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Settlement of Redshank *Tringa totanus* following winter habitat loss: effects of prior knowledge and age

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The ability of animals to survive habitat loss is likely to be dependent not only on the proximity of alternative habitat but also on the ability of individuals to relocate. Here, we examine influences on the settlement behaviour of Redshank *Tringa totanus* following winter intertidal habitat loss resulting from the construction of a barrage at Cardiff Bay, on the Severn Estuary, UK. Results supported previous studies showing that the species is highly faithful to its wintering sites. Redshank were reluctant to leave Cardiff Bay in the first winter following habitat loss: birds used the site at all tidal stages for eight days after barrage-closure and thereafter continued to roost there. Birds moved at most 19 km, the distances that individuals moved being inversely related to their age, indicating that young birds were less attached to the bay and so more plastic in their response to change. Settlement also appeared to be influenced by prior knowledge – notably, one site previously only used nocturnally by 'Cardiff Bay' birds was used diurnally post-closure despite being heavily disturbed during the day. Birds initially ranged more widely following their displacement, but over the three winters post-closure, became increasingly concentrated into one recipient site, just 4 km from the bay. It is suggested that individuals' fidelity to Cardiff Bay post-closure and lack of knowledge of alternative foraging sites would have been to their detriment.

Key words: age, habitat loss, prior knowledge, Redshank, settlement, *Tringa totanus*

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INTRODUCTION

In many parts of the world, the habitats used by wintering waders have been affected by human activities (Davidson *et al.* 1991). Land-claim, for industry, agriculture, harbours and housing, as well as barrage schemes, have caused substantial habitat loss (Evans 1978/79, Lambeck *et al.* 1996) and remain threats to a number of important sites (Barter 2002). The impacts of such changes on local populations are primarily dependent upon the proximity of alternative habitat and whether these sites have the resources to support additional birds (Goss-Custard *et al.* 2002). If available resources are limited, increased densities may lead to an intensification of interference competition and depletion competition (Goss-Custard 1980) and thus potentially increased mortality (Burton *et al.* 2006).

However, while there is significant comprehension of these processes, there remains a need to understand how the ability to relocate following

habitat loss varies between species and individuals. Among waders, for example, species such as Sanderling *Calidris alba* which regularly move to exploit varying food resources (Evans 1981, Myers *et al.* 1988, Roberts 1991) might be expected to have better prior knowledge of alternative habitat and thus exhibit greater behavioural plasticity in response to the loss of any one site. In contrast, species with more reliable food resources, such as Turnstone *Arenaria interpres*, may be more site-faithful (Metcalfe & Furness 1985, Burton & Evans 1997) and thus have limited knowledge of alternatives. Furthermore, residency may be adaptive as it may confer competitive advantages (Whitfield 1985, Cristol *et al.* 1990, Senar *et al.* 1990, Snell-Rood & Cristol 2005) and so better access to resources; thus individuals may be reluctant to leave a site if habitat is lost and at a disadvantage due to decreased status once they do. Attachment to wintering sites also tends to develop from autumn into winter in an individual's first year (Ralph & Mewaldt 1975, Benvenuti & Ioalè 1980, Myers *et al.* 1988, Baccetti *et al.* 1995, 1999) though between-year site-fidelity may develop over a longer period (Baccetti *et al.* 1999; see Ketterson & Nolan 1990 for definitions of attachment and site-fidelity). Thus young birds might be expected to relocate to new sites more readily than older individuals following habitat loss.

Here we investigate the behaviour of Redshank *Tringa totanus* following winter habitat loss at Cardiff Bay, on the Severn Estuary, UK. The intertidal habitat of Cardiff Bay was impounded by a barrage on 4 November 1999, the resulting freshwater lake now forming the centre point for the redevelopment of Cardiff's former docklands. The loss of this habitat provided an unique opportunity to examine the strength of site-fidelity in the species and the factors affecting individuals' behavioural responses to change.

Previous work suggests that Redshank are highly faithful to their wintering sites (Burton 2000, Rehfisch *et al.* 1996, 2003) and thus our first prediction was that individuals would remain close to their former wintering site, at least for the first winter after barrage-closure. We secondly investigated whether the settlement of displaced birds might not only be explained by the proximity (and size) of alternative foraging sites but also individuals' prior knowledge and age, predicting that older individuals would be more attached to Cardiff Bay and so disperse less far. We use the term knowledge as we examine whether birds moved to sites that they had previously visited and thus knew of, rather than solely examining if movements were affected by whether birds had experience of using alternative sites. Finally, although displaced birds were predicted to initially range more widely following habitat loss, in part due to increased competition, we also examined whether the pattern of settlement became more stable over time. Data were gathered through observations of both colour-ringed and radio-tagged birds.

STUDY AREA AND SPECIES

Redshank winter at a number of sites around the Severn Estuary, primarily where rivers or other freshwater flows intersect mudflats (Burton *et al.* 2003a). Cardiff Bay (hereafter also 'the bay') (51°27'N, 3°10'W) was formed by the combined estuaries of the Rivers Taff and Ely and, before its impoundment, encompassed 200 ha of intertidal habitat. Here, a peak of 296 Redshank was recorded in winter 1998/99 (Burton *et al.* 2003b).

The nearest alternative feeding habitat is found by Cardiff Heliport (35 ha), 2.5 km northeast along the Welsh coast of the Severn (Fig. 1), where a sewage outfall discharges onto mudflats – though this site was not used diurnally prior to barrage-closure (Burton & Armitage 2005). The more extensive mudflats at the Rhymney River (260 ha), 4 km distant, supported a peak of 625 Redshank in winter 1998/99 (Burton *et al.* 2003b). Further northeast, smaller numbers of Redshank are found at Peterstone (100 ha, including a small area of habitat at the adjacent Sluice House Farm), 11 km from the bay, and the estuaries of the Rivers Usk and Ebbw (100 ha), 19 km away. Few Redshank utilise the open coast between these flows and the species is rarely found on the rocky coast west of Cardiff.

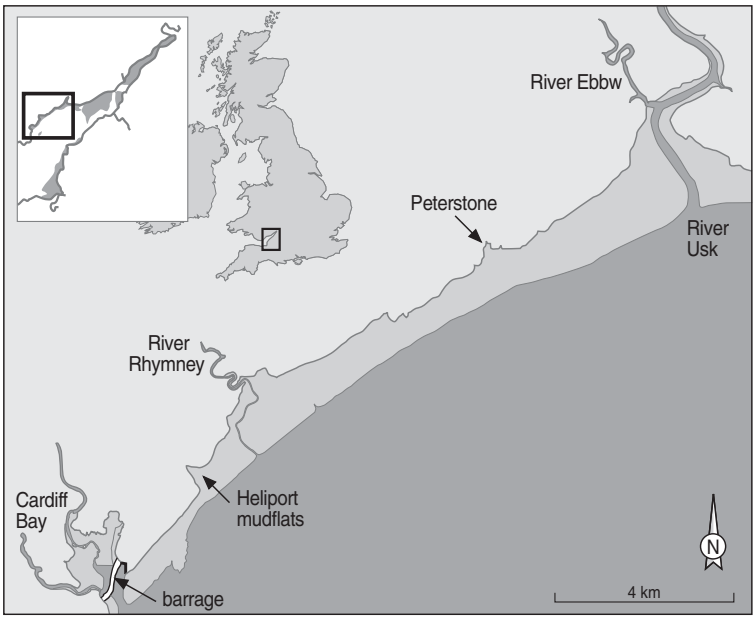

Figure 1. The study area showing intertidal habitat, the main locations discussed and their position on the Severn Estuary, UK; the whole area shown was searched for colour-ringed individuals.

Previous tracking studies had shown that, before barrage-closure, individual Redshank were highly faithful to the bay within a winter, though that use of other sites increased at night; a high proportion of adults also returned to the Cardiff study area each winter (Burton 2000, Burton *et al.* 2006).

METHODS

Colour-ringing and radio-tagging

Redshank were caught for marking by cannon- or mist-netting at high-tide roosts both at Cardiff Bay and the Rhymney River, beginning in 1991. Birds were fitted with metal rings and aged according to plumage characteristics (Prater *et al.* 1977) as either adult or first-winter.

Up until September 1994, Redshank caught in the bay were fitted with single yellow and white Darvic plastic rings on the right or left tarsus to identify them as 'Cardiff Bay' birds. Thereafter, until October 1999, the majority of Redshank caught at Cardiff Bay (and a small number trapped at Rhymney) were fitted with unique combinations of colour-rings to aid subsequent field-identification. A total of 454 birds were individually colour-ringed – 396 in the bay (322 adults, 69 first-winter birds and five birds of indeterminate age) and 58 adults at Rhymney (39 previously caught in the bay and 19 marked as part of radio-tagging studies).

Twenty individuals (19 adults and one first-winter bird) caught in Cardiff Bay on 15 and 21 October 1999 were also fitted with radio-transmitters in order to examine the movements of Redshank in more detail. A comparison of the diurnal and nocturnal movements of these birds before barrage-closure was provided by Burton & Armitage (2005). Here analyses focus on temporal changes in the movements of Redshank following barrage-closure. Seven further adult Redshank (all originally caught and ringed at Cardiff Bay) were fitted with transmitters at Rhymney on 20 and 24 January 2000.

Transmitters (model TW-4, Biotrack Ltd, Wareham, UK) weighed 2.5 g and were attached to clipped feathers on the birds' lower backs using cyanoacrylate glue (Warnock & Warnock 1993). Individuals weighed 125–173 g and thus transmitters were 1.4–2.0% of their body mass. Signals could be detected 1.5 km away and batteries had a life expectancy of three months. Every Redshank fitted with a transmitter was also individually colour-ringed. Radio-tagged Redshank were located in the field using a three-element Yagi antenna and either a Mariner 57 receiver (Mariner Radar, Lowestoft, UK) or an Australis 26K scanning receiver (Titley Electronics, Ballina, Australia).

The pattern of settlement in winter 1999/2000

The pattern of settlement of displaced Redshank in the first winter post-closure was examined using data from surveys for colour-ringed birds. Both in October 1999 and winter (November-February) 1999/2000 (and subsequently the winters of 2000/01 and 2001/02), Cardiff Bay and other parts of the Severn known to support wintering Redshank (Burton *et al.* 2003a) were surveyed for colour-ringed birds. Figure 1 shows the extent of the area surveyed, which extended east to the River Wye (51°37'N, 2°39'W) and Berkeley Pill, Gloucestershire (51°42'N, 2°29'W) and south to the River Parrett, Somerset (51°11'N, 3°03'W) and, in detail, the main locations discussed. Our own data were supplemented by information received from volunteer birdwatchers.

In addition to details of any colour-ringed birds sighted, the proportions of colour-ringed birds in flocks of Redshank were recorded. No other studies have colour-ringed Redshank on the Severn and thus those marked birds seen would either have been from Cardiff Bay (with the exception of the few radio-tagged and thus colour-ringed at Rhymney) or been ringed in the breeding season. Three Redshank colour-ringed on Scottish breeding grounds were seen in the area during the study (Burton *et al.* 2002).

Differences in the proportions of colour-ringed Redshank seen in flocks at different sites before (October 1999) and after (winter 1999/2000) barrage-closure were investigated using generalized linear models (GLMs; PROC GENMOD: SAS Institute 2002–2004), assuming binomial errors and a logit link function, and tested for using likelihood ratio tests.

Due to their previous site-fidelity, Redshank displaced from the bay were predicted to move to the closest (and largest) sites available to them. Given that the Heliport mudflats were not used diurnally prior to barrage-closure (Burton & Armitage 2005), the larger Rhymney River mudflats thus represented the most likely recipient site for displaced birds.

Effects of prior knowledge and age

The possible effects of prior knowledge on the settlement of displaced Redshank in the first winter post-closure were examined in two ways. Firstly, we investigated whether 'Cardiff Bay' birds that were known to have previously used alternative feeding sites were quicker to respond to the loss of habitat. The presence in the bay of those individuals radio-tagged there in October 1999 was thus monitored diurnally at high and low tide for the first fortnight after barrage-closure (4–18 November – post-closure period 1, see below). (Although intertidal habitat was lost, some former high-tide roost sites remained.) A GLM, again with binomial errors and a logit link function, was used to examine whether the proportions of occasions that individuals were present in the bay in this period were related to whether they had been recorded outside the bay pre-closure (15–31 October, see below), either during the day or night. This analysis excludes data from one individual whose transmitter failed prior to 18 November, thus $n = 19$.

Secondly, using data from surveys for colour-ringed birds, we examined whether displaced Redshank used the Heliport mudflats in winter 1999/2000. Although close to both Cardiff Bay and the Rhymney River, this site had previously been avoided in the day, probably due to disturbance from helicopters. Thus, Redshank displaced from Cardiff Bay might not have been expected to use the site during the day, but instead bypass it to join the large flocks using the Rhymney River

mudflats, had it not been for the fact that some Cardiff Bay birds were known to have previously used the Heliport mudflats at night (Burton & Armitage 2005). We determined whether any flocks of Redshank that used this site diurnally post-closure had wholly or partly originated from the bay by comparing the proportions of colour-ringed birds within them to those recorded in the bay immediately pre-closure.

In addition to examining the effects of prior knowledge, we also investigated whether the distances that colour-ringed Cardiff Bay Redshank moved in the first winter post-closure were influenced by their age. Locations where birds were recorded were classified according to their distance from the bay (i.e. the Heliport mudflats, Rhymney River, Peterstone and Rivers Usk and Ebbw) and a non-parametric Jonckheere Test (Siegel & Castellan 1988) then used to determine whether the furthest distances that individuals were seen from the bay in winter 1999/2000 were related to their age. This analysis was first undertaken for birds of known age (i.e. those caught and ringed as first-winter birds), and then repeated to include all birds originally ringed at Cardiff Bay, by calculating each individual's minimum known age in winter 1999/2000.

Temporal changes in movements and settlement

Data from Redshank radio-tagged in October 1999 were used to examine temporal changes in the use of different sites and the extent of movements over 1999/2000, the first winter post-closure. Location data for these individuals were collected during three periods: 15–31 October 1999 (*Pre-closure*), 4–18 November 1999 (*Post-closure period 1*) and 26 November – 20 December 1999 (*Post-closure period 2*). For those tagged in January 2000, data were collected during two further periods: 24 January – 16 February 2000 (*Post-closure period 3*) and 21–29 February 2000 (*Post-closure period 4*) (periods differed in length primarily due to tides). During each period, using triangulation from fixed stations along the coast, we attempted to determine the location of each individual three times, diurnally and nocturnally, each hour of the intertidal (foraging) period, i.e. from four hours before to four hours after low tide (thus 27 times in all).

Changes in the sites used by tagged birds are illustrated graphically. Data are only shown for those individuals for which transmitter-life allowed 27 points to be obtained for every possible period, either diurnally or nocturnally. Location data for post-closure period 1 were only collected once individuals were first recorded away from the bay during daylight hours.

We also estimated the diurnal and nocturnal 'ranges' used by each individual in each period. As it was predicted that it would take time for birds' movements to stabilise post-closure, the areas estimated do not conform to any traditional definition of an animal's home range (e.g. Burt 1943, see White & Garrott 1990). However, by using a fixed number of radio-locations (for each tidal stage) it was possible to compare ranging behaviour between periods even though the full extent of the areas used may have been underestimated. Data were plotted, at a resolution of 40 m, in an ArcView Geographic Information System (ESRI 1999) project. Fixed kernel home ranges (Worton 1989) were calculated for the 95% volume contour, using the Home Range Extension developed by Rodgers & Carr (1998). The area of intertidal shore (i.e. the habitat between mean high- and low-tide marks) contained within the 95% volume contour was defined as the individual's home range. Additionally, we calculated the maximum distance between the locations used to calculate each range. These values and the sizes of individuals' ranges were log10 transformed prior to analysis and compared between periods using paired t-tests (tests for normality and the equality of variances, and t-tests were undertaken using PROC UNIVARIATE and PROC TTEST in SAS). In making these comparisons, it should be noted that the extent of movements might be affected by the different lengths of time taken to collect data.

Data from surveys for colour-ringed birds were used to examine changes in the pattern of settlement over the two subsequent winters (for field methods, see above).

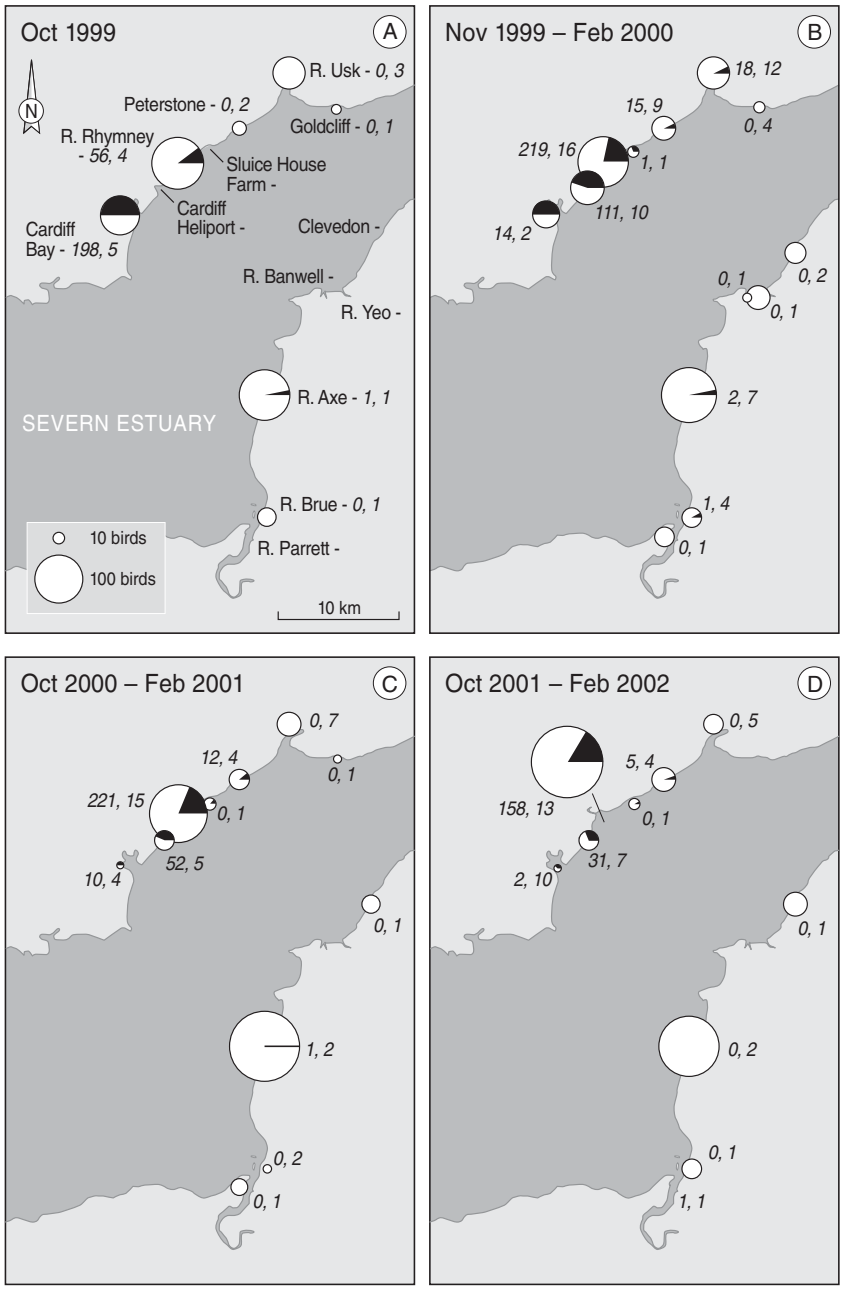

Figure 2. Mean proportions of colour-ringed individuals in flocks of Redshank in (A) October 1999, immediately before closure of the Cardiff Bay barrage; (B) November 1999 – February 2000, the first winter post-closure; (C) October 2000 – February 2001 and (D) October 2001 – February 2002. Proportions are indicated by black segments and circle size reflects the mean size of flocks surveyed; figures indicate the number of colour-ringed individuals identified at a site and the number of surveys undertaken. No colour-ringed Redshank were seen in winter beyond the area shown.

RESULTS

The pattern of settlement in winter 1999/2000

Pre-closure, in October 1999, a mean of 49% of the Redshank in Cardiff Bay were colour-ringed and, in total, 198 colour-ringed individuals were recorded there (Fig. 2A). By contrast, only 11% of the Redshank at the Rhymney River were colour-ringed and only 56 colour-ringed individuals were recorded there. No colour-ringed Redshank were recorded (diurnally) on the Heliport mudflats or east of the Rhymney River and only one on the English (southern) side of the Severn.

Post-closure, in winter 1999/2000 (excluding radio-tracking records) just 14 colour-ringed Redshank were observed in the bay (Fig. 2B). Most marked birds were recorded at the two nearest sites, i.e. the Heliport mudflats (111 individuals) and the Rhymney River (219). The percentage of colour-ringed birds in flocks at the Rhymney River increased significantly to 21% ($\chi^2_1 = 28.97$, $P < 0.0001$). Colour-ringed Redshank were also seen at Peterstone and the neighbouring Sluice House Farm (16 individuals) and as far east as the Rivers Usk and Ebbw (18) during winter 1999/2000. No colour-ringed Redshank were seen further up the Severn, in spite of repeated surveying of this area. Two further colour-ringed individuals were seen on the English side of the Severn.

Effects of prior knowledge and age

Post-closure, radio-tagged Redshank continued to be recorded in the bay both at high and low tide for eight days, though more often at high tide. A maximum of six tagged birds was recorded in the bay at low tide during post-closure period 1, compared to 15 at high tide. Thereafter, the bay was primarily used just as a high-tide roost site. Tagged individuals that had been recorded outside the bay diurnally pre-closure were, on average, recorded less frequently in the bay during post-closure period 1 than those that had not (Fig. 3; $\chi^2_1 = 16.84$, $P < 0.0001$). In contrast, use of other sites nocturnally pre-closure had no such effect ($\chi^2_1 = 0.71$, $P = 0.40$).

The Heliport mudflats, which were only used nocturnally by Redshank before barrage-closure (Burton & Armitage 2005), were used intensively both diurnally and nocturnally post-closure. An average of 45% of the Redshank that used this site diurnally in winter 1999/2000 were colour-ringed, a similar percentage to that recorded in the bay immediately before barrage-closure ($\chi^2_1 = 0.74$, ns).

There was a strong inverse relationship between the ages of individually colour-ringed Redshank and the maximum distances that they were recorded away from Cardiff Bay (along the Welsh Severn coast) in winter 1999/2000 (for birds of known age, $n = 39$, see Table 1: Jonckheere Test $z = 2.27$, $P = 0.023$; for birds of minimum age, $n = 225$, see Table 2: $z = 4.19$, $P < 0.0001$). Individuals that were recorded only as far as the Heliport mudflats were on average the oldest, whilst those that moved to the Rivers Usk and Ebbw were the youngest. Only three of 94 Redshank known to be at least five years old were recorded further than the Rhymney River, i.e. just 4 km from the bay.

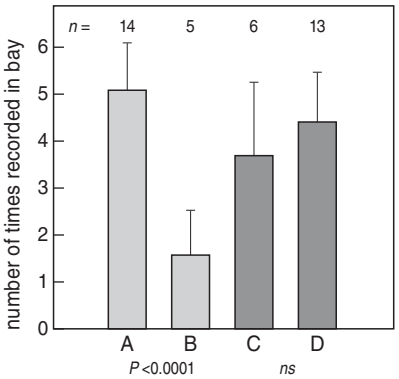

Figure 3. The number of times that radio-tagged Cardiff Bay Redshank were recorded in Cardiff Bay over 15 (high and low tide) surveys in post-closure period 1. Data are means ±1 SE. (A) Individuals that had not been recorded outside the bay during the day pre-closure. (B) Individuals that were recorded outside the bay during the day pre-closure. (C) Individuals that had not been recorded outside the bay during the night pre-closure. (D) Individuals that were recorded outside the bay during the night pre-closure.

Table 1. The furthest distances that individually colour-ringed Cardiff Bay Redshank of known age were seen away from the bay (along the Welsh Severn coast) in the winter after barrage-closure (November 1999 – February 2000). Given are the numbers of birds of specified age that were recorded no further from the bay than the specified site.

Site		Heliport	Rhymney River	Peterstone[a]	Usk and Ebbw	Mean distance moved (km)	*n* (birds)
Distance from Cardiff Bay (km)		2.5	4.0	11.0	19.0		
Age (years)	1	0	1	0	2	14.0	3
	2	1	21	4	2	6.0	28
	3	1	0	0	0	2.5	1
	4	0	0	0	0	-	0
	5	0	3	0	0	4.0	3
	6	0	2	0	0	4.0	2
	7	1	1	0	0	3.3	2
Mean age (years)		4.0	2.8	2.0	1.5		
n (birds)		3	28	4	4		39

[a]Including birds seen at Sluice House Farm (see Fig. 2).

Table 2. The furthest distances that individually colour-ringed Cardiff Bay Redshank were seen away from the bay (along the Welsh Severn coast) in the winter after barrage-closure (November 1999 – February 2000) in relation to their minimum known age.

Site		Heliport	Rhymney River	Peterstone[a]	Usk and Ebbw	Mean distance moved (km)	*n* (birds)
Distance from Cardiff Bay (km)		2.5	4.0	11.0	19.0		
Minimum age	1	0	1	0	2	14.0	3
(years)	2	4	53	7	9	6.4	73
	3	6	33	4	4	5.7	47
	4	1	6	0	1	5.7	8
	5	1	11	0	0	3.9	12
	6	1	10	0	0	3.9	11
	7	7	29	1	0	3.9	37
	8	4	16	0	1	4.4	21
	9	0	1	0	0	4.0	1
	10	0	2	0	0	4.0	2
	11	3	6	0	1	5.1	10
Mean (min) age (years)		5.7	4.6	2.8	3.1		
n (birds)		27	168	12	18		225

[a]Including birds seen at Sluice House Farm (see Fig. 2).

Temporal changes in movements and settlement

Radio-transmitters on a number of individuals failed prior to the end of post-closure period 2 and, as a result, site use and home ranges could only be compared across the first three periods for 12 adults diurnally and, due to failing signals, only eight of these nocturnally. Home ranges were estimated for all seven adults for post-closure periods 3 and 4 (see methods for definitions of periods used in the analyses of radio-tracking data). Radio-tracking confirmed the results from observations of colour-ringed birds, that most Cardiff Bay Redshank were displaced to the Heliport and Rhymney River mudflats (Fig. 4). During post-closure period 1, adult Redshank radio-tagged at Cardiff Bay were recorded (during the intertidal period) between the bay and River Usk. By post-closure period 2, radio-tagged birds had become more limited to the Heliport and Rhymney River mudflats. Results from adults tagged (at Rhymney) in January 2000, show a continuation of this pattern in January and February (post-closure periods 3 and 4) with the Rhymney River mudflats favoured and decreasing use of the Heliport mudflats, both diurnally and nocturnally.

Diurnal and nocturnal radio-locations and estimated home ranges for the first three periods are shown for one adult (representative of those first displaced to the Heliport) in Fig. 5. Pre-closure, this individual was only recorded in the bay diurnally, though also used the Heliport mudflats at night. In post-closure period 1, it used the bay, the Heliport mudflats and Rhymney River mudflats during the day, whereas, nocturnally, all but one record came from the Heliport mudflats. By post-closure period 2, this bird had stopped using the bay and most records came from the Rhymney River.

Maximum distances between observations of radio-tagged individuals within periods and estimated home ranges are shown in Table 3. In post-closure period 1, the maximum distances separating diurnal observations of radio-tagged Redshank increased, as birds ranged more widely (t_{12} = 4.57, P = 0.0008). Two individuals were recorded both at Cardiff Bay and on the River Usk in this period – a distance of 19 km. Diurnal ranges also increased in size between pre-closure and post-closure period 1 (t_{12} = 2.25, P = 0.046). In contrast, there were no clear differences in the extent of nocturnal movements (maximum distances: t_8 = 0.52, P = 0.64; ranges: t_8 = 2.20, P = 0.064). In post-closure period 2, radio-tagged Redshank continued to range more widely than pre-closure during the day (maximum distances: t_{12} = 4.03, P = 0.002; ranges: t_{12} = 1.69, P = 0.12). However, movements appeared more restricted at night (maximum distances: t_8 = 2.45, P = 0.044; ranges: t_8 = 1.09, P = 0.31).

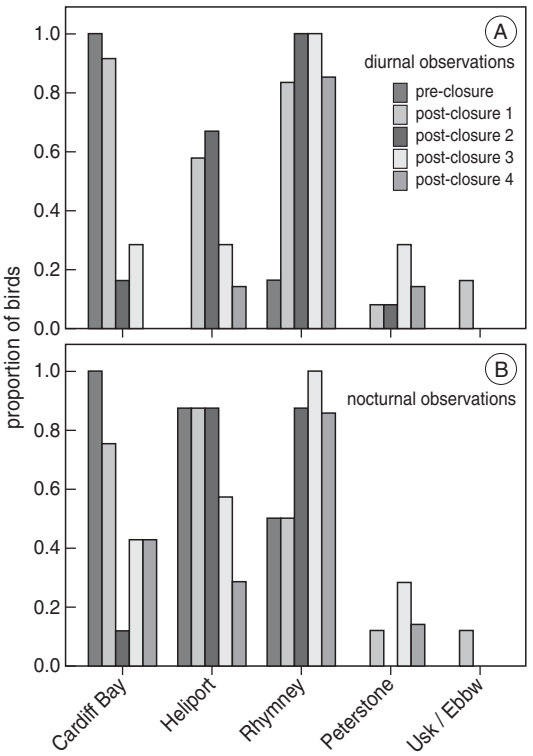

Figure 4. The proportions of adult, radio-tagged Cardiff Bay Redshank recorded at sites between Cardiff Bay and the Rivers Usk and Ebbw by period. (A) Diurnal observations ($n_{\text{columns 1–3}}$ = 12; $n_{\text{columns 4–5}}$ = 7) and (B) nocturnal observations ($n_{\text{columns 1–3}}$ = 8; $n_{\text{columns 4–5}}$ = 7). Note that, in each period, individuals may have been recorded at more than one site, thus proportions add up to more than 1.

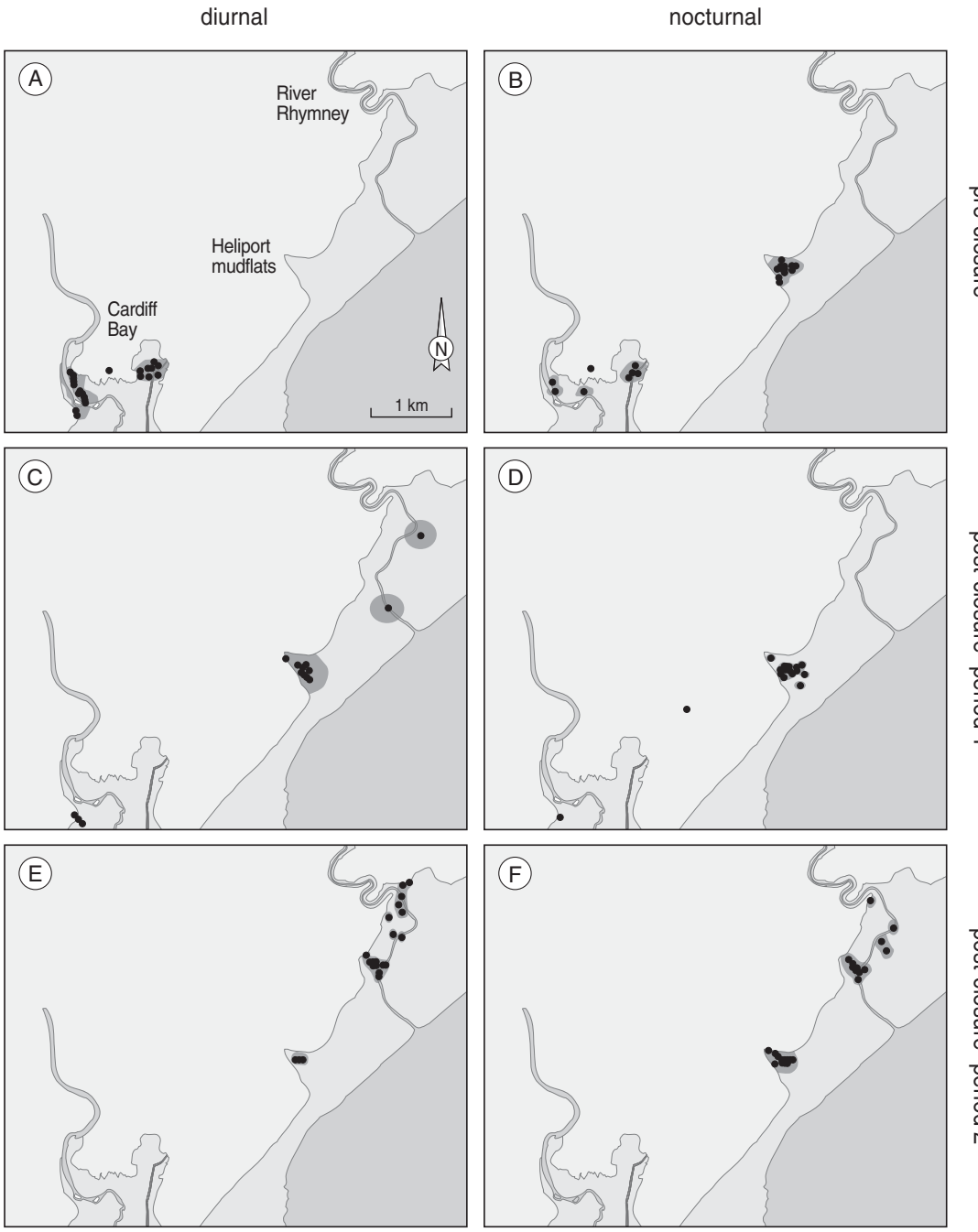

Figure 5. The radio-locations and estimated home ranges (shading) of adult Redshank RD19, radio-tagged at Cardiff Bay on 21 October 1999 by time of day (diurnal or nocturnal) and period.

Table 3. Mean maximum distances (km) between observations of individual adult Redshank radio-tagged at Cardiff Bay in October 1999 and their mean home range areas (ha) in pre- and post-closure periods.

Period		Day				Night			
		Mean	*n*	Min	Max	Mean	*n*	Min	Max
Pre-closure	Distance	1.45	12	0.76	5.56	4.26	8	1.20	7.51
	Range	14.7	12	1.1	76.9	36.8	8	16.7	85.2
Post-closure period 1	Distance	5.82	12	1.81	18.69	4.84	8	2.90	15.28
	Range	45.4	12	11.5	297.7	19.2	8	7.5	222.2
Post-closure period 2	Distance	3.33	12	1.25	8.46	2.43	8	1.46	3.40
	Range	31.8	12	9.3	108.0	24.2	8	2.4	70.1
Post-closure period 3	Distance	2.91	7	1.41	8.65	4.16	7	1.15	8.59
	Range	27.1	7	10.5	82.2	38.6	7	7.1	130.7
Post-closure period 4	Distance	1.11	7	0.63	2.61	2.66	7	0.94	3.99
	Range	11.1	7	3.7	20.6	20.6	7	6.9	31.9

Data from adults tagged in January 2000 indicated that by the end of winter 1999/2000 the extent of movements of displaced Redshank was similar to that pre-closure. The sizes of ranges decreased significantly between post-closure periods 3 and 4, diurnally ($t_7 = 3.32$, $P = 0.016$) and nocturnally ($t_7 = 2.63$, $P = 0.039$), though the maximum distances separating observations did not (diurnally: $t_7 = 2.27$, $P = 0.064$; nocturnally: $t_7 = 1.17$, $P = 0.29$).

In subsequent winters, colour-ringed Redshank displaced from the bay became more concentrated at the Rhymney River (Figs. 2C & 2D), though the percentage of colour-ringed birds in flocks there fell to 15% by 2001/02. A total of 238 different individuals were seen at the Rhymney River over these winters, in comparison to just 12 in the bay, 65 at the Heliport mudflats and 13 at Peterstone. Only one colour-ringed Redshank was seen on the Rivers Usk and Ebbw after 1999/2000 and two colour-ringed birds on the English side of the Severn.

DISCUSSION

Fidelity to Cardiff Bay after barrage-closure

The results of this study support previous work that has shown that Redshank are highly faithful to their wintering sites (Burton 2000, Rehfisch *et al.* 1996, 2003). In spite of the loss of intertidal habitat, Redshank appeared extremely reluctant to leave Cardiff Bay following its impoundment. Flocks of Redshank, including a large proportion of radio-tagged individuals, were present in the bay both at high and low tide for at least eight days after barrage-closure. Although few Redshank subsequently used the bay over the intertidal period, continued use over high water indicated that a strong fidelity to the site was maintained through the first winter post-closure. During that winter, radio-tagged Redshank fed in the bay on two of six occasions when the bay was temporarily drained overnight to help maintain water quality (eight of 13 birds with active transmitters on the first, two of seven on the second). This use of the bay was probably opportunistic, some of the birds having roosted in the bay over the preceding high tide.

The majority of Redshank from Cardiff Bay settled at the nearest alternative foraging sites, i.e. the Heliport and Rhymney River mudflats. This greatly increased the densities of birds recorded on these mudflats (Burton *et al.* 2006). Comparatively few moved further – despite extensive searches, marked birds were recorded only as far as the Rivers Usk and Axe, both 19 km distant.

Effects of prior knowledge and age

There was some evidence that the movements and settlement of Redshank displaced from Cardiff Bay were influenced by prior knowledge. Radio-tracking indicated that the speed of individuals' initial response to the loss of habitat was dependent on prior use of alternative feeding sites. Tagged individuals that had previously been recorded outside the bay diurnally left the bay more frequently in the first fortnight after its impoundment than those that had not.

The similarity in the proportion of colour-ringed birds in flocks of Redshank at the Heliport mudflats in 1999/2000 to that recorded in the bay immediately pre-closure indicates that the majority of Redshank using this site were birds displaced from the bay. However, it seems likely that the diurnal use of the Heliport mudflats by displaced birds was not solely the result of its proximity to the bay. This sewage-enriched foraging site had previously been avoided during the day, probably due to disturbance from helicopters, and thus it might not have been expected that displaced Redshank would have used the site. However, previous studies had shown that at least some Cardiff Bay birds frequented the site at night when the Heliport was unused (Burton & Armitage 2005). Although previously less favoured and disturbed, therefore, it seems probable that many Redshank displaced from the bay foraged at the Heliport mudflats diurnally as it was a site that they were familiar with and where they would be free from competition from other groups of Redshank. Fewer Cardiff Bay Redshank visited the Rhymney River mudflats pre-closure. Those that tried to settle there post-closure were likely to have faced intense depletion and interference competition for food, not only due to increased densities (Goss-Custard 1980, Burton *et al.* 2006) but also due to being less familiar with the locations of food resources and possibly of lower status to those birds already resident at the site (Whitfield 1985, Cristol *et al.* 1990, Senar *et al.* 1990, Snell-Rood & Cristol 2005).

There is one further piece of evidence to suggest that prior knowledge may have affected movements: one individual that crossed the Severn following barrage-closure – to the River Axe – had been reported on breeding grounds nearby in spring 1996, suggesting that it probably already knew this site. The other three individuals seen on the English side of the Severn were believed to have been colour-ringed at Cardiff on autumn passage, never having been recorded in the bay during winter.

Previous studies, e.g. of Dunlin *Calidris alpina* (Baccetti *et al.* 1995, 1999), have shown that attachment to wintering sites typically develops early in an individual's first winter. Thus at the time of barrage-closure, in early November 1999, the attachment of first-winter Redshank to Cardiff Bay is likely to have been limited. Only three first-winter Redshank were colour-ringed in the bay pre-closure; however, two were subsequently recorded on the River Usk – the furthest that any individuals were found to move. In common with many other birds, the extent of within-winter movements in Redshank also tends to be greater in first-winter birds than adults (Rehfisch *et al.* 1996, 2003).

Townshend (1985), studying Grey Plover *Pluvialis squatarola*, reported that patterns of spatial defence and the adoption of a wintering site were typically determined in the first autumn of an individual's life. Our results suggest, though, that the fidelity of individual Redshank to wintering sites may continue to develop over several years – as suggested for Dunlin by Baccetti *et al.* (1999). Older birds appeared less plastic in response to the loss of habitat, only moving to the nearest sites (the Heliport and Rhymney River mudflats) in the winter following barrage-closure, while younger birds (not just those in their first-winter) moved further. This variation in response could perhaps in part have been due to an inherent decline in behavioural plasticity with age, but likely also reflects the development of individual status. In Oystercatchers *Haematopus ostralegus*, for example, individuals become more dominant as they grow older, though this is at the expense of a decrease in range size (Goss-Custard & Durell 1987, Caldow *et al.* 1999, see Ens & Cayford 1996

for a review). Here, the small size of some home ranges pre-closure suggests that some, probably older, Redshank might have held territories in the bay (see Goss-Custard 1970), and any such individuals would have been particularly reluctant to leave. Young birds, though they returned to Cardiff each winter, may have been less attached to the bay due to a more subordinate status. For the same reason, these birds may also have avoided the high densities at the Heliport and Rhymney River mudflats post-closure (Ens & Goss-Custard 1984, Burton *et al.* 2006), so leading to their greater dispersal.

Temporal changes in movements and settlement

In spite of their fidelity to Cardiff Bay and use of sites that they had had prior knowledge of, displaced radio-tagged Redshank ranged more widely in the first two months following barrage-closure than they had previously. In part this reflects the fact that Redshank at the Rhymney River had inherently larger ranges than those at Cardiff Bay (Burton & Armitage 2005), though also may have been due to increased competition and the displaced birds' likely reduced status and limited knowledge of profitable foraging sites outside the bay. In Germany, Ganter *et al.* (1997) similarly found that Brent Geese *Branta bernicla* displaced by a loss of saltmarsh ranged more widely than a group of control birds.

Subsequent observations of colour-ringed birds and the increase in numbers of Redshank at the Rhymney River mudflats (Burton *et al.* 2006) indicated that displaced Redshank became concentrated into this site over the following winters, suggesting that birds were adapting to their new conditions. Although Redshank had continued to roost in Cardiff Bay in winter 2000/01 (when a peak of 91 birds and 10 different colour-ringed individuals were recorded there), use of the bay subsequently diminished (a maximum of just 30 Redshank and just two colour-ringed individuals were recorded in the bay in winter 2001/02).

Implications

Previous studies of Oystercatchers in The Netherlands have shown that birds displaced by habitat loss can be limited in where they can settle if alternate areas already hold high densities (Lambeck *et al.* 1996). Here, due to regional declines in numbers prior to barrage-closure, it is likely that there was spare capacity for Redshank at the time of the bay's loss (Burton *et al.* 2006) and thus settlement patterns will have largely reflected the species' inherent adaptability.

Evidence from marked birds has revealed that while the increase in densities at the Heliport and Rhymney River mudflats post-closure had no impact on the survival of those adult Redshank already resident there, adults displaced from Cardiff Bay experienced a 44% increase in annual mortality (Burton *et al.* 2006). The present study suggests that this difference was likely to have been partly due to a lack of behavioural plasticity in response to change. Displaced birds only moved short distances and settlement also appeared to be influenced by birds' previous knowledge. The Heliport mudflats, previously only used nocturnally by 'Cardiff Bay' birds, were used diurnally post-closure despite being heavily disturbed. It is suggested that birds' fidelity to the bay post-closure and lack of knowledge of and, perhaps, status at suitable alternative foraging sites would have been to their detriment as it would have prevented them from fully exploiting available resources. Notably, the oldest individuals, i.e. those likely to be the most experienced breeders, appeared least able to respond and should these individuals have suffered greater mortality as a result, there could have been additional effects on the birds' breeding productivity.

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SAMENVATTING

Of dieren bij verlies van habitat kunnen overleven hangt af van de nabijheid van alternatieve plekken en het vermogen om deze nieuwe plekken te vinden. In het onderhavige onderzoek werd onderzocht welke factoren van invloed waren op het verspreidingspatroon van Tureluurs *Tringa totanus* toen hun overwinteringsgebied, de Baai van Cardiff (UK), werd afgesloten met een zeekering. De Tureluurs bleken zeer trouw aan hun overwinteringsplek, zoals ook al uit eerder onderzoek aan de soort was gebleken. De Tureluurs waren in de eerste winter na de afsluiting amper bereid de baai te verlaten. Toen het gebied afgesloten werd, bleven de vogels er acht dagen lang rondhangen zonder dat ze er voedsel konden vinden. Daarna bleven ze naar het gebied terugkeren om er te slapen. De vogels verplaatsten zich maximaal 19 km van hun oorspronkelijke overwinteringsplek. Hoe jonger de vogels waren, des te verder trokken ze weg. Dit wijst erop dat jonge vogels het minst gehecht waren aan hun plek van overwinteren en dus het meest flexibel in gedrag waren. Het vinden van een nieuwe plek bleek ook af te hangen van eerder opgedane kennis. Dit werd geconcludeerd op grond van de waarneming dat een plek die de vogels oorspronkelijk alleen 's nachts bezochten na de afsluiting ook overdag werd gebruikt als voedselgebied ondanks forse verstoring door helikopters. Na de afsluiting werden de Tureluurs op talloze nieuwe plekken waargenomen, maar binnen drie jaar na de afsluiting concentreerden de vogels zich in een gebied dat slechts 4 km van de baai verwijderd was. Er wordt geopperd dat de sterke trouw aan de baai na het afsluiten ervan en een gebrek aan kennis van alternatieve voedselgebieden ongunstig moeten zijn geweest voor hun overlevingskansen.
(DH)

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