energy or protein.

In this chapter, focal-animal sampling is used to investigate activity patterns across the study range in different seasons (6.3.1), and success rates in different habitats (6.3.2). Vigilance behaviour and disturbance caused by other Choughs and by other species, including humans (which affected feeding efficiency) were also investigated, as were the responses of Choughs to disturbance, and consequent minimum flight distances (6.3.3).

6.2 METHODS

The basic methodology is described in Section 2.5.3. Altmann (1973) discussed observational sampling methods, and recommended "focal-animal sampling" in which "all occurrences of specified (inter)actions of an individual... are recorded during each sample period"; a record is made of the length and the time during which the focal individual is in view. "Once chosen, a focal

individual is followed to whatever extent possible..." (*ibid.*). Focal-animal sampling was chosen as a means of providing relatively complete data. The sampling regime involved behaviours being recorded for one minute on every hour and half-hour (one was additionally taken at the first opportunity in case the subject moved out of sight). The exclusive behaviour categories are listed in Table 6.1. Food ingestions were recorded, as were environmental and climatic data. Inter- and intra-specific interactions and their outcomes were recorded as and when they occurred.

Table 6.1 Behaviour categories recorded during focal-animal sampling,with symbols used in subsequent tables

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Behaviour	Symbol	Description
Foraging	F	Exclusive feeding, *i.e.* head-down hunting
Vigilance	V	Head-up wariness, scanning for predators etc.
Ground-movement	G-M	Walking translocation: between foraging patches where this did not include 'F'. *Note:* birds so engaged would also be to some extent 'V'
Relocation	ReL	Flighted translocation between foraging areas or sites of other behaviour
Hunting	H	Incorporating all activities integral to F: 'F+V+G-M', does not include 'ReL'
Active	A	Activities *per se*: all behaviours requiring movement: 'H+ReL' or components thereof
Inactive	InA	All static behaviours, *e.g.* resting, loafing, preening. *Note:* also includes periods within roost, shelter or nestsite
Other	O	Any other 'A' behaviour: *e.g.* interactions with other individuals, spiralling flight etc

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Analyses were undertaken both for individual study areas and for the *region* (=all study areas combined). Foraging success was assessed by successful peck rate and calculated for different habitats in the range of study areas.

6.3 RESULTS

6.3.1 ACTIVITY PATTERNS

In Wales, 240 focal periods, mainly of *ca.* 60s duration ($\bar{x}$ = 61.2s), were recorded (Table 6.2) over 68 days in all seasons. Birds were not marked, and therefore individuals could not normally be identified; the sampling rationale described in Section 2.5.3 helped to reduce bias, and focal periods are treated as independent. During the earlier Cornish study, 112 were achieved in addition to 34 longer observations devoted to specific inquiries (Meyer 1990, see Appendix IV). It can be

Table 6.2 Distribution of focal periods (f.p.) ±1 s.e. between study areas and mean proportions of time (seconds) spent in activity patterns (Act =active, InA =inactive); mean proportion of time spent hunting (H), the principal 'Act' component, is also shown

Locality	Mean time f.p.	s.e.	Mean proportions of time						N
			Act	s.e.	InA	s.e.	H	s.e.	
W1/Mwnt-Cemaes	62.21	1.53	.95	.02	.05	.02	.77	.04	82
W2/Strumble	64.55	4.97	.94	.04	.05	.03	.77	.07	33
W3/Newgale-Solva	58.68	1.32	.95	.03	.05	.03	.66	.08	31
W4/Marloes	59.80	1.67	.90	.03	.10	.03	.55	.06	56
WR/Ramsey Island	60.82	1.34	1.0	-	0	-	.91	.02	38
Region	61.29	0.98	.94	.01	.06	.01	.73	.03	240
Kruskal-Wallis 1-way ANOVA (excluding WR)	K		4.374		6.104		11.613		
	P		N.S.		N.S.		<0.01		

Pair underlined is significantly different, multiple comparison test P <0.05

Table 6.2

seen from Table 6.2 that the greatest proportion of time (.94) was spent in active behaviour; Choughs at Mwnt-Cemaes and Strumble were almost identical in the amount of time spent hunting. Since data were non-normal and proportional, non-parametric statistics were used: Kruskal-Wallis 1-way ANOVAs were applied to the data sets to determine differences between the 4 main study areas (*i.e.* excluding the Ramsey Island summer inquiry, see Appendix V). Where significant differences were found, the particular pairs of study areas involved were identified by a multiple comparison test (Siegel & Castellan 1988). It was thus shown that Choughs spent significantly less time hunting at Marloes in the south of the study range than at Strumble in the north ($P<0.01$).

The mean time per focal period spent in different activities is given in Table 6.3, and converted to proportions in Table 6.4. In line with the above findings, Choughs spent more time foraging at Strumble than elsewhere, again very significantly more so than at Marloes ($P<0.01$). This is at the expense of vigilance and time spent in other activities. The north/south dichotomy often appears but, interestingly, the Choughs at Strumble were much less vigilant than those at neighbouring Mwnt-Cemaes ($P<0.001$), where, otherwise, there is usually close agreement. They did, however, spend significantly less time in non-hunting activities than Choughs at Marloes ($P<0.01$). It is certainly possible that the apparently better foraging performance of Choughs at Marloes is a consequence of the larger flock sizes generally seen there. [The Strumble birds unlike those at Marloes, and despite very low numbers being recorded (usually only one pair), successfully bred; although, as pointed out elsewhere (6.4), failure at Marloes was probably due to human disturbance (see also Appendix VIII)].

Table 6.4 also shows that while there was a significant difference in variance between the study areas in ground activity whilst feeding, no significant difference at the 5% level was found between individual study areas; however birds at Strumble were least mobile (as they were least vigilant) at a level very close to 5% significance compared to the other northern area, Mwnt-Cemaes. Neither was there a significant difference between individual study areas in the proportion of time spent flying.

The two southerly, more agriculturally improved, study areas were both 'worked' significantly less intensively than the two northern more pastoral areas (Tables 6.5 and 6.6); additionally, the amount of time spent in plumage maintenance and other non-hunting activities was very significantly greater in the south ($P=0.007$). Analysis of food finding rates suggests that not only was feeding less intensive in the south, it was also more successful (6.3.2).

Seasonal breakdowns (winter = November-February, breeding season = March-June, post-breeding season = July-October) for the Welsh region are given in Tables 6.7 - 6.9a-d. Although no significant difference was found between the seasons in the proportions of time spent hunting, even though less time was spent in this activity during the breeding season due to opposing reproductive demands, the proportion of time spent actually foraging (*i.e.* in head-down feeding mode) during the breeding season was significantly less than in the other two seasons (Table 6.8). The greatest proportion of time spent hunting was in the post-breeding season, when the birds were also more vigilant, although not to a significant extent (see Section 6.4). Significantly more time was spent in flight (between foraging patches) during the winter ($P<0.05$), in accord with the observations made during the early Cornish study (see Section 6.4 and Appendix IV).

The mean proportion of time spent hunting in winter in the Welsh region (.74) was exactly the same as that recorded in Cornwall during the earlier (winter) study (Meyer 1990, see Appendix IV). Similar proportions of time were also spent in winter 'head-down' foraging: *i.e.* Wales =.58, Cornwall =.60 (Table 6.8 *cf. ibid.*). Significantly less time was spent in preening and other activities

Table 6.3 Activity patterns, mean time ±1 s.e. per focal period: F =foraging, V =vigilance, G-M =ground-movements (all within hunting bouts); ReL =relocations, i.e. flights, O =other; and periods of inactivity (InA), largely resting or loafing; sample sizes as in Table 6.2

Mean time (seconds)

Locality	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	InA	s.e.
W1/Mwnt-Cemaes	31.7	2.2	13.4	1.0	3.2	1.0	2.8	0.8	6.2	1.5	2.9	1.3
W2/Strumble	42.8	5.9	7.6	1.4	1.3	0.6	8.3	3.4	0.8	0.5	2.9	2.0
W3/Newgale-Solva	28.4	4.0	8.7	1.4	2.1	0.6	4.1	1.4	11.7	3.9	2.6	1.7
W4/Marloes	22.0	3.1	12.2	1.6	2.3	0.6	6.5	2.1	10.6	2.3	7.4	2.2
WR/Ramsey Island	46.3	1.9	8.6	0.8	0.4	0.2	0	-	5.6	1.1	0	-
Region	32.8	1.5	11.0	0.6	2.8	0.4	4.2	0.8	7.1	0.9	3.4	0.8

Table 6.3

Table 6.4 Activity patterns: mean proportions of local period time ±1 s.e. spent foraging (F), vigilant (V), moving on the ground (G-M), in relocation flights (ReL), in other (O) activities and inactive (InA) by study area and region; sample sizes as in Table 6.2

Mean proportion of time

Locality	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.
W1/Nant-Cemaes	.51	.03	.21	.01	.08	.01	.05	.02	.10	.02
W2/Strumble	.65	.06	.11	.02	.02	.01	.14	.06	.01	.01
W3/Newgale-Solva	.47	.07	.15	.02	.04	.01	.08	.03	.19	.07
W4/Marloes	.37	.05	.21	.03	.04	.01	.12	.04	.16	.02
WR/Ramsey Island	.76	.02	.14	.01	.01		0		.09	.02
Region	.53	.02	.18	.01	.04	.01	.08	.01	.11	.01
Kruskal-Wallis 1-way ANOVA (excluding WR)										
K	13.872		16.725		9.220		1.758		14.489	
P	<0.01		<0.001		<0.05		N.S.		<0.01	

Column pairs underlined are significantly different, multiple comparison test $P < 0.05$

Table 6.4

Table 6.5 Mean proportions of focal period time ±1 s.e. spent active (Act) and inactive (InA) in northern (W1+W2) and southern (W3+W4) study areas; the mean proportion of time spent hunting (H), the principal 'Act' component, also shown

	Mean proportion of time						
Season	Act	s.e.	InA	s.e.	H	s.e.	N
W1+W2 (north)	.95	.02	.05	.02	.77	.04	115
W3+W4 (south)	.92	.02	.09	.03	.59	.05	87
z-value	0.89		-1.35		3.07		
P	N.S.		N.S.		0.003		

Table 6.6 Activity patterns, mean proportions of focal period time ±1 s.e. spent in different activities (F =foraging, V =vigilance, G-M =ground-movements, ReL =relocations, i.e. flights, O =other) in northern (W1+W2) and southern (W3+W4) study areas; sample sizes as in Table 6.5

	Mean proportion of time									
Locality	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.
W1+W2 (north)	.55	.03	.18	.01	.06	.01	.08	.02	.07	.02
W3+W4 (south)	.41	.04	.19	.02	.04	.01	.11	.03	.18	.03
z-value	2.82		-0.25		1.78		-0.90		-2.75	
P	0.005		N.S.		N.S.		N.S.		0.007	

Tables 6.5 & 6.6

Table 6.7 Mean proportions of focal period time ±1 s.e. spent active (Act) and inactive (InA) by season within Welsh region; mean proportion of time spent hunting (H), the principal 'Act' component, is also shown

Season	Act	s.e.	InA	s.e.	H	s.e.	N
Winter	.98	.01	.02	.01	.74	.07	38
Breeding	.93	.02	.07	.02	.68	.04	124
Post-breeding	.96	.02	.05	.02	.80	.04	78
All	.94	.01	.73	.03	.06	.01	240
Kruskal-Wallis 1-way ANOVA (excluding WR) K	5.556	N.S.	2.211	N.S.	2.563	N.S.	

Table 6.8 Activity patterns, mean proportions of focal period time ±1 s.e. spent in different activities (F =foraging, V =vigilance, G-M =ground-movements, ReL =relocations *i.e.* flights, O =other) by season within Welsh region; sample sizes as in Table 6.7

Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.
Winter	.58	.06[a]	.16	.02	.04	.01	.15	.05	.06	.03[a]
Breeding	.46	.03[a,b]	.17	.01	.07	.01[a]	.08	.02	.14	.03[a]
Post-breeding	.62	.03[b]	.20	.02	.01	0[a]	.04	.02	.09	.02[b]
All	.53	.02	.18	.01	.04	.01	.08	.01	.11	.01
K-W 1-way ANOVA (excluding WR) K	11.995		1.343		24.274		8.839		11.6	
$P<$	0.01		N.S.		0.001			0.05		0.01

Superscript signifies column pairs significantly different, multiple comparison test P<0.05

Table 6.9a-d Activity patterns: mean proportions of focal period time ±1 s.e. spent in various activities (F = foraging, V = vigilance, G-M = ground-movements, ReL = relocations i.e. flights, O = other) by season in study areas; mean proportion of time spent hunting (H = elements of F+V+G-M), the principal activity, is also shown

Table 6.9a Study Area W1/Mwnt-Cemaes

Mean proportion of time

Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	H	s.e.	N
Winter	.40	.10	.26	.04	.06	.04	.09	.05	.18	.09	.61	.14	12
Breeding	.50	.04	.20	.02	.09	.02	.06	.02	.08	.03	.78	.05	54
Post-breeding	.63	.07	.21	.03	.04	.02	0	-	.12	.06	.87	.07	16
All	.51	.03	.21	.01	.08	.01	.05	.02	.10	.02	.77	.04	82

Table 6.9b Study Area W2/Strumble

Mean proportion of time

Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	H	±s.e.	N
Winter	.65	.12	.12	.03	.04	.03	.18	.12	.01	.01	.79	.13	10
Breeding	.68	.08	.11	.03	.02	.01	.16	.08	0	-	.81	.08	18
Post-breeding	.53	.22	.09	.02	0	-	0	-	.07	.04	.60	.24	5
All	.65	.06	.11	.02	.02	.01	.02	.01	.01	.01	.77	.07	33

Table 6.9a-b

Table 6.9c Study Area W3/Newgale-Solva

Mean proportion of time

Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	.e.	O	s.e.	H	s.e.	N
Winter	.78	.13	.20	.15	.03	.03	0	-	0	-	1.0	0	2
Breeding	.42	.08	.14	.03	.05	.01	.09	.04	.25	.08	.60	.09	24
Post-breeding	.61	.13	.17	.03	.01	.01	.08	.06	.01	.01	.79	.13	5
All	.47	.07	.15	.02	.04	.01	.08	.03	.19	.07	.66	.08	31

Table 6.9d Study Area W4/Marloes

Mean proportion of time

Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	H	s.e.	N
Winter	.66	.10	.09	.02	.03	.01	.20	.10	0	-	.77	.11	14
Breeding	.28	.06	.19	.03	.06	.02	.06	.04	.27	.06	.46	.09	28
Post-breeding	.26	.09	.37	.08	.01	.01	.17	.08	.11	.04	.50	.12	14
All	.37	.05	.21	.03	.04	.01	.12	.04	.16	.03	.55	.06	56

Table 6.9c & d

during the winter than at all other times ($P<0.01$); most time was spent in these behaviours during the breeding season ($P<0.01$), with the post-breeding season supporting a central position (Table 6.8 and see Section 6.4).

Sheep and cattle were by far the commonest herbivores on pasture foraged over by Choughs, their presence was noted during 41 (17.1%) and 23 (9.6%) focal periods respectively; only 2 focal periods were recorded on pasture grazed by equines (Table 6.10 *cf.* Table 4.5), but horse-grazed fields existed only at Cemaes and Strumble (=*ca.* 0.4% of available pasture). Rabbits were patchily distributed, and the effects of their presence not always noticeable during focal sampling (but see Table 4.5 and Chapter 7 for appraisals of their importance). Birds were slightly more mobile on sheep-grazed pasture probably due to the less clumped nature of the dung; this is confirmed by the significantly reduced amount of time spent actually foraging on sheep pasture ($P<0.05$), while no such significance existed in the amount of time spent hunting (Table 6.10).

Foraging performance during time spent in different biotopes was also examined (Table 6.11). Cliffs are by far the most important single biotope in terms of time spent therein (see *e.g.* Figure 4.10) and also in their productivity to Choughs (6.3.2, 6.4); indeed >47% of all focal periods were recorded on the 'vertical' cliffs (excluding contiguous maritime habitats), and yet significantly less time per focal period was spent hunting there than within the old pasture categories ($P<0.001$). This is explained by the fact that cliffs were used more for non-hunting behaviours; for example, Choughs were inactive there for longer periods ($P<0.01$; Table 6.11). Less time was spent in 'head-down' foraging than on unimproved pasture ($P<0.05$). They also moved less on the ground in the cliff environment than elsewhere ($P<0.01$). Vigilance was only marginally affected by habitat; no two affected it significantly although there was a difference in overall variance ($P<0.05$). Stubble was excluded from these analyses because it involves a non-comparable feeding regime. Comparison of the proportion of time spent in flight (=relocation) in different habitats (Table 6.11) is of dubious value because it only accurately records relocation within the same habitat; if the focal bird disappeared from sight it was obviously not possible to be sure of its destination: some flights would have been to similar habitats, and some to different ones.

Activity patterns were also examined in relation to various environmental variables, *ie.* temperature, windforce, precipitation and cloud cover (Table 6.12). In these results, due to the large number of comparisons, $P<0.01$ is taken as the appropriate level of significance; levels at *ca.* 0.05 may be seen by reference to the table. Choughs spent a greater part of their active time during rainy weather hunting and less in some other activities ($P<0.02$); foraging and vigilance spans within hunting bouts were not significantly affected by any of the climatic variables measured, although warm weather increased the proportion of time spent foraging. Choughs were slightly more mobile, both on the ground and in the air, during cold weather ($P<0.02$), but significantly more likely to fly during very cloudy or overcast conditions ($P=0.002$). It has already been shown that 'other activities', *e.g.* plumage maintenance, sunning etc., occur very largely within the cliff environment (Table 6.11, $P<0.001$); as might be expected, warm weather seemed to affect these behaviours (Table 6.12), while rain, to some extent ($P=0.013$), decreased them. Indeed, the greatest climatic effect was caused by cloud cover, or the lack of it, on such behaviours: heavy cloud cover very significantly decreased the amount of time spent in behaviours other than hunting ($P<0.001$), and it might also have increased the amount of time spent inactive, though not significantly at the 1% level (Table 6.12). Wind less than Beaufort force 7 did not significantly affect the amount of time spent hunting or in secondary behaviours, although in strong winds they chose to feed in sheltered sites, as demonstrated by Bullock (1980), and strong wind also impaired foraging *success* (6.3.2). Very little Chough activity, during focal sampling, was recorded in winds stronger than force 5 or 6: in fact, only one period each at forces 7 and 8. During gales and severe weather, Choughs remained in regular shelters in both the Welsh and Cornish phases of the study.

Table 6.10 Activity patterns:: the mean proportion of time ±1 s.e. spent on land grazed by sheep and cattle in region (F =foraging, V =vigilance, G-M =ground-movements, ReL =relocations *i.e.* flights, O =other); time spent hunting (H =elements of F+V+G-M), the principal activity, also shown

Grazer					Mean proportion of time										
	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	InA	s.e.	H	s.e.	N
Sheep	.51	.04	.21	.02	.09	.02	.11	.04	.07	.03	0	-	.79	.05	41
Cattle	.66	.05	.22	.03	.04	.02	.03	.02	.04	.03	0	-	.90	.06	23

Mann-Whitney test

	F	V	G-M	ReL	O	InA	H
z	-2.156	-0.070	-1.825	-0.587	-1.025	0	-1.695
P	<0.05	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

Table 6.10

Table 6.11 The effect of habitat type on activity patterns. Mean proportion of focal period time ±1 s.e. H =all hunting time, including elements of F+V+G-M; F =foraging; V =vigilance; G-M =ground-movements; Rel =relocations; Rel =relocations, i.e. flights; O =other

Mean proportion of time

Habitat	H	s.e.	F	s.e.	V	s.e.	G-M	s.e.	Rel	s.e.	O	s.e.	InA	s.e.	N
Marit. grass/Q pstr/spp-rich/<5cm	.87	.06[a]	.56	.05[a]	.23	.02	.10	.03[a]	.08	.04	.03	.02	0	-	24
Cliff complex	.58	.04[a,b]	.41	.04[a]	.17	.02	.04	.01[a]	.10	.02	.17	.03[a]	.12	.03	113
Marit. heath	.63	.18	.41	.14	.21	.06	.03	.02	.34	.16	0	-	0	-	8
Marit. heath/burnt	.95	.02	.72	.03	.21	.02	.02	.01	0	-	.05	.02	0	-	14
Marit. scrub	.03	-	0	-	.03	-	0	-	.33	-	.63	-	0	-	1
Evap. hollow/spp-r	.88	.03	.78	.3	.10	.01	.13	.05	0	-	.12	.03	0	-	24
Ant-rich	.97	.01	.68	.08	.16	.03	.01	.00	.01	.01	.01	.01	0	-	10
Walls	.68	.15	.54	.13	.18	.14	.08	.03	.02	.02	.25	.12	0	-	9
S-Imp. pstr <5cm	.91	.05[b]	.62	.05	.23	.03	.01	.01	.03	.02	.02	.01[a]	0	-	24
Imp. pstr <1cm	.67	.33	.60	.30	.08	0	0	-	0	-	.31	.31	0	-	3
Stubble	.92	.06	.79	.07	.14	.03	0	-	.08	.06	0	-	0	-	10
All	.73	.03	.53	.02	.18	.01	.04	.01	.08	.01	.11	.01	.06	.01	240
Kruskal-Wallis 1-way ANOVA: main habitats (underlined) K	21.720		10.641		10.673		14.787		2.702		19.497		14.695		
P	<0.001		<0.05		<0.05		<0.01		N.S.		<0.001		<0.01		

Superscript denotes column pairs significantly different, multiple comparison test P <0.05

Table 6.11

Table 6.12 The effect of extremes of various climatic variables on activity patterns in region over all habitats; the mean proportion of focal period time ± s.e spent hunting (H =elements of F+V+G+M), the principal activity, is also shown

Variable	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	InA	s.e.	H	s.e.	N
Temperature <11°	.46	.05	.16	.02	.07	.02	.13	.03	.12	.03	.06	.02	.65	.06	61
Temperature >15°	.59	.03	.17	.01	.03	.01	.05	.02	.10	.02	.05	.02	.78	.03	97
Mann-Whitney test z	-1.940		-1.060		-2.517		-2.422		-1.970		-1.099		-0.364		
P	0.052		N.S.		0.012*		0.015*		0.049*		N.S.		N.S.		
Windforce <2	.61	.03	.17	.01	.04	.01	.06	.02	.09	.02	.01	.01	.81	.03	118
Windforce >5	.56	.08	.22	.05	.03	.02	.05	.04	.09	.05	.06	.06	.75	.09	18
Mann-Whitney test z	-0.267		-0.145		-0.621		-0.601		-1.421		-0.492		-0.526		
P	N.S.		N.S.		N.S.		N.S.		N.S.		N.S.		N.S.		
No precipitation	.52	.02	.17	.01	.04	.01	.08	.01	.12	.02	.06	.01	.71	.03	213
Precipitation	.60	.07	.24	.04	.07	.02	.09	.07	.01	.01	0	-	.90	.07	14
Mann-Whitney test z	-0.298		-1.768		-1.827		-0.107		-2.478		-1.260		-2.371		
P	N.S.		0.077		0.067		N.S.		0.013*		N.S.		0.018*		
Cloud cover <1/4	.57	.03	.16	.01	.04	.01	.05	.02	.16	.03	.03	.01	.74	.04	103
Cloud cover >3/4	.50	.04	.18	.02	.05	.01	.09	.02	.06	.02	.11	.03	.70	.05	65
Mann-Whitney test z	-1.060		-0.135		-1.783		-3.096		-3.856		-1.923		-.407		
P	N.S.		N.S.		0.075		0.002**		<0.001***		0.055		N.S.		

Table 6.12

6.3.2 FORAGING SUCCESS

Feeding success, as measured by rate of successful pecks (seconds per swallow), during 'head-down' foraging and over all hunting time, is shown in Table 6.13. During actual foraging, ANOVA shows a significant difference between the study areas, although not between any individual couple. The data suggest that feeding was not only less intensive in the two southern areas (6.3.1), it was also more successful: items were found >3s faster when foraging, and >4s faster over all hunting time (Table 6.14), but the data do not take into account nutrititive return per item (see Section 5.3).

Success in different habitats is given in Table 6.15. The success rate is predictably increased during surface-gleaning on stubble-fields and where birds are feeding on clumped prey (*e.g.* at anthills), otherwise there is no significant difference in success rate between the habitats most frequently used, nor is there any significant difference between the cliff region and semi-natural zone (Table 6.16). Since it concerns future discussion, however, it should be noted that during foraging prey was found nearly 1s more frequently within the cliff complex than in the second most successful habitat (excluding ant-rich), short semi-improved pasture, and >1s faster over all hunting time; the mean success rate during which was 1 swallow per 17.2 seconds (1/17.2s). The winter rate on cliffs and semi-natural habitat was 1/13.2s, and the mean rate during winter over all Wales was 1/10.8s; seasonality did not significantly affect foraging success (Table 6.17). The effects of climate extremes on foraging success are given in Table 6.18. In contrast to its lack of effect on the actual proportion of time spent feeding (4.3.1), strong wind significantly reduced foraging success (P=0.02; see Section 6.4).

Although the success rate was better on cattle-grazed pasture, Mann-Whitney U-tests revealed no significant differences between sheep-grazed and cattle-grazed pasture over either actual feeding time (cattle = 1/8.9s, sheep = 1/11.7s; Z=-.3717, n = 58) or generalised hunting time (cattle = 1/11.9s, sheep = 1/17.5s; Z=-.4218, n = 58).

Table 6.13 Mean swallowing rate (seconds/swallow) ±1 s.e. during head-down feeding time (=foraging 'F') and all hunting time (H) in study areas and combined (=region) in focal periods

Locality	Mean rate during				
	F	s.e.	H	s.e.	N
W1/Mwnt-Cemaes	10.19	1.76	14.93	2.51	71
W2/Strumble	15.98	4.02	21.44	5.26	18
W3/Newgale-Solva	8.06	2.30	13.37	3.79	21
W4/Marloes	8.37	2.75	11.13	3.37	36
WR/Ramsey Island	23.07	3.16	27.46	3.80	38
All (=region)	12.82	1.24	17.23	1.61	184
Region excluding WR	10.15	1.25	14.57	1.70	146
Kruskal-Wallis 1-way ANOVA	K 7.823	P <0.05	6.215	N.S.	

Table 6.14 Mean swallowing rate (seconds/swallow) ±1 s.e. during foraging time (F) and over all hunting time (H) in northern (W1+W2) and southern (W3+W4) study areas, excluding Ramsey Island

Locality	Mean rate during				
	F	s.e.	H	s.e.	N
W1+W2 (north)	11.36	1.63	16.25	2.27	89
W3+W4 (south)	8.25	1.92	11.95	2.53	57
t value	1.23	N.S.	1.26	N.S.	

Tables 6.13 & 6.14

Table 6.15 Mean swallowing rate (seconds/swallow) ±1 s.e. in focal periods during foraging time (F) and over all hunting time (H) in different habitats in Welsh region

Habitat	Mean rate during				
	F	s.e.	H	s.e.	N
Maritime grass - old pasture/					
spp-rich/<5cm	12.56	3.25	19.05	5.05	23
Cliff complex	9.88	2.08	13.51	2.65	68
Maritime heath	13.25	4.93	25.75	9.11	4
Maritime heath/burnt	19.24	6.09	24.80	7.73	14
Maritime scrub	0	-	0	-	1
Evaporated hollow/spp-rich	25.31	3.56	29.02	4.09	24
Ant-rich habitats	6.51	2.60	13.03	6.24	10
Walls	14.89	8.47	18.39	10.54	7
Semi-improved pasture <5cm	10.85	2.37	15.09	3.18	23
Improved pasture <1cm	17.67	-	20.00	-	1
Stubble (surface grain-feeding)	3.49	0.76	4.64	1.16	9
All	12.82	1.24	17.23	1.61	184

Kruskal Wallis 1-way ANOVA between
principal habitats (underlined) K 1.654 N.S.   1.469 N.S.

Table 6.16 Mean swallowing rate (seconds/swallow) ±1 s.e. in focal periods during foraging time (F) and over all hunting time (H) in main biomes (excluding stubble-feeding)

Biome	Mean rate during				
	F	s.e.	H	s.e.	N
Clifflands	13.66	1.58	18.19	2.00	130
Semi-natural	12.13	2.22	16.93	3.09	44
Mann-Whitney z-value	0.242	N.S.	0.098	N.S.	

Tables 6.15 & 6.16

Table 6.17 Mean swallowing rate (seconds/swallow) ± 1 s.e. in all habitats, and natural cliff and semi-natural habitats during foraging time (F) and over all hunting time (H) in focal periods

Mean rate in

Season	All habitats during					Natural & semi-natural during				
	F	s.e.	H	s.e.	N	F	s.e.	H	s.e.	N
Winter	10.84	3.50	14.18	4.48	23	13.24	4.61	17.25	5.90	17
Breeding	10.19	1.45	15.54	2.11	90	10.10	1.46	15.49	2.13	89
Post-breeding	16.79	2.34	20.37	2.83	71	17.42	2.41	21.14	2.92	68
Year	12.82	1.24	17.23	1.61	184	13.27	1.30	17.87	1.68	174
Kruskal Wallis 1-way ANOVA K	0.829 N.S.		0.405 N.S.			1.175 N.S.		0.429 N.S.		

Table 6.17

Table 6.18 The effects of climate on foraging success in Welsh region.
Mean swallowing rate (seconds/swallow) ±1 s.e. during foraging time (F) and
over all hunting time (H) in focal periods

Variable		Mean rate during				
		F	s.e.	H	s.e.	N
Temperature <11°		8.04	2.07	12.03	3.01	40
Temperature >15°		15.04	1.93	18.94	2.38	81
Mann-Whitney test	z	-1.698		-1.538		
	P	0.0895		N.S.		
Windforce <2		14.60	1.72	18.82	2.17	99
Windforce >5		6.15	5.01	7.53	5.89	12
Mann-Whitney test	z	-2.321		-2.142		
	P	0.0203*		0.0322*		
No precipitation		13.60	1.38	18.21	1.78	160
Precipitation		8.28	2.72	12.23	3.90	13
Mann-Whitney test	z	-0.914		-0.793		
	P	N.S.		N.S.		
Cloud cover <1/4		16.24	1.97	21.03	2.49	80
Cloud cover >3/4		11.26	2.58	15.45	3.39	40
Mann-Whitney test	z	-1.780		-1.642		
	P	0.0750		N.S.		

Table 6.18

6.3.3 INTERSPECIFIC INTERACTIONS

All visible interactions with other species were recorded as and when they occurred. Table 6.19 shows the causes of disturbance to Choughs at different times of the year and for all year. Human disturbance (excluding observer pursuit disturbance), though not agonistic, is clearly the most frequent, accounting for more than 40% of all incidents and increasing during the summer. Only the Raven caused frequent disturbance throughout the year; although this was matched in the breeding season by the Carrion crow, this species was not a serious problem at other times. Early in the breeding season (March/April), however, Carrion crows represented the most serious disturbing influence for they made direct attacks straight at feeding Choughs, even, on occasions, low-level 'hedge-hopping' approaches from some 200 metres distance. The only other disturbing influence recorded at a frequency of >10% was aircraft activity during the summer.

Most serious disturbances to feeding Choughs occur at flight distances of <10 metres (Table 6.20); this increases through the year as birds become concentrated on nest sites or dependent young. Potential danger is usually noticed at 50-100m when evasive action is taken. Virtually all flights from a distance of <10m were as a result of surprise encounters. On >36% of occasions the Choughs resettled nearby (Table 6.21), and usually continued feeding within 12 minutes, often after a period of vigilance and/or preening on a nearby vantage point, usually a fence post. On a greater number of occasions (45% of those timed, and 54% of all records), Choughs departed from the immediate vicinity; a slight increase during the breeding season was the result of birds' visiting their nest-site. Of disturbances specifically attributed and numbering ≥10, those occasioned by Carrion crows and humans caused the greatest disturbance in that they caused the Choughs to leave areas altogether (on 58% & 57% of occasions respectively). Of disturbances caused by aeroplanes and helicopters, 30% occasioned the Choughs to leave a feeding area, while of 27 caused by Ravens, only 22% resulted in the Choughs' departure. Table 6.22 shows the different responses caused by the main initiators: after only 3% of those caused by humans did the Choughs resume feeding immediately, compared to a third of all those attributed to Ravens. Of all initiators, Carrion crows caused the most serious response and, over and above the 58% complete departures from feeding areas, not once did the Choughs begin feeding again immediately (n=12). Peregrines caused only 6 recorded disturbances.

If agonistic interactions are separated out from all others, the Raven accounted for nearly half all records and the Carrion crow for exactly half and the Peregrine for nearly 10% (Table 6.23). In the winter, only the Raven and Peregrine caused disturbance, while in the breeding season, the Carrion crow emerged as the most formidable threat with the Raven in second place, and the Peregrine scoring only the same as the Rook and Magpie, although, of course, its attention was potentially more serious.

The Chough itself harried the Raven more during the breeding season than *vice versa*: >50% of 23 recorded instances of Choughs attacking other species; over the year as a whole, the Chough gave the Raven almost 'as good as it got' (45:48%) (Table 6.24)! The Jackdaw received >1/4 of all attacks (these were generally deterrents from feeding in close association) and the Buzzard nearly 14 percent.

Table 6.19 The causes of disturbance towards Choughs in different seasons (W =winter, B =breeding season, P-B =post breeding season)

	Percentage interactions			
Initiator	W	B	P-B	All
Human	28.6	47.2	50.0	41.2
Raven	33.3	12.4	13.3	19.8
Carrion crow	1.6	13.5	3.3	7.7
Helicopters/aeroplanes	1.6	5.6	13.3	5.5
Peregrine falcon	6.3	5.6	0	4.9
Extrinsic noise (eg. gunshot)	4.8	4.5	3.3	4.4
Jackdaw	3.2	5.6	0	3.8
Starling	7.9	0	0	2.7
Fox	3.2	0	6.7	2.2
Rook	3.2	1.1	0	1.6
Buzzard	0	0	6.7	1.1
Thrush	3.2	1.1	0	1.1
Dog (unaccompanied)	1.6	0	3.3	1.1
Windblown debris	1.6	1.1	0	1.1
Unknown	0	2.2	0	1.1
Magpie	0	1.1	0	0.5
Interactions (N)	63	89	30	182

Table 6.20 Approximate flight distances at which Choughs respond to disturbance in different seasons (W =winter, B =breeding season, P-B =post breeding season)

	Percentage occurrences			
Flight variable (m)	W	B	P-B	All
<10	49.0	37.5	23.5	40.2
10-25	7.8	20.3	23.5	17.4
25-49	9.8	17.2	23.5	15.9
50-99	29.4	15.6	11.8	20.5
>100	2.0	7.8	5.9	6.1
Occurrences (N)	51	64	17	132

Tables 6.19 & 6.20

Table 6.21 Responses by Choughs to disturbance in different seasons
(W —winter, B -breeding season, P-B —post-breeding season)

	Percentage responses			
Response	W	B	P-B	All
Depart from area	46.9	58.8	48.0	54.4
Resettle	10.9	12.5	4.0	10.7
Settle nearby out of sight	9.4	10.0	4.0	8.9
Resettle same site	9.4	5.0	16.0	8.3
Settle on vantage point vigilant or preen	7.8	5.0	12.0	7.1
Scramble, circle in flight	7.8	5.0	4.0	5.9
Some resettle/some depart	4.7	1.3	0	2.4
Evade and continue	3.1	2.5	0	2.4
Responses (N)	64	80	25	169

Table 6.21

Table 6.22 Frequency distribution of mean time elapses before recommencement of feeding by Choughs following disturbance by various causes in different seasons. Time categories: A =immediate; B =2-12mins; C =part then C; D =vigilant then C; E =flock separated, part-A/part-C (total n = 147)

No. within span/season

Initiator	Winter					Breeding					Post-breeding					All				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
Human	0	5	10	1	0	2	15	15	4	0	0	4	4	0	0	2	24	29	5	0
Raven	6	4	2	0	1	1	7	1	0	2	2	0	3	0	0	9	11	6	0	1
Carrion crow	0	2	0	0	0	0	1	7	0	0	0	0	0	1	0	0	3	7	0	2
Aircraft	0	0	1	0	0	1	0	2	0	2	1	5	0	0	0	2	5	3	0	0
Peregrine	0	0	2	0	0	0	4	0	0	0	0	0	0	0	0	0	4	2	0	0
Starling	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0
Jackdaw	0	2	1	0	0	0	2	1	0	0	0	0	1	0	0	0	4	2	0	0
Extrinsic noise	0	0	3	0	1	0	0	1	0	0	0	0	0	0	0	0	0	5	0	1
Rook	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	1
Fox	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1
Buzzard	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Raptor sp.	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
Other	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	0	0
Unknown	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	2	0	0
All	12	14	23	1	3	4	30	30	4	2	5	10	8	1	1	21	54	61	5	6

Table 6.22

Table 6.23 Agonistic interactions towards Choughs in different seasons
(W = winter, B = breeding season, P-B = post-breeding season)

	Percentage interactions			
Initiator	W	B	P-B	All
Raven	80.0	27.3	50.0	47.7
Carrion crow	0	45.5	16.7	25.0
Peregrine falcon	20.0	4.5	0	9.1
Buzzard	0	0	33.3	4.5
Rook	0	4.5	0	2.3
Magpie	0	4.5	0	2.3
Interactions (N)	15	22	6	44

Table 6.24 Agonistic interactions by Choughs in different seasons
(W = winter, B = breeding season, P-B = post-breeding season)

	Percentage interactions			
Receiver	W	B	P-B	All
Raven	0	52.2	20.0	44.8
Jackdaw	100.0	30.4	0	27.6
Buzzard	0	13.1	20.0	13.8
Rock dove	0	0	40.0	6.9
Magpie	0	0	20.0	3.4
Interactions (N)	1	23	5	29

Tables 6.23 & 6.24

6.4 DISCUSSION

Choughs spend at least 90% of their time active, about 75% hunting for food, and approximately half all daylight time actually in 'head-down' foraging mode. The study area where Choughs spent least time feeding was Marloes, at the southern edge of the study range (Tables 6.2 & 6.4). In this area, previously considered to be less well favoured for Choughs due to its more improved agriculture, not only did the Choughs spend less time feeding, their success rate was also better than farther north in apparently more suitable pastoral country (Tables 6.13 & 6.14). The reason for this could be due to availability of preferential habitat and the *quality* of the clifflands. The cliffs to the north of Pembrokeshire trend to a north-westerly aspect and receive less solar radiation, less wind exposure and reduced oceanicity; the slopes tend to be more scrubby, unless actively managed as on the Cemaes Head reserve. On slopes with a south-westerly aspect, there is more short/open vegetation, which not only gives improved access to food but allows greater insolation, which of itself actually promotes invertebrate activity, *e.g.* ants. The Marloes peninsula (Figure 2.9, and see Appendix VIII) illustrates this well: the northern side with predominantly scrub vegetation was <u>never</u> seen to be used by the Choughs, whilst the southern side was in continual use, and, as stated above, with considerable foraging success.

Results presented in Chapter 4 (*cf.* Figure 4.7) show the increased amount of time spent on the cliffs of the Marloes peninsula: about 75%, compared to less than 40% at Mwnt-Cemaes. Cliffs rendered of a high quality by environmental forces might be preferentially selected by Choughs in favour of contiguous traditional pastoralism, and, therefore, compensate for unsuitable agriculture even to the extent of over-riding its state altogether. There is little doubt though that without sufficient high-quality <u>natural</u> cliffscape, some management is probably essential to enable Choughs to maximise their potential in any particular area. Mixed grazing of cliffslopes can, by the reduction of sward height, creation of open areas, and input of organic material, only be beneficial.

Table 6.11 shows that, whilst on the cliffs, Choughs spend significantly less time active than when on adjoining (semi-)natural pasture, and more time there in other behaviours. Reference to Table 6.15, however, reveals that foraging success is somewhat better than in grassland, so it would be unwise to associate reduced activity in a particular habitat as an indication that it is less suitable. The discussion on ant-feeding (4.3.5) perhaps illuminates this. The 'north/upland/pastoral' and 'south/ lowland/improved' dichotomy (Tables 6.5, 6.6 & 6.14) appeared to be a convenient way of demonstrating the benefits of pastoralism but in fact the results were inconclusive: in some tests no significant difference was found between the two categories; in others, however, there were surprising differences, *i.e.* significantly less time was spent hunting in the south but foraging success was greater there.

Comparison of activity patterns within separate study areas (Tables 6.9a-d), suggests that winter foraging in the southern areas is as time-consuming, or more so, as in the north (mean proportion hunting time Marloes =.77 *cf.* Mwnt-Cemaes =.61); in contrast, summer foraging at Marloes occupied only .48 of daytime, compared to .83 at Mwnt-Cemaes. One of the reasons, of course, depressing the summer values of time spent hunting and foraging are other demands associated with breeding and rearing young (*e.g.* incubation and brooding) but this is a fairly constant demand across all areas irrespective of habitat quality except where this might be so different as to affect reproductive success.

Choughs spend more time hunting in the <u>post</u>-breeding season than in any other; this is perhaps surprising when one considers the demands of provisioning altricial young. However, it was found that Choughs feeding nestlings make great use of clumped food, especially ants. Since Choughs throughout the year spend about three-quarters of their active time hunting, it seems that

recourse to densely clumped food reserves, such as ants, on account of the nutritional benefits discussed below <u>and</u> the cost benefits, is of crucial importance during the nestling period. It was also shown, due largely no doubt to the demands of incubation, that Choughs spent significantly more time engaged in non-hunting activities during the breeding season ($P<0.01$). Therefore, during the post-breeding season, parent Choughs will need to replenish their energy reserves.

More time will need to be spent feeding during the post-breeding season because changes, as a result of breeding constraints, in habitat-use and, therefore, diet (5.3.3) do not significantly affect foraging success (Table 6.17). The rate is somewhat faster during the breeding season, when an increased number of smaller items, such as ants, are collected quickly to present to the young in the form of a bolus. A slowing of the intake rate, by as much 42%, during the post-breeding season could be due to juvenile care, a constraint on selecting optimum habitats because of such care, or to seasonal and climatic effects on food supply and accessibility (*e.g.* dry, hard ground). Only during the breeding season does the success rate in natural and semi-natural habitats (10.1s/ swallow) exceed the mean for all others (12.8s; Table 6.17), suggesting that cliffs during the early summer are the most invertebrate-productive habitat; indeed, ant-rich habitat was the most productive of all (excluding cereal-stubble). Very often such habitat was to be found on the cliffslopes, but mainly during this study the two were considered separately; if combined, ant-rich habitat would increase still further the cliff success rate (*cf.* Table 6.15). It was shown in Figure 5.4 that Choughs made considerable use of ant-rich habitats during the breeding season and immediately afterwards.

That time spent foraging decreases during the breeding season, and rises to a peak immediately afterwards (Table 6.8), but that success increases during the breeding season (Table 6.16), reflects the parents' need to feed their young, and confirms that a modification of dietary behaviour will influence the selection of habitat (see Section 5.4). Were this not so, it might be expected that Choughs would select habitats which offered similar returns to those selected at other times of the year. The Choughs were considerably less mobile yet more vigilant in the post-breeding season, both on the ground and in the air (Table 6.8) presumably due to the constraints imposed by caring for less mobile juveniles and possibly because they were present in small groups. Still (1989) found that young Choughs tend to be found in smaller flocks. However, she concurred with Dunnet *et al.* (1969) that young corvids move around more, possibly to avoid competition; however, while this may be true of young birds feeding independently, flocks of any size greater than family units were very rare in my study areas, and, consequently, almost no intraspecific conflicts were recorded throughout the entire study. Increased mobility in the winter suggests either that it is necessary in order to visit a range of habitats <u>or</u> that breeding constraints discourage mobility.

Vigilance did not seem to be affected by the patchiness of food resources (Table 6.10) but if the increase noted in translocations both on the ground and in the air (which include vigilance but to a degree which was impossible to measure accurately without sophisticated video recording equipment) are taken into account, vigilance associated with feeding on sheep-grazed pasture and dung would be expected to increase in line with that noted by Still (1989). However, she proposed that patchy food increased vigilance because it represented definable resources which were worth defending from members of the same species. If this had been the case during the present study, the proportion of time spent vigilant *while feeding* would be expected to be greater but, as noted above, no intraspecific agonistic behaviour was recorded, and so it is reasonable to assume that the usual pattern of vigilance decreasing with increasing flock size (Pulliam 1973) is countered if very small flock sizes remove the need to defend resources.

Pulliam (*ibid*), Caraco (1982), Pulliam *et al.* (1982), Hart & Lendrem (1984) and Lima (1987) all state that vigilance scans are instantaneous and unpredictable. Lendrem *et al.* (1986) stated that this was to prevent predators being able to forecast the inter-scan interval and thus make a final uncovered

hunting approach. Data gathered during the course of this study, together with equivalent data from other workers has shown by spectral analysis of series that there are non-random fluctuations in the magnitude of scans and intervals (Desportes *et al.* 1991, see Appendix IX).

The reduced mobility of Choughs on the ground within the cliff environment (Table 6.11) is probably a reflection of their preference for this habitat for such activities as sunning, sheltering and preening. The post-breeding season, as represented by the amount of time Choughs seem to have at their disposal for such behaviours (Table 6.8), occupies a midway position: possibly where opposing demands reach a peak. Sample sizes are small for some seasons in some areas, and this might explain some of the low levels of agreement seen in Tables 6.9a-d; local conditions are also likely to have important effects.

Bullock (1980) showed that Choughs are influenced in their choice of feeding sites by wind direction and velocity; it was not possible in the present study to gain comparable data (due to the extensive nature of the project) but it was shown that a wind strength of less than force 5 did not significantly affect the activity budget (Table 6.12). However, in force 5 or 6 on the Beaufort scale, slightly less time was spent feeding and slightly more time visually vigilant (the calls of other birds on several occasions caused Choughs to abandon feeding, and in conditions with a high wind-noise factor these would be harder to hear); more time was also spent in other activities such as sheltering, resting and preening.

Evans (1976) has reviewed the effects of wind on foraging shorebirds, and buffeting is known to be a problem for long-legged species like the Redshank (Speakman 1984). The noise factor of windy conditions, depending on how important the sense of hearing is to hunting Choughs (do they use the vibrations set up by worms for example?, see also Section 1.3.1), might also explain the decreased feeding success given in Table 6.18. Strong winds might impair hunting efficiency, and buffeting affect the ability of the birds to balance, but is difficult to see how it could affect subterranean prey invertebrates. No other climatic variable appeared to affect foraging efficiency within the Welsh region. That a lack of cloud cover, rather than temperature, very greatly increased the amount of time spent in non-hunting activities, probably only merits the conclusion that sunny conditions are indeed utilised *a priori* for activities which are not possible at other times, such as sunning!

Unfortunately, no summer evidence exists for Choughs in Cornwall, however evidence presented in Chapter 5 shows that invertebrate abundance and diversity is greater in Cornwall than Wales, and this could accordingly be expected to enhance foraging success there proportionally. The success rate achieved in Cornwall during the earlier short-term study (Meyer 1990, Appendix IV) was better but the two studies are not directly comparable since the main habitat used in Cornwall was a dung-rich stubble-turnip field, the equivalent of which in Wales was only found at Mwnt-Cemaes, and at a location farther from the coast, which would have decreased its usage.

Human encroachment into Chough habitat occurs mainly during the summer (June-August), spanning the breeding and post-breeding phases of the Chough's life cycle: >30% of all recorded disturbances were by humans at that time (Table 6.19). Many Chough nests are placed well away from casual human reach, and these are seldom disturbed during the critical breeding phase (March-June). Where a traditional nest-site is situated at a human 'honey-pot' area such as occurred at the north end of the Mwnt-Cemaes study area (at the end of a footpath *cul-de-sac*), and at Marloes, breeding success can be affected: both these nests failed to produce young in 1988. At Marloes, steps were taken to reroute a path thus creating a buffer zone of about 100m radius round the clifftop above the nest, an area the Choughs often frequented. This diversion might have been instrumental in the success of the site in 1989 (2.3.2). As can be seen from Table

6.20, a buffer zone of 100m radius around nest-sites should be sufficient to provide the necessary security.

As the summer progressed, human disturbance fell off from 42 to 15 occurrences (there were 18 winter disturbances), however it is when young birds have left the nest and yet are much in evidence nearby - calling, following their parents, and reluctant to fly - that disturbance from walkers, picnickers and curious sightseers can be most troublesome. At this time minimum flight distances increase: during the winter almost half of all flights were occasioned from a distance of <10m. This dropped by >75% during the post-breeding season; in other words, the birds were less tolerant of disturbance.

No other source with the possible exception of the Raven in the winter, and the Carrion crow during the breeding season caused serious disturbance. During the post-breeding phase (Table 6.21), Choughs were more likely to resettle in the same site or nearby on a prominent perch than at other times of the year, again this was apparently due to the presence of juveniles, however, by far the most frequent response to disturbance at all times was to quit the area altogether; this is more likely following human and Carrion crow disturbance than after that initiated by Ravens (Table 6.22). Gunshots, even when distant, always caused evacuation from an area, unlike aircraft noise, which, on 7 out of 10 occasions, merely interrupted feeding. Irrespective of cause and season, Choughs left feeding areas on *ca.* 45% of occasions and remained in >50%. Otherwise, the flock separated: individual birds doing one or the other. In the breeding season, the ratio was 50:50. No human disturbance was intentionally agonistic, the only species to cause actual physical threat were the Raven, Carrion crow and Peregrine (Table 6.23).

It has been shown that Magpies can be very seriously affected by agonistic Carrion crows (Baeyens 1981); the Magpie was the only other corvid frequently seen feeding, usually in pairs, near Choughs, *e.g.* in the same field, in both Wales and Cornwall during this study. Lovari (1981) advanced the theory that *Pyrrhocorax* was phylogenetically related to *Pica* and *Cyanopica* as well as *Corvus*. Magpies employ various methods of avoiding Carrion crow attacks, and Rowley (1973) and Roell (1978) noted that flocks of a usually subordinate species (in these cases, Magpies and Jackdaws) would sometimes 'swamp' the aggressor and deter territorial aggression. Baeyens (*ibid.*) quotes an instance of reversed dominance, in which Magpies chased away Carrion crows, in much the same way as Choughs during this study were occasionally seen to chase Ravens away; he also suggests that the Magpie's ability to resist Carrion crow attacks is influenced by habitat.

The theory that Jackdaws were a principal reason for the Chough's decline in some areas is not supported by the results in Table 6.24, which shows that all serious interactions with Jackdaws were instigated by Choughs. Some depletion of food resources is possible but the respective diets of the two species are not broadly comparable (1.3.1); Darke (1971) saw a possibility of competition when the two species were rearing young in close proximity. No disturbance by domestic livestock was witnessed. At one site (Marloes), Starlings appeared to cause disturbance during the winter by their extremely close association with Choughs, at which times the Starlings seemed to be using them as cues to locate food.