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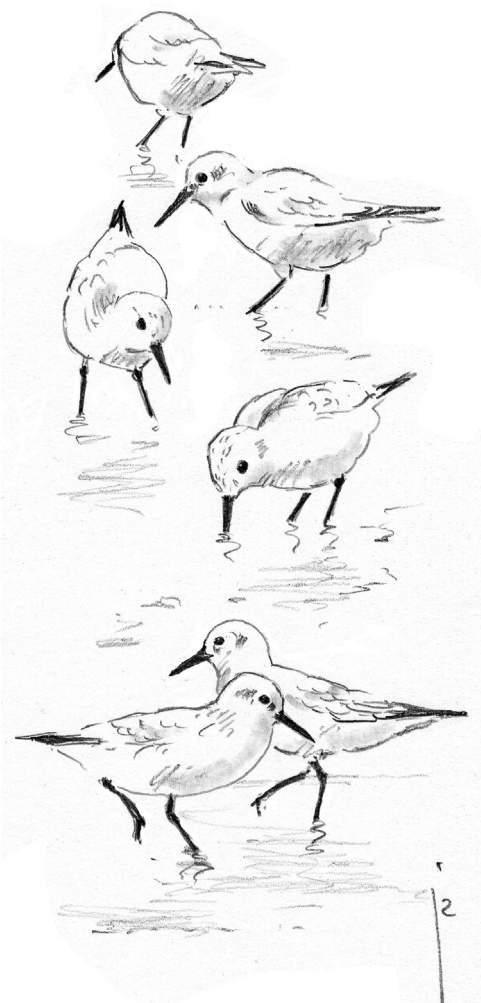
To be able to set priorities in species conservation planning, we need to know how these species prioritize the environment themselves, i.e. what they consider to be better and worse sites. We present a unique and relevant case from tropical West-Africa based on 20 years of monthly counts of wetland sites spread along the 550 km long coast of Ghana. The Ghanaian Sanderling *Calidris alba* population increased almost fourfold from average monthly total counts of c. 1350 Sanderlings to 4850 during the study period. Interestingly, with this considerable increase, the sites with the larger numbers at the start of the survey showed the smallest relative increases during 20 years of monitoring. This pattern is consistent with a buffer effect and suggests that with an increasing overall population the best quality sites are filled up, so that additional birds will be forced to use lower quality sites. The preferred site in Ghana, a stretch of beach near the village of Esiama between the Amansuri-Ankobra estuaries, is now entirely unprotected. We argue that the site should be placed higher on the conservation agenda given the fact that up to 3.5% of the Sanderling population connecting Greenland with West- and southern Africa rely on this site.

Key words: buffer effect, density-dependence, population regulation, coastal wetlands, waterbirds, flyway conservation

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The buffer effect concept describes density-dependent patterns of habitat and resource use. At low densities, individuals would occur predominantly at the most profitable sites, but with sustained population increase a higher proportion of individuals are forced onto poorer quality sites (Kluyver & Tinbergen 1953, Brown 1969, Sutherland 1996). As more birds start using sites of lower quality, population growth will slow down because of decreases in average survival (Gill *et al.* 2001) and/or reproduction (Ferrer & Donazar 1996). The concept, first described by Kluyver & Tinbergen (1953), has been developed to define the carrying capacity of areas and has been applied to several species in both breeding and non-breeding seasons and at a range of scales from patches within a site to sites across a country (Fretwell & Lucas 1970, Zwarts 1976, Goss-Custard 1977, 1980, Sutherland 1996). So far, the buffer effect has been demonstrated in only two wintering shorebirds, both from Great Britain; Grey Plover *Pluvialis squatarola* by Moser (1988) and Black-tailed Godwit *Limosa limosa islandica* by Gill *et al.* (2001).

In this study we test for evidence of the buffer effect using a 20-year monthly count series of a growing population of Sanderling *Calidris alba* in Ghana, West-Africa. Sanderlings are long-distance migrant shorebirds that breed in the High Arctic tundra of eastern Canada, Greenland and central Siberia (Piersma *et al.* 1996). In the non-breeding season they are widely distributed in coastal areas, particularly along sandy beaches (Reneerkens *et al.* 2009a). Ring recoveries

indicate that Ghana's coastal wetlands are visited by Sanderlings of Greenlandic breeding origin and serve as staging areas for individuals that continue further south to spend the winter months in Namibia and South Africa, and also as residential habitat for those that remain in Ghana (Gudmundsson & Lindström 1992, Reneerkens *et al.* 2009a, Ntiamoa-Baidu & Reneerkens unpubl. data).

The Sanderling population in Europe and Africa that uses the East Atlantic flyway has increased substantially from c. 70,000 in the 1980s to 123,000 in the 1990s (Reneerkens *et al.* 2009a, Scott 2009). An increased abundance of Sanderlings in Ghana is expected to lead to an increased use of less profitable sites when the preferred sites have reached their carrying capacity. The long-term counts in Ghana thus offer an ideal opportunity to examine the occurrence of a buffer effect, and as the buffer effect indicates which sites are preferred by birds themselves, we explore the potential value of our analysis to support conservation priority setting.

METHODS

Counts

Sanderlings were counted as part of the waterbird population monitoring in coastal Ghana that has been running since 1986 (Ntiamoa-Baidu & Grieve 1987, Ntiamoa-Baidu 1991, 1993, Ntiamoa-Baidu *et al.* 1998). Initial familiarisation visits undertaken in 1985/86 covered the entire Ghanaian coast and waterbirds were counted on all the coastal lagoons and sandy beaches. Subsequent surveys focused on 17 sites that regularly held significant populations of waterbirds. Our analysis is based on Sanderling counts spanning over a 20 year period (1987–2006; Figure 1) from 11 of the sites (Amisa Lagoon, Narkwa Lagoon, Densu delta, Elmina salt pans, Esiama beach, Keta Lagoon, Lalui Lagoon, Muni Lagoon, River Whin mouth, Sakumo Lagoon and Songor Lagoon; Table 1) . The 11 sites vary in size from under 5 km² to over 300 km² and comprise varying habitat types. Esiama is a 13 km sandy beach between two estuaries (Figure 2). Keta and Songor Lagoon are the large lagoons associated with the Volta River estuary consisting of open water bodies and extensive mudflats and flood plain, The rest are open or closed brackish water lagoons associated with the estuaries of smaller rivers along the coast. Four of the sites, Densu delta, Elmina salt pans, Lalui and Songor, are associated with commercial and traditional salt winning ventures (see also Ntiamoa-Baidu 1991 for descriptions of sites). Although Sanderlings were sometimes encountered at all the 17 sites, the 11 sites were the ones counted every month throughout the 20 year survey, thus excluding any biases due to missing data. Together the 11 sites accounted for 99% of all Sanderlings recorded on Ghana's coast. Each site was visited once in the first week of every month by teams of two to three people. All waterbirds observed were counted on foot using telescopes and binoculars.

Data analysis

Based on the observed seasonal patterns of occurrence of Sanderling in Ghana (Ntiamoa-Baidu 1991, see Figure 1), the population trends and site selection

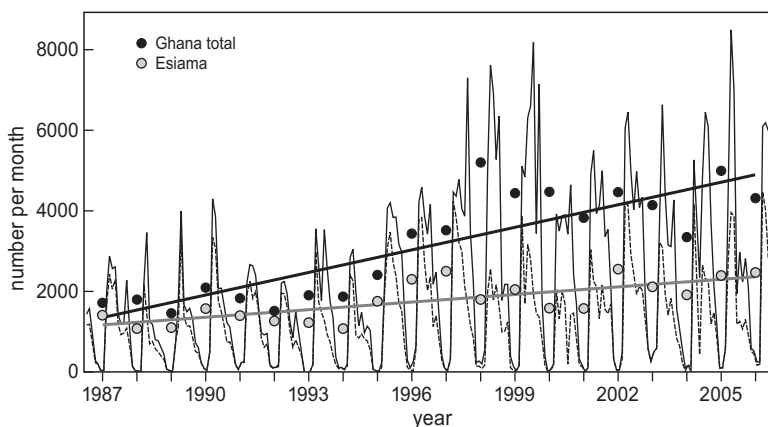**Figure 1.** Monthly counts of Sanderling on the coast of Ghana over a 20-year period (1987–2006). The solid line shows total numbers recorded every month at all the eleven study sites and the broken line numbers recorded at Esiama. The ticks on the x-axis indicate June each year, the month with lowest numbers of Sanderlings counted. Regression lines show the monthly averages in September–April for the total of all sites and for Esiama.

analysis were based on the September–April counts, thus focusing the analysis on the period with relatively stable non-breeding population. The reasons for excluding the four months, May–August, were that they represent (1) periods of active migration, with birds arriving from the northern autumn migration (August), (2) months of departure on northern spring migration (May), or (3) breeding periods when very low numbers are present on the Ghanaian coast (June–July).

We analysed the increase in the numbers counted each month in each year ('total annual bird count') at each study site in comparison with the total annual count for all sites. The difference in the slopes of the two linear regression lines of bird numbers during the census period (Figure 1) for Esiama and for all other sites together was tested using a simple ANCOVA. The total annual bird count was calculated based on the actual numbers counted each month, as we found no difference in the outcome of the analysis when bird-days (calculated as the count in any one month at a particular site multiplied by the number of days in the particular month) were used. The rate of change at each site was calculated as the slope of the linear regression of the $\log_{10}$(total annual bird count) at the site against the $\log_{10}$(total count for all sites). To examine the existence of a buffer effect, the rate of change for each site was plotted against $\log_{10}$(initial population size) at the site. The initial population size was estimated from the average annual counts of the first three years of the study (1986/87–1989/90). Data were analysed using Microsoft Excel and R v. 2.12.2 (R Development Core Team 2011).

RESULTS

Sanderlings started arriving on the Ghanaian coast from their northern breeding grounds in August, with peak numbers occurring in September–October, after which the numbers dropped to about half of the autumn peak. In some years a smaller peak was observed in March–April (Figure 1).

During the non–migration period, September–April, an average of 3117 ± 1295 (SD) Sanderlings was counted monthly at the monitored sites. The monthly average population increased significantly (almost

Table 1. Characteristics of the 11 coastal sites in Ghana included in the analysis, with monthly average peak counts of Sanderlings recorded in the initial five years of the survey (1986/87–1990/91) and final years of the survey (2000/01–2005/06).

Site	Characteristics (estimated beach length/lagoon perimeter used by foraging Sanderlings)	Monthly average peak count in first five years of survey (range)	Monthly average peak count in last five years of survey (range)
Amisa Lagoon	Brackish water lagoon, sandy beach front (3 km)	82 (18–153)	127 (72–187)
Densu delta	Commercial salt industry, several reservoirs, brackish water lagoons, sandy beach front (10 km)	114 (37–203)	796 (695–999)
Elmina salt pans	Small scale salt pans and reservoir (4.5 km)	83 (2–368)	278 (140–589)
Esiama beach	Sandy beach between Ankobra and Amansuri Rivers (13 km)	2743 (2221–3429)	3898 (3225–4238)
Keta Lagoon	Large brackish water lagoon and mudflats associated with the Volta River delta, extensive fishing activities, shallot farming in coastal flood plain (63.5 km)	479 (228–658)	1618 (1506–1776)
Lalui Lagoon	Small scale salt production, salt pans and edges of concentration ponds used by feeding and roosting waders (0.5 km)	35 (10–71)	138 (70–216)
Muni Lagoon	Brackish water lagoon, occasionally link to sea opens with heavy rains, sandy beach front (3 km)	95 (44–148)	331 (234–499)
Narkwa Lagoon	Brackish water lagoon, sandy beach front (6 km)	12 (0–27)	81 (18–170)
River Whin mouth	River estuary with small mud/sand flats (0.5 km)	48 (32–67)	178 (32–482)
Sakumo Lagoon	Brackish water closed lagoon, intensive fishing (1 km)	142 (69–229)	286 (123–452)
Songor Lagoon	Brackish water closed lagoon, limited fresh water inflow, seepage of sea water through sand dunes, commercial salt production in northern sections, traditional salt collection during dry season (17 km)	386 (212–700)	1358 (795–1784)

Figure 2. A roosting flock of sanderlings on Esiama beach (22 January 2008) is disturbed by a fisherman. Although Sanderling occur at Esiama beach in numbers of international and national importance, the site is currently not designated as a protected area (Photo Jeroen Reneerkens).

fourfold) from c. 1350 to 4850 during the study period ($r^2 = 0.73$, $P < 0.0001$; Figure 1). From the beginning of the survey, Sanderlings occurred on all sites, but a single site, Esiama beach, accounted for an average of 73% of the total annual counts during the first ten years of the survey period (Table 1). The numbers of Sanderling at the other sites increased considerably faster than at Esiama beach (ANCOVA $t_{37} = -6.56$, $P < 0.0001$; Figure 1), resulting in a decrease in the degree of importance of Esiama relative to the other sites and an increase in the relative importance of the other sites. In the last five years of the survey, numbers at Esiama had dropped to 55% of the total counts. There was much variation in the extent of increases at the different locations (Figure 3), and a negative relationship between the initial numbers and the rate of increase at a site during the 20 year study period was observed ($r^2 = 0.51$, $P < 0.05$; Figure 4).

The 11 sites vary considerably in size with respect to the beach/lagoon edges commonly used by Sanderlings (Table 1). The estimated length of the beach or lagoon edges (Sanderlings always forage along water edges) varies from less than 0.5 km to 63.5 km across the different sites. However, there was no relationship between the size of the sites and the average number of Sanderlings that used them in the first three years of the study (linear regression on $\log_{10}$-transformed data, $F = 1.70$, $P < 0.20$).

DISCUSSION

The extensive, scattered distribution of non-breeding Sanderlings on sandy beaches worldwide (Scott 2009, Reneerkens *et al.* 2009a) makes population monitoring particularly difficult. A 20-year series of uninterrupted monthly counts in coastal Ghana presented a unique opportunity for analysis of population trends. The population of Sanderling using the East Atlantic flyway was estimated at 123,000 birds in the 1990s (Stroud *et al.* 2004), a considerable increase from the estimated 70,000 in the 1980s (Smit & Piersma 1989). The almost fourfold increase of the Ghanaian non-breeding population parallels the increase of the flyway population.
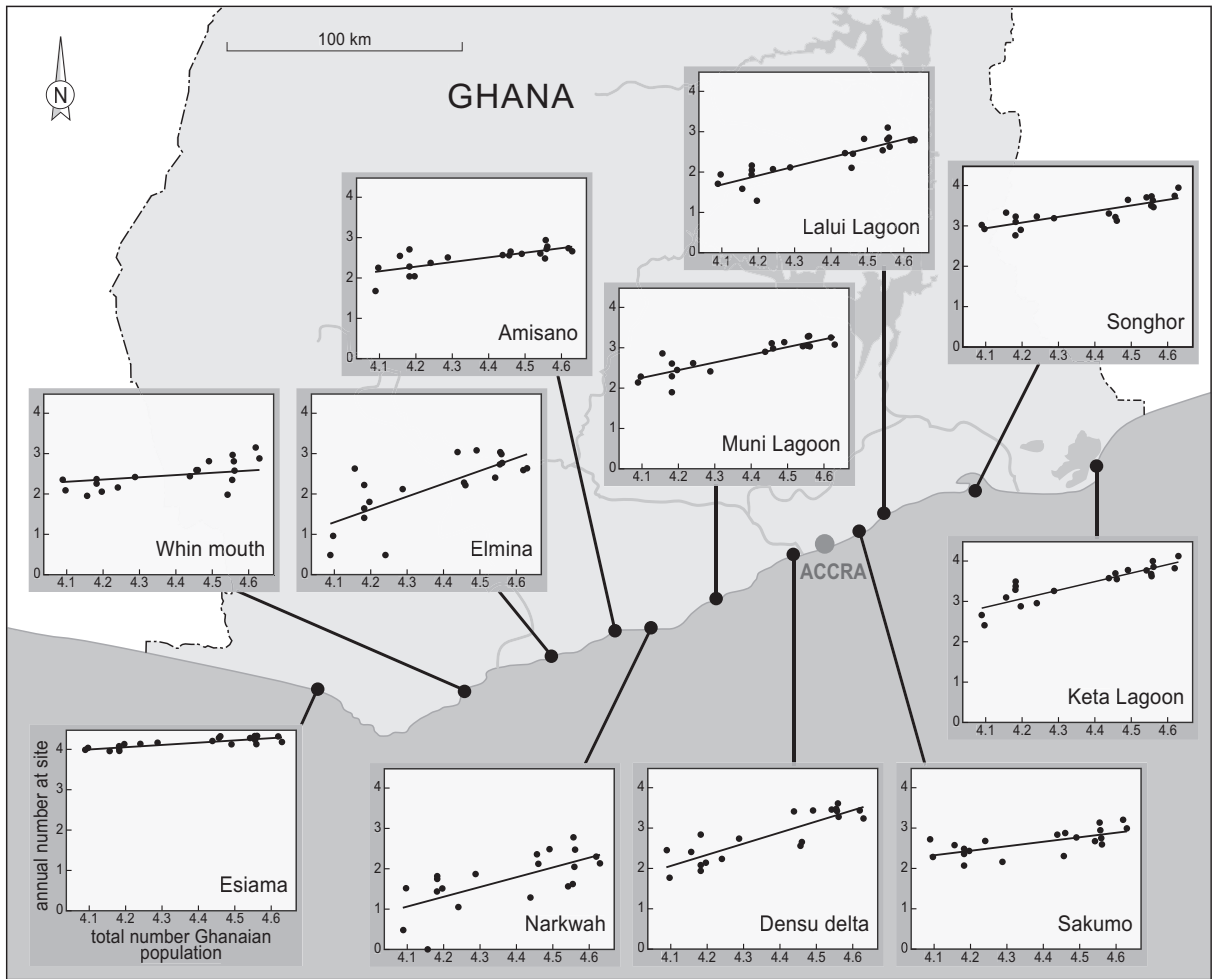
Figure 3. Rates of change of Sanderling numbers at 11 different sites along the coast of Ghana. Total annual Sanderling counts (log$_{10}$-transformed) for each site are expressed against those of the total Ghanaian coast. Axes are identical on all graphs.
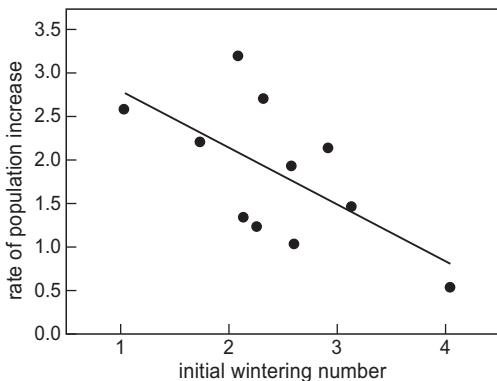

Figure 4. Rate of change in Sanderling populations at the different sites relative to initial wintering numbers (mean local numbers from 1987–1989 plotted on log$_{10}$–log$_{10}$-scale). Linear regression: $r^2 = 0.40$, $P < 0.05$.

The negative correlation between the rate of increase at the sites and the initial total population is consistent with a buffer effect at a large-spatial and temporal scale (e.g. Sutherland 1996). The buffer effect had hitherto been demonstrated in two shorebird species (Moser 1988, Gill *et al.* 2001) all using British estuaries, and on the breeding grounds in Iceland (Gunnarsson *et al.* 2005), and also in four other water-birds (Great Crested Grebe *Podiceps cristatus*, Whooper and Mute Swans *Cygnus cygnus* and *C. olor*, and Wigeon *Anas penelope*, Jackson *et al.* 2004). A buffer effect can occur with an overall growing population across a range of sites that differ in quality. As the preferred sites reach their carrying capacity, additional individuals are forced to move to other, less preferred, locations. An assumption here is that the (relative) quality of sites remains constant over the time of study. We cannot

exclude the possibility that the pattern found can be explained by a change of habitat quality over time at the different sites, with individuals increasingly using sites that increased in quality in concert with the growing overall population. We have not measured food availability, intake rate, predation risk or other parameters that could indicate the quality of the sites (Piersma 2012), but instead use the pattern to indicate which of the sites are considered to be of high or low quality by the birds themselves. Ongoing comparative studies focusing on the quality and use of the Esiama site and other selected sites on Ghana's coast used by Sanderlings is expected to provide more insight.

There was no indication of a relationship between the size of the sites and Sanderling numbers on the site, and therefore no indication that small populations occurred on small sites and big populations on big sites. Sanderlings showed a clear preference for the c. 13 km stretch of sandy beach between the Ankobra and Amansuri Rivers near the village of Esiama. In the early years of the counts, when the overall Sanderling population in Ghana was lower, over 70% of the population occurred at this site. The situation of the Esiama beach between two estuaries makes it potentially one of the most productive beaches in the country, especially with respect to young and small individuals of the bivalve *Donax pulchellus* which occurred in enormous densities of 5700–14,300 individuals/m^2. This species was the single important prey for Sanderlings in 2008 and 2009 (Reneerkens *et al.* 2009b). In the earlier years, Sanderlings were observed to forage also on large quantities of coconut waste thrown on the beach from the coconut oil extraction industry (Ntiamoa-Baidu unpubl. obs.).

Priority setting for conservation investment has hitherto often focused on centres of diversity, endemism and unique wildlife areas with globally or nationally threatened species and/or large populations (Olson & Dinerstein 1998, Isaac *et al.* 2007, Stephenson & Ntiamoa-Baidu 2009). It is usually implicitly assumed that these high conservation value sites also would be the preferred sites from the viewpoint of the target species themselves. The buffer effect analysis provides an additional, and a potentially powerful tool for selection of priority sites for conservation investment based on choices made by the target species themselves and should be encouraged for all species for which long-term count data are available. In the specific case of waterbird populations, presently, the 1% threshold of a flyway population is the criteria used most frequently for designation of wetland sites of international importance (Rose & Scott 1997, www.ramsar.org). The buffer effect implies that a site which

holds 1% or more of a species, and therefore qualifies for international importance at a particular point in time, could lose its international status as the population of the species increases. Such a site, however, may still hold the highest numbers and constitute the most important site for the species in a particular region; therefore although the numbers may not meet the 1% threshold, the site would deserve conservation attention. The buffer effect analysis also enables identification and prioritization of sites that would absorb the spill-over of an increasing population and also provide alternate sites in situations where the preferred site is threatened. Of the 11 Ghanaian coastal sites monitored, only five are designated as Wetlands of International Importance following the Ramsar Convention. Esiama, the most important site for Sanderlings that supports up to 3.5% of the East Atlantic flyway population (Scott 2009) is not as yet designated under any protected area category. The potential threat from the recent discovery and subsequent exploration and extraction of oil offshore in the western region of Ghana makes it even more urgent that the beaches of Esiama should be given priority on the national conservation agenda.

ACKNOWLEDGEMENTS

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SAMENVATTING

In de laatste jaren is de populatie Drieteenstrandlopers *Calidris alba* die gebruikmaakt van de Oost-Atlantische trekroute sterk gegroeid. De tellingen die de afgelopen twintig jaar maandelijks langs alle voor Drieteenstrandlopers geschikte gebieden langs de 550 km lange kust van Ghana zijn gehouden, laten die groei duidelijk zien. Het gemiddelde aantal per maand nam met bijna een factor vier toe, van ca. 1350 tot 4850 individuen. De grootste aantallen werden tijdens de najaarstrek (september–oktober) geteld. Ook de herfstpiek groeide gedurende de onderzoeksperiode sterk, van ca. 2900 tot 8500. Tijdens deze ongekend sterke populatiegroei raakten bepaalde gebieden langzaam vol en werden vogels gedwongen om andere, kennelijk minder geprefereerde, locaties op te zoeken. De aantallen Drieteenstrandlopers in de gebieden die al in het begin van het onderzoek de meeste vogels herbergden, groeiden namelijk minder hard dan gebieden die aanvankelijk gemeden werden. Dat patroon wordt het 'buffer-effect' genoemd, een bekend theoretisch principe in de ecologie waar tot nog toe maar een handjevol studies empirisch bewijs voor hebben geleverd. De door Drieteenstrandlopers meest geprefereerde locatie was het strand bij het dorp Esiama, waar de vogels voornamelijk de hoge dichtheden aan de kleine tweekleppige *Donax pulchellus* als voedselbron benutten. Ondanks dat dit strand door een aanzienlijk deel van de totale populatie Drieteenstrandlopers wordt gebruikt, geniet het momenteel geen enkele bescherming.