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DIURNAL AND NOCTURNAL TERRITORIALITY IN THE GREY PLOVER AT TEESMOUTH, AS REVEALED BY RADIO TELEMETRY

By A. G. Wood

During the non-breeding season individuals of many species of shorebirds defend foraging territories (Myers et al. 1979). The decision by an individual to defend or not defend an area, and for how long, is affected by many factors such as prey density, density of conspecifics and habitat type (Myers et al. 1981).

A number of workers have shown that many wader species, including Grey Plovers (*Pluvialis squatarola*), may continue to forage at night (Dugan 1981a, Knights 1979, Pienkowski 1983, Sutherland 1982), but the behavior of individuals is unknown. Recent work on Grey Plover wintering at Teesmouth has revealed that up to 40% defend foraging territories in the intertidal zone by day (Dugan 1982, Knights 1979, Townshend et al. 1984). Direct visual observation of color-marked individuals has provided much information on the use of areas of the mudflats by different birds. However, two important questions concerning the social and foraging behavior of Grey Plovers remain to be answered. Firstly, where do the birds go and what do they do at night? Secondly, does a territorial bird use and defend the same area during both diurnal and nocturnal low water periods? Answers to these questions have important implications for the accurate determination of time and energy budgets of individuals.

METHODS

This study was carried out on the estuary of the River Tees in NE England (54°37′N, 1°12′W) (Fig. 1), particularly on Seal Sands, an area of 140 ha of mudflats remaining after extensive reclamation of intertidal land. Seal Sands is exposed and available to foraging shorebirds for 7–8 h in each tidal cycle. If birds cannot obtain enough food during that period of exposure, they may move to the higher tidal flats of North Gare as the tide rises.

Birds were caught, individually color-ringed and had radio transmitters attached using a harness similar to that used by Brander (1968). Bird locations were monitored from the ground using an AVM LA 12 receiver and a 3 element hand-held Yagi antenna. Observations were made with 10 × 50 binoculars and a 15–60 × 60 telescope. At least 14 d elapsed before any data were used from the radio-tagged birds, to reduce the chance of including abnormal short-term effects of the transmitters on the birds' behavior.

The location of a radio-tagged bird was obtained by triangulation. Directional fixes on a bird were made in quick succession from two or

more points. For each radio fix the direction of maximal signal strength for an individual was determined and drawn as a line on specially prepared field maps. Data were collected only when the birds were on the mudflats, and hence moving around slowly (Wood 1984). Any errors induced by the time lag between successive fixes were considered unimportant when compared to the errors in triangulation (Heezen and Tester 1967, Springer 1979). Data from the field maps were transferred to computer file in the form of digitized co-ordinates. Information on the time of day and state of tide were also recorded.

As each radio fix has an inherent error associated with it (Heezen and Tester 1967), use of a point location to represent the position of a bird would imply greater accuracy than the detection system can produce. Therefore in the maps that follow a circle has been used to represent the position of a bird deduced from triangulation. The area of the circle was determined as the approximate area of one bird's territory. This individual could be observed, and radio triangulation of its position could not reveal whether it was positioned at one or other extreme edge of its territory. A bird was assumed to be using the same foraging location if the error circles around its triangulated positions on different dates overlapped.

RESULTS

In mid January 1981, 15 Grey Plovers were radio-tagged, and their behavior monitored for a total of 18 days and 12 nights until the end of March 1981. This period of the year is one in which the population of territorial individuals at Teesmouth is relatively constant (Dugan 1981b, Townshend 1982).

Diurnal observation allowed these birds to be classified into one of three behavioral types (Townshend et al. 1984); long-term territorial birds—individuals that defended the same foraging site against conspecifics over a period of several months; short-term territorial birds—individuals that fed non-territorially for the majority of the time, but defended one or more foraging sites for short periods; non-territorial birds—individuals that fed without a territory at all times. Figures 2–4 show radio-telemetric data for examples of each of these categories of Grey Plovers.

Figure 2 shows data typical of long-term territorial individuals. They are characterized by having radio-triangulated locations heavily clustered about one site, this being the known diurnal low-water foraging territory. This territory was also used very regularly during the nocturnal low-water periods, as both diurnal and nocturnal triangulated locations were indistinguishable in the area covered.

Short-term territorial birds (Fig. 3) clearly exhibited clustering of triangulated locations in more than one site during the study period. At times these birds would use the same locations by day as by night, but later in the study period other sites were preferred for a number of days and nights.

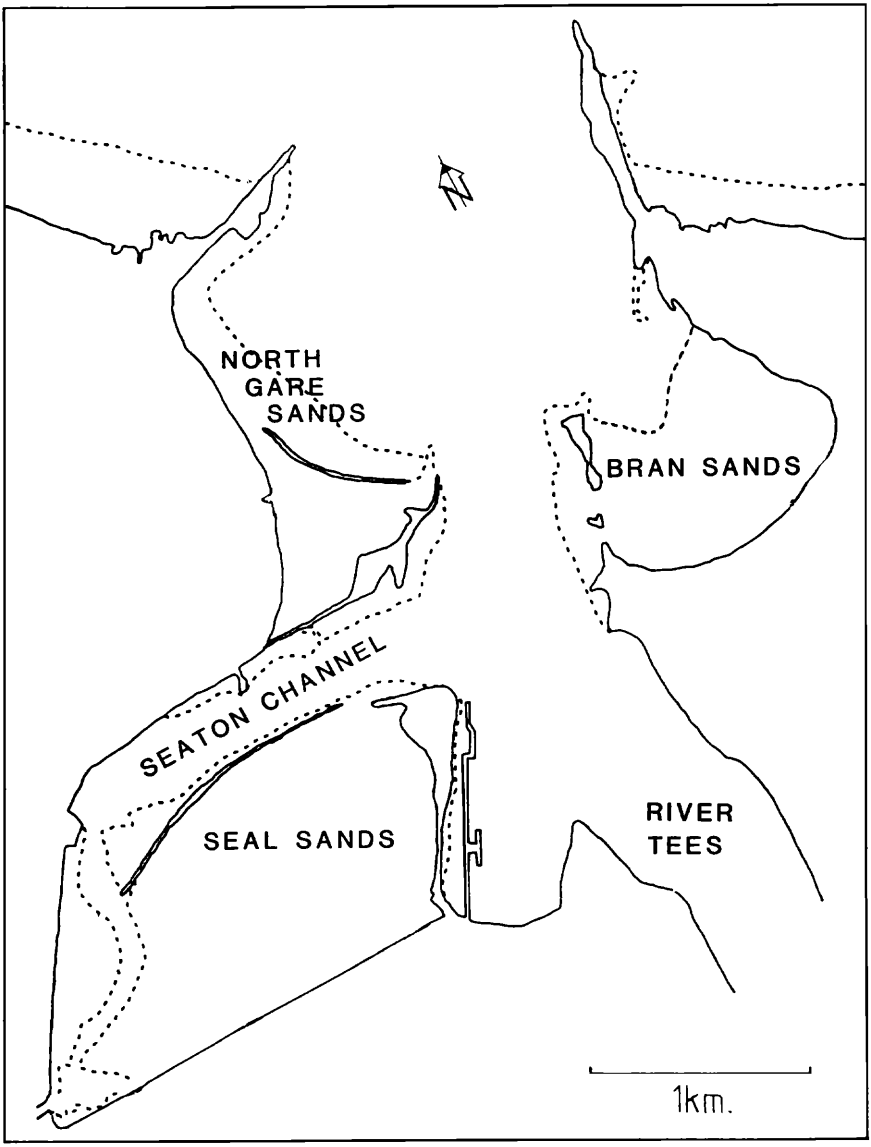

FIGURE 1. Map showing details of the estuary of the River Tees in NE England. ----- indicates position of mean low water, spring tides.

It was clear from subsequent nocturnal observations of territorial Grey Plover (Wood 1984) that they were actively defending their low-water foraging locations. Indicating that, particularly in long-term territorial Grey Plover, the use and defense of a low-water foraging territory, were regular diurnal and nocturnal activities.

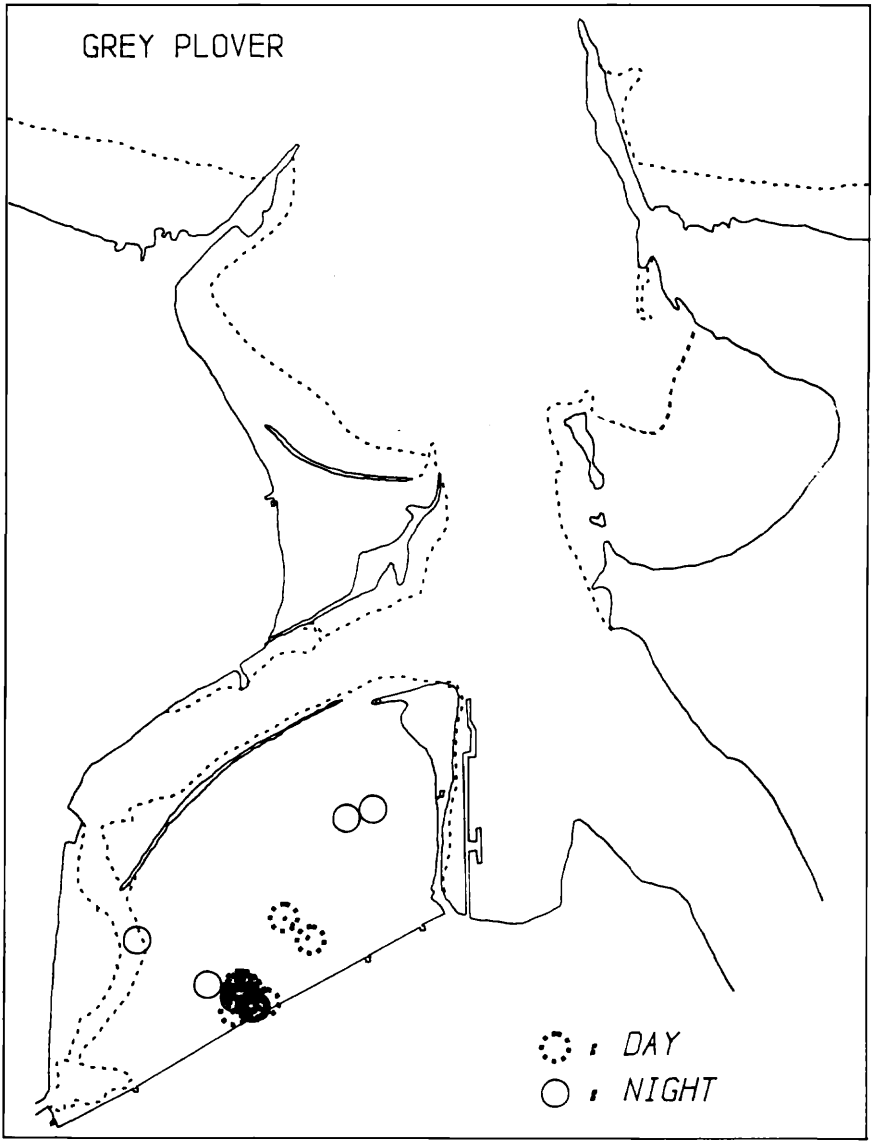

FIGURE 2. Low-water foraging locations of territorial Grey Plovers, January–March 1981. A line joins two or more different foraging locations used on the same date.

Finally, non-territorial Grey Plover, typified by the example in Figure 4, were consistent in the wide range of radio-triangulated locations found throughout the study period. These birds exhibited very little consistent use of one site, and were found in low-water foraging locations away from the main mudflat area of Seal Sands.

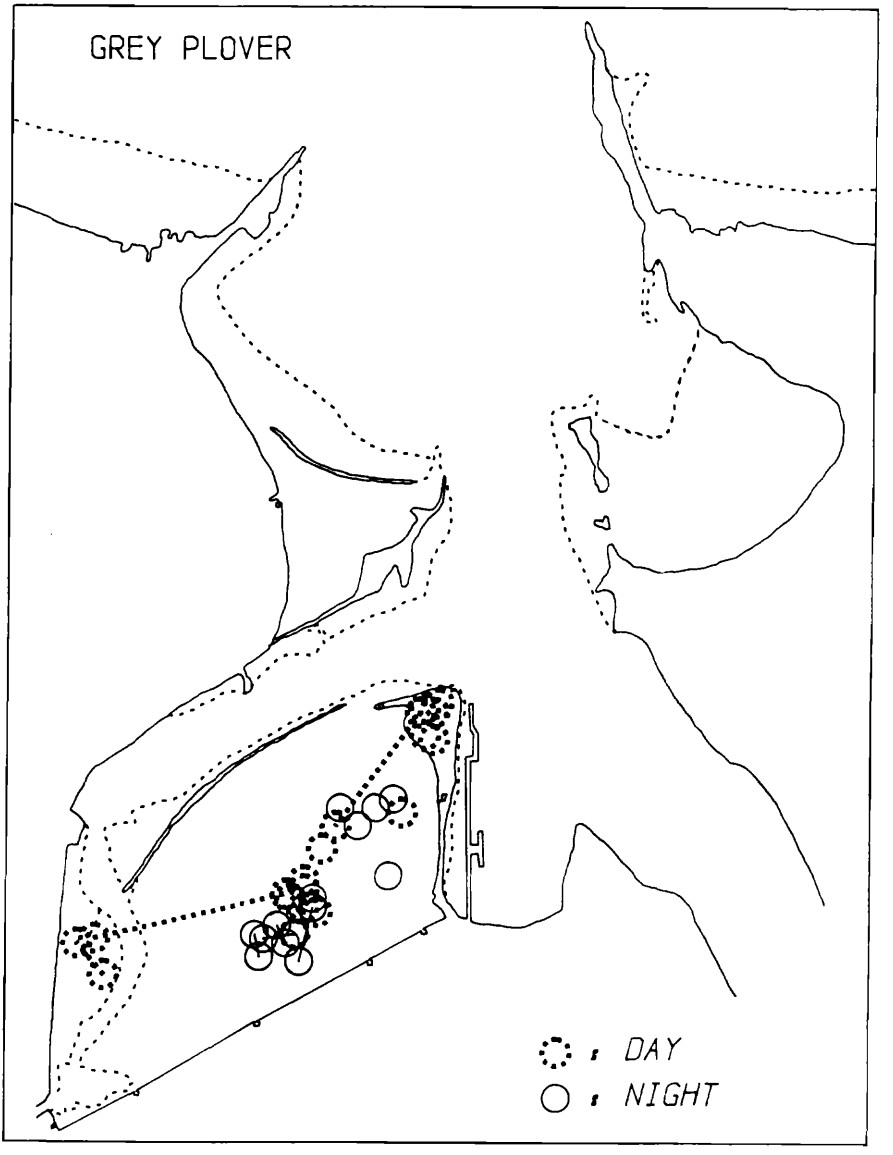

FIGURE 3. Low-water foraging locations of short-term territorial Grey Plovers, January–March 1981. A line joins two or more different foraging locations used on the same date.

Both long- and short-term territory holders occasionally used sites other than their normal territories. The data on site fidelity in Table 1 show that long-term territorial Grey Plover spent significantly more time on their territories by day than by night ($\chi^2 = 5.6$, $P < 0.05$); but they

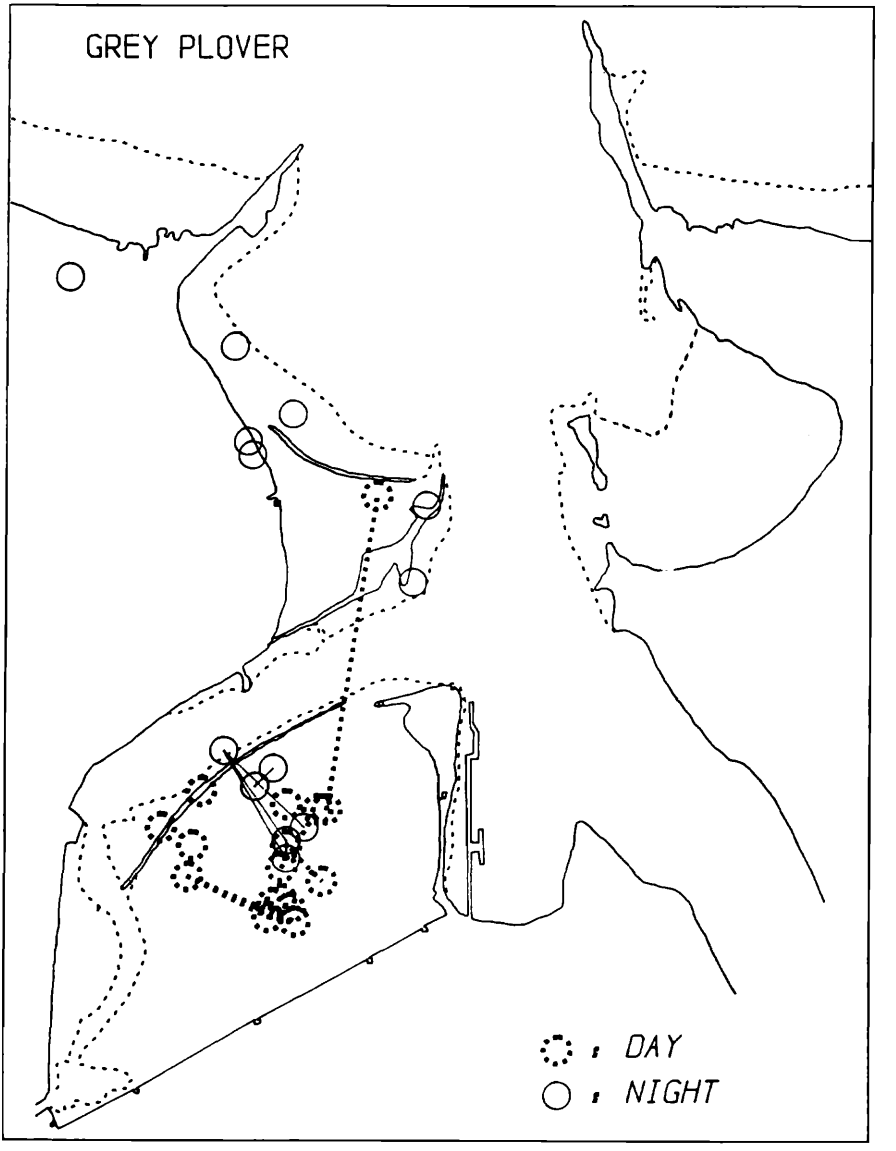

FIGURE 4. Low-water foraging locations of non-territorial Grey Plovers, January–March 1981. A line joins two or more different foraging locations used on the same date.

used their territories more frequently than non-territorial foraging locations. Short-term territorial birds showed no significant difference between diurnal and nocturnal use of their numerous defended sites ($\chi^2 = 3.1$, $P > 0.05$); and over the study period they used territorial locations

TABLE 1. Percentage of total number of bird days/nights on which a defended site was occupied, data obtained by radio telemetry.

		Percentage of bird days/nights on defended site	Total no. bird days/nights
Long-term territorial (5 birds)	Day	91	65
	Night	75	60
Short-term territorial (3 birds)[a]	Day	56	39
	Night	36	36

[a] The data for short-term territorial individuals refer to the use of more than one location by any one bird.

as frequently as non-territorial locations. The data for the short-term territorial birds show a trend for the use of territorial locations diurnally, and non-territorial locations nocturnally. Dugan (1981a, and in Townshend et al. 1984) suggested that such movements might occur to take advantage of more abundant food at lower tidal levels, particularly at night. However, the data in Table 2 indicate that there was no significant difference ($t = 1.76$, $P > 0.05$) between the mean predicted height of low water on dates on which normal territorial behavior was observed, and dates on which long-term territorial birds used an atypical foraging location.

Other factors that could have affected the behavior of these birds include, most importantly perhaps, the prevailing weather conditions. Dugan et al. (1981) found that the weather conditions under which Grey Plovers lost weight were associated with higher than normal chill factors. A chill factor is related to the rate of heat loss by a bird, and is derived from the effect of wind speed on the metabolic rates of birds at temperatures below thermoneutrality (Gessaman 1973). Chill factors were adequate predictors of the choice of foraging location by long-term territorial Grey Plovers (Table 2). The mean chill factor for dates on which normal territorial behavior was observed was significantly lower ($t = 2.88$, $P < 0.01$) than that calculated for dates on which birds used a different foraging location. These long-term territorial birds moved to a

TABLE 2. Physical parameters associated with the temporary changes in foraging strategies of long-term territorial Grey Plover.

	For dates of normal territorial behavior	For dates when a new temporary foraging site used	*N*
Mean predicted height of low water (m) ± SE	1.4 ± 0.13	1.1 ± 0.11	29
Mean chill factor ± SE (Dugan et al. 1981)	11.7 ± 1.95	21.7 ± 2.88	29

new temporary foraging site under more extreme environmental conditions, as characterized by dates with high chill factors.

DISCUSSION

The use of radio telemetry to study the foraging and social behavior of the Grey Plover at Teesmouth has substantiated a number of previous speculations. Diurnal classification of the degree of territoriality exhibited by individual birds was confirmed by the radio telemetry results. The diurnal classification also appeared to hold for the nocturnal low-water periods, when the birds followed the same behavior as that observed by day.

The costs and benefits of territoriality in the Grey Plover have recently been reviewed by Townshend et al. (1984). They concluded that the benefits of holding long-term territories must also be evaluated in the long-term. Presumably the short-term changes in behavior of normally territorial individuals has some significance, and may represent the birds monitoring different foraging locations in order to determine the costs and benefits of remaining at a particular site (Davies 1976).

The suggested reasons for a particular bird having or lacking long-term territorial behavior are numerous (Townshend et al. 1984). The final result may be determined by a bird's behavior in the early years of its life (Townshend 1985). The factors that determine where a non-territorial bird will forage may be additionally influenced by the decisions of territorial individuals, if density of conspecifics is high (Goss-Custard 1977). This could explain the much wider range of sites used by non-territorial Grey Plovers during the low-water period.

SUMMARY

Radio telemetric data on Grey Plovers (*Pluvialis squatarola*) at Teesmouth confirmed diurnal observations that some birds consistently defended the same low-water foraging territories, and that other individuals were either non-territorial, or defended a foraging site for only a short time. Similar data collected at night showed that the behavior exhibited by an individual during the day was maintained during the nocturnal low-water period. Territorial birds were not totally faithful to one foraging location, but on a few days and nights used other areas of the intertidal mudflats.

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