Year-round territoriality in long-lived birds: rethinking the concept of carrying capacity

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Adult African Black Oystercatchers Haematopus moquini are sedentary and territorial year round, with juveniles expressing strong natal philopatry. At four South African study sites (two mainland and two islands) breeding numbers more than doubled between the late 1970s/early 1980s and 2005 in response to improved protection and increased food availability, providing large-scale, natural experiments that could not have been simulated by manipulation. Oystercatcher population increases did not occur at constant rates – in each case breeding numbers remained stable for long periods both before and after periods of rapid population increases. At all sites, patterns of stability and change in breeding densities could be explained by (1) territorial adults reducing average territory size in a delayed response to improved resources, and (2) a resultant rapid influx of previously excluded sexually mature birds into new breeding territories. Our results bring into question whether a minimum territory size (and associated maximum breeding density) is ever reached as a result of competitor-induced territorial compression. Thus, for shorebird populations limited at high densities by interference competition, we suggest that it is most realistic to use equilibrium numbers (ultimately due to a balance between birth and death rates) as a basis to define carrying capacity.

Keywords: delayed breeding, density dependence, intraspecific competition, population regulation, territoriality

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Introduction

The concept of carrying capacity is central to population ecology (Begon et al. 1996) and has been used extensively to understand the population biology and conservation requirements of shorebirds (Sutherland and Dolman 1994; Dolman and Sutherland 1995; Goss-Custard et al. 1996a; Durell et al. 1997; Goss-Custard and West 1997). However, its use has been plagued by ambiguity because (1) the term has frequently been used without a clear definition being supplied and (2) the factors determining carrying capacity (however it is defined) vary considerably with both species’ biology and environmental conditions. This in turn influences the way in which carrying capacity has been defined and measured (cf. Goss-Custard and West 1997; van Gils et al. 2004). In the context of shorebirds, all definitions contain the central and necessary notion that there must be an upper limit to the number of birds that one area can support (Goss-Custard and West 1997). However, the factors limiting numbers of shorebirds (including density-dependent effects with negative feedbacks) may vary considerably across species. For example, many estimates of the carrying capacity of local habitats for shorebirds have been linked to prey abundance, because the systems studied were ones where bird numbers are regulated by exploitative competition (e.g. Holling 1959; Piersma et al. 1995; van Gils et al. 2004). However, other studies, particularly on Eurasian Oystercatchers Haematopus ostralegus, have highlighted the (often overriding) importance of interference competition and territorial exclusion as the main processes limiting populations (e.g. Harris 1970; Ens et al. 1995; Goss-Custard et al. 2001).

Territoriality is widespread in monogamous birds (Lack 1968; Davies 1978) and frequently precludes sexually mature birds from breeding (floaters, i.e. non-breeding adults). This can be an important form of population regulation if the number of floaters is large (Harris 1970; Ens 1992; Goss-Custard et al. 1995; Newton 1998; Heg 1999). Characteristics of populations regulated by territorial exclusion include rapid occupancy of breeding vacancies and the presence of many floaters close to prime breeding and/or feeding habitat (Newton 1998). The presence of many floaters means that breeding populations are tightly regulated, with little change in numbers unless habitat

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quality changes (Krebs 1970; Klomp 1980; Patterson 1980). Among Eurasian Oystercatchers the size of the breeding population is influenced by the number of birds available to breed, even though a much larger proportion of potential breeders remain excluded (Harris 1970; Safriel et al. 1984; Ens et al. 1995; Heg et al. 2000; Bruinzeel and van de Pol 2004), some of which are as old as 10 years (Ens 1992).

African Black Oystercatchers Haematopus moquini are less well studied, but two sources of evidence suggest that territorial exclusion is likely to be the key mechanism limiting breeder numbers at high population densities. First, many sexually mature birds (up to at least 10 years old) do not breed, and these are found both adjacent to and within prime breeding habitat (DL and PARH unpublished data). Second, although only one, small removal experiment has been undertaken (in which pairs were rapidly replaced; PARH unpublished data), two much larger natural removal experiments strongly suggest that many floaters are excluded from high-quality habitats. In 1978, an outbreak of paralytic shellfish poisoning (PSP) virtually halved oystercatcher breeding populations on five islands off South Africa’s west coast (Hockey and Cooper 1980). Despite the fact that densities of oystercatcher breeding pairs on these islands were high (Hockey 1983), these losses were replaced rapidly: one year later, populations were already at 80% of pre-PSP levels (Hockey and Cooper 1980). In 1999, breeding populations on two islands were reduced by approximately 30% due to avian cholera, yet breeder numbers had recovered by the following breeding season (DL and PARH unpublished data).

Although territorial breeding populations generally are tightly regulated, territory size may vary in response to changes in resource (e.g. food) abundance (Krebs 1970; Klomp 1980; Patterson 1980; Carpenter 1987a). Even if resource levels remain constant, conspecific pressure may cause territorial shrinkage (Vines 1979; Patterson 1980), with territory size being inversely related to the size of the floater population (Krebs 1970), as has been demonstrated for Eurasian Oystercatchers (Goss-Custard et al. 1996b). The regulatory importance of territorial behaviour has been addressed extensively, primarily using Eurasian Oystercatchers as a model (Goss-Custard et al. 1996a, 1996b; Goss-Custard and West 1997; Goss-Custard et al. 2001). For this species, both resource abundance (e.g. food availability) and competitor density have been incorporated in definitions of local carrying capacity and used to model the population consequences of habitat loss (Sutherland and Dolman 1994; Dolman and Sutherland 1995; Goss-Custard et al. 1996a; Goss-Custard and West 1997). Unlike the Eurasian Oystercatcher, the African Black Oystercatcher is sedentary and territorial year round (despite extensive juvenile movements; Hockey et al. 2003), and the species also has a predictable food supply (Hockey 1996).

In general, however, whether models of local shorebird carrying capacity have been based largely on negative feedback processes of exploitative competition, interference competition or even density-dependent predation (van Gils et al. 2004), or some combination of these, the focus has been on defining and estimating the short-term carrying capacity of local habitats for migratory species (e.g. van Gils et al. 2004; Goss-Custard et al. 1996a, 1996b). For example, where interference competition is deemed primarily responsible for limiting shorebird densities, it has been argued that carrying capacity should be defined as the point at which further increases in competitor density no longer influence breeder density (Goss-Custard et al. 1996a). Dhondt (1992), by contrast, argued that carrying capacity should simply be defined as the point at which a population stabilises due to demographic processes.

In light of these differences, the aims of this study were to (1) develop a simple model of African Black Oystercatcher population dynamics that encapsulates the relative importance of resource levels/habitat quality, territorial behaviour, and population densities/demographic rates; (2) use population data from four sites, spanning periods of population stability and change, to test the model’s validity and assess whether the potential breeding population exerts a density-dependent effect on the realised breeding population, and the relative importance of habitat quality and conspecific pressure in determining breeder densities; and (3) assess the validity/usefulness of models of carrying capacity as they might apply to sedentary (rather than migratory) shorebirds.

Methods

Definition and characterisation of local populations

Four South African breeding populations of African Black Oystercatchers were studied, two on islands off the west coast (Malgas Island, 33°03′ S, 17°56′ E; and Jutten Island, 33°05′ S, 17°58′ E), and two at sites on the south coast mainland (De Hoop Nature Reserve, 34°29′ S, 20°30′ E; and Goukamma Nature Reserve, 34°04′ S, 22°50′ E). Based on very high levels of both site fidelity and natal philopatry (DL and PARH unpublished data), all four populations were considered to be closed.

In terms of population demographics, breeding adults were treated as being territorial year round (Hockey 1996) and were assumed to experience constant habitat/resource conditions (Wieters 2006). Only breeding numbers at each locality were counted annually (aside from Goukamma where corresponding estimates of floater numbers have also been made on a yearly basis). For the purposes of establishing starting conditions (see Model Calibration and Application, this section), numbers of floaters, immatures and juveniles for each local population were established by running a population model incorporating the following key components: age at sexual maturity (three years for females, four for males; Hockey 1996), age-related survival rates, site-specific fledging success rates and density-dependent exclusion of sexually mature birds on the breeding grounds during the breeding season. Even though young birds regularly forage in flocks (Rao 2005), especially at ‘nursery grounds’ in Namibia (Leseberg 2001), aggressive interactions and kleptoparasitism are rare (Leseberg 2001) when compared with Eurasian Oystercatchers (Ens and Goss-Custard 1984; Sitters 2000) and have no measurable impact on food intake rates (Leseberg 2001). Based on these factors, and coupled with very low mortality rates (Leseberg 2001), our model ignored density-dependent effects operating among sexually immature birds and investigates only the possible density-dependent
effect of the potential breeding population on the realised breeding population. A full description of and rationale for the model development of this density-dependent effect is provided in Supplementary Appendix S1.

**Model calibration and application**

Estimating the density-dependence parameter $b$ (Appendix S1) is problematic because both the numbers of breeders and floaters must be known. In addition, $b$ can only be estimated if population numbers change substantially over time (Goss-Custard et al. 1996a). Under non-equilibrium conditions, the density-dependent effect of the potential breeding population on the realised breeding population will vary unpredictably due to inertial effects such as delays in territory establishment. Because of these constraints, even for Eurasian Oystercatchers — one of the best-studied shorebirds in the world — only two studies have attempted to estimate $b$ (Goss-Custard et al. 1996a). This study assumes that $b$ is a species-specific trait that is constant across sites and across a wide range of population densities.

For African Black Oystercatchers, there is only one site (Goukamma) where the population has both changed over time and where the potential and realised breeding populations have been quantified. We therefore adopted a different approach to estimating $b$, using changes in breeding populations over time at the four study sites.

**Count data**

The yearly breeder populations were determined from averages of 2–4 counts per year at each site during the mid- and late-breeding season, except for 1976 and 1980, when only single, mid-breeding season counts were made. Counts made early in the breeding season were excluded because they are the ones most likely to include floaters (Heg 1999).

At Goukamma, in every year when breeders were counted (except for 1980), nests and chicks were also monitored. From the mid-1980s and in all years from 1998 (Loewenthal et al. 2005), nests and chicks were also monitored for African Black Oystercatchers. To estimate breeding numbers accurately, the proportion of birds present at these island sites were breeding pairs and count data for the two islands were assumed to represent the breeding population. Island-reared floaters spend most of their time on the adjacent mainland coast from where they make periodic forays to the islands (DL and PARH unpublished data). Densities on the mainland close to islands in the mid- to late-breeding season are high, averaging 10–15 birds km$^{-1}$, nearly four times the average density on west coast rocky shores (DL and PARH unpublished data), suggesting that a large proportion of these are birds excluded from the islands by territory holders.

At all sites, populations have increased since the late 1970s/early 1980s, but these increases have not been steady. Rather, at all sites, numbers remained stable up to the late 1980s/early 1990s, then increased rapidly (particularly at De Hoop and Goukamma) before once again stabilising (Figure 1). At Malgas and Jutten islands, this pattern is less convincing due to larger inter-annual fluctuations in numbers. However, despite fluctuations at both islands, the lowest counts since 1995 have been higher than the highest counts pre-1995: statistical analysis confirms this conclusion (Table 1). Two main factors have been hypothesised as driving population increases – enhanced protection and/or increased food availability (Loewenthal et al. 2015). De Hoop Nature Reserve was proclaimed in 1957. However, prior to 1986, when the area was declared a Marine Reserve, angling, bait-collecting and off-road vehicles were all permitted along the coastline. Goukamma Nature Reserve was proclaimed in 1960, but the area was only designated a Marine Reserve in 1990 when all bait-collecting and night-time angling was stopped, along with the use of off-road vehicles associated with commercial oyster harvesting (Leseberg et al. 2000). Although the islands have always been largely undisturbed, the protection status of Jutten and Malgas islands was significantly improved in 1985 when they were incorporated into the West Coast National Park. Prior to this there was much seasonal human disturbance on Malgas Island associated with guano collecting (Crawford et al. 1995). At the islands there was also a dramatic increase in the proportion of the alien invasive Mytilus galloprovincialis (Mediterranean mussel) in the oystercatchers’ diet between the early 1980s and the early 1990s (Hockey and van Erkom Schurink 1992), reflecting the mussel’s progressive invasion of the shore. From the mid-1990s onwards, the proportion of Mytilus in the birds’ diet remained constant (Loewenthal 2007), indicating that the intertidal invertebrate community had restabilised. This novel food source led to a dramatic increase in intertidal mussel biomass (Robinson et al. 2005) and certainly increased food availability for oystercatchers on these islands (Hockey and van Erkom Schurink 1992). If, as hypothesised, protection and improved food supply have benefited oystercatchers independently, there is nonetheless a lag phase of 3–7 years between the time at which conditions improved and the time at which breeder numbers increased (Figure 1). In attempting to assess the strength of density dependence ($b$) in regulating population numbers, we also attempt to explain this lag phase.

**Model calibration**

A regression of the count data for all populations indicated that they were stable until the late 1980s/
For all simulations, mean juvenile, immature and adult survival rates were kept constant (at 61%, 83% and 96%, respectively; DL and PARH unpublished data). Breeding success data (fledglings pair⁻¹ y⁻¹) were obtained from the following sources:

De Hoop Nature Reserve: Breeding success of 15–20 breeding pairs was documented from 1984–1990 (Scott 2007). These data cover two years before the area was declared a Marine Reserve and four years subsequently. Average fledging success was 0.77 fledglings pair⁻¹ y⁻¹ and did not differ before and after establishment of the marine reserve.

Goukamma Nature Reserve: All (9–17) breeding pairs and their performance were monitored from 1990–2004, after the area was proclaimed a Marine Reserve in 1990. Average breeding success was 0.41 fledglings pair⁻¹ y⁻¹ and there was no significant trend in breeding success (Loewenthal 2007).

Malgas and Jutten islands: No detailed nest-monitoring data exist for these two islands. Breeding success was assumed to be 0.91 fledglings pair⁻¹ y⁻¹ based on the productivity of 48–69 pairs y⁻¹ monitored over four years at nearby Dassen Island (33°26′ S, 18° 05′ E).

Based on the hypotheses that either breeding success has improved (modelled as an increase in fledglings pair⁻¹ y⁻¹) and/or the average optimal territory size of breeding birds has decreased (modelled as an increase in $N_t'$; see Appendix S1) following protection and/or improved food supply, both of these parameters were manipulated in the model for a given $b$-value and compared with field data.

To explore the possible effect of a change in $N_t'$ on breeder numbers, average breeding success (BS) and $b$ were held constant. $N_t'$ was then adjusted to give the correct mean breeding population size before the population increases of the late 1980s/early 1990s (Table 1). $N_t'$ was then increased by varying amounts at the time at which protection and/or food supply improved and the effect of this on breeding numbers was compared with the field data. The procedure was repeated for a range of values of $b$.

Although data from De Hoop and Goukamma indicate no significant increase in breeding success following protection (Figure 2), at Malgas and Jutten islands breeding success did appear to improve in the 1980s, in concert with an increased proportion of Mytilus in the diet (Hockey and van Erkom Schurink 1992). Therefore, to investigate the possible effect of improved breeding success on breeding success.
populations, a range of much lower values for breeding success were arbitrarily chosen, for a given value of \( b \). For each of these, a value of \( N'_t \) was obtained for the mean breeder population between the late 1970s and early 1990s (Table 1). The same procedure was followed as above, except that \( N'_t \) was held constant and breeding success was increased by varying amounts (up to and beyond current mean values). The effects of these manipulations on modelled population changes were then compared with the field data.

**Estimating upper limits to breeding populations**

Because of uncertainty in the estimation of \( b \), model projections were made for populations at each site for a range of \( b \)-values. All projections assumed the same site-specific mean breeding success and the same mean age-linked survival rates. Projections were made beyond the duration of the simulations that were used to calibrate the model.

**Results**

Breeder numbers at all sites have increased over the last 25+ years (Figure 1). Most of this increase occurred in a short period between the early and mid-1990s and was preceded and followed by periods of stability (Figure 1, Table 1). This replicated pattern provided the basis for model calibration. At De Hoop, breeding success was not affected by improved protection (Scott 2007). At Goukamma, although breeding success data only exist for the years following protection, there was no trend of increasing breeding success over this period (Figure 2). At both islands, breeding success increased following invasion of the shore by *Mytilus* (Hockey and van Erkom Schurink 1992).

**Model calibration**

**Manipulation of fledging success, keeping \( N'_t \) constant**

At the two mainland sites, the lag between enhanced protection and increases in breeder numbers was 3–5 years (Figure 1). At Malgas Island, the lag following improved protection was approximately 7 years. There also appears to have been a lag following increased food abundance at both Malgas Island and Jutten Island. Between 1982 and 1988, the proportion of *M. galloprovincialis* in the diet of oystercatchers at Malgas and Jutten almost doubled (Hockey and van Erkom Schurink 1992), yet an increase in breeder numbers at these sites could only be detected by 1992, at which stage *Mytilus* formed more than 60% of the hard-shelled diet of oystercatchers (Hockey and van Erkom Schurink 1992). At all sites, if modelled breeding success was increased following protection, the number of breeders increased with a lag phase that compared well with observed population trends.

Although models appeared able to predict the lag phases, they could not explain the rapid rates of increase or the subsequent sudden stabilisation of numbers. Even when average fledging success was increased to more than double current values (a highly unlikely scenario), growth in breeder numbers was still much slower than the observed rates of increase. This remained true even when using very low values of \( b \), simulating high floater pressure for breeding space.

Small values of \( b \) did eventually stabilise breeder numbers, but at levels far higher than those observed. For example, doubling the current breeding success at De Hoop and using very low \( b \)-values predicted that breeder numbers would stabilise after approximately 50 years at c. 150 individuals, more than double the stable population size (Figure 3). To achieve stable breeding numbers approximating the current average, a much weaker density-dependent effect (higher \( b \)-value) was required. Although achieving the ‘correct’ end result, this model still predicted a much slower increase in breeder numbers and a much longer period to stability than that observed. Only one example is illustrated here (Figure 3), but results from all sites were comparable.

**Manipulation of \( N'_t \), keeping breeding success constant**

Using small \( b \)-values, manipulation of \( N'_t \) following either
increased food availability or increased protection resulted in initial, rapid increases in breeder numbers at all sites. Even at Goukamma, where breeding success is low, the initial floater population was large enough to account for this increase. However, a secondary effect of increasing $N_t'$ was a continued increase in the breeding population, albeit at a much slower rate, with the population eventually stabilising. This pattern was repeated at all sites, although for low values of $b$ the long-term increase in breeder numbers on islands was much faster than on the mainland (results from one mainland site and one island site are illustrated in Figure 4 and 5, respectively; similar results

**Figure 4:** Results of simulations used to attempt to quantify the constant $b$ (a measure of the influence of adults competing for territories on the realised breeding density of oystercatchers) using count data from De Hoop Nature Reserve. BS = Mean breeding success (fledglings pair$^{-1}$ y$^{-1}$); $N_t'$ (bef) = the value of $N_t'$ needed to fit the model to mean breeding numbers before protection; $N_t'$ (aft) = the new value of $N_t'$, used to fit the model to the average stable breeding population size after it increased; $b$ = the strength of density-dependence (a low $b$-value reflects strong density dependence and vice versa)

**Figure 5:** Results of simulations used to attempt to quantify the constant $b$ (a measure of the influence of adults competing for territories on the realised breeding density of oystercatchers), using count data from Malgas Island. BS = Mean breeding success (fledglings pair$^{-1}$ y$^{-1}$); $N_t'$ (bef) = the value of $N_t'$ needed to fit the model to mean breeding numbers before protection; $N_t'$ (aft) = the new value of $N_t'$, used to fit the model to the average stable breeding population size after it increased; $b$ = the strength of density-dependence (a low $b$-value reflects strong density dependence and vice versa)
were obtained from the other two study sites). In all cases, however, simulated increases were out of phase (too early) with real increases by 3–7 years. If the real time lags were taken into account in the model, then simulated population dynamics corresponded well with the field data, but only if relatively high \( b \)-values were used. As \( b \) was increased from 0.4 to 0.8, simulated populations fitted observed trends with increasing accuracy (Figures 4 and 5). On the mainland, breeder numbers became insensitive to increases in \( b \) once \( b \) exceeded 0.6; the corresponding \( b \)-value at islands was 0.8 (Figures 4 and 5). The key to estimating \( b \) was thus to minimise a model-generated, secondary increase in breeder numbers (a pattern not observed in the field).

Intersite differences in the sensitivity of breeder numbers to changes in \( b \) (and especially at low values of \( b \)) reflect different reproductive rates. At islands, where fledging success is high, changing \( N_f \) (i.e. allowing non-breeders to establish territories without resistance from established breeders) dramatically increases population-level reproductive output. This in turn leads to a much more rapid increase in the number of floaters relative to sites where reproductive output is less.

Estimating the strength of density dependence based on a hypothesised increase in \( N_f \) assumes that past, present and future reproductive rates are/will be the same. However, estimates of \( b \) might change if breeding success was lower before environmental conditions improved. A series of simulations was therefore run in which \( N_f \) was manipulated as before, but historical stable breeding populations were established using reduced breeding success (down to 50% of current estimates) and were then increased at the time when conditions improved (Hockey and van Erkom Schurink 1992). Only at Goukamma did reducing historical breeding success compromise the estimate of \( b \). At this site, increasing \( N_f \) caused an initial rapid increase in breeder numbers, followed by a slow decrease. These decreases were accelerated by reducing \( b \)-values. This result can be explained by the low reproductive output of Goukamma birds and the resultant small pool of floaters available to settle. When breeding success was set to c. 50% of the current average, there were insufficient floaters to counter breeder mortality. Faster decreases with lower \( b \)-values resulted from conspecific pressure having an increasing influence on breeder numbers. However, despite these predictions, breeder numbers have not decreased at Goukamma over the last 12 years (Table 1), so it seems unlikely that breeding success was indeed significantly lower before protection was enhanced.

Model application
Population projections and local, long-term carrying capacity
Based on uncertainty in the precise value of \( b \), population projections were initially made using a range of \( b \)-values from 0.6 to 1 for each site. At mainland sites, \( b \)-values >0.9 made no difference to breeder numbers and projections for these two sites are therefore based on \( b \)-values of 0.6–0.9. At islands, the density-dependent effect had little influence on breeding population projections once \( b > 0.95 \). Thus, projections for these two sites are based on \( b \)-values of 0.6–0.95 (Figure 6). At Goukamma, \( b \)-values of 0.6 and 0.9 yielded estimates of 47 and 34 breeders, respectively; corresponding figures at De Hoop were 95 and 72. Island population projections were more sensitive to variations in \( b \). At Malgas Island, \( b \)-values of 0.6 and 0.95 yielded breeder numbers of 182 and 132, respectively; the corresponding figures at Jutten Island were 290 and 233. However, based on both estimates, there were similar deviations from the modelled means at all sites (Goukamma: 16%; De Hoop: 14%; Malgas: 16%; Jutten:

\[ N_t' = \frac{N_t}{\left(1 - \frac{b}{100}ight)} \]

Figure 6: Long-term population projections for estimated breeding numbers at four localities around the coast of South Africa. Projections illustrate the variability in stable upper limits to breeding populations based on uncertainty in the estimation of the density-dependent effect \( b \). Population trajectories simply represent projections of population simulations used to calibrate the model and to estimate \( b \) (refer to Figures 4 and 5).
11%). Assuming no regulatory effects on immatures and floaters, it is possible to estimate the maximum stable size of the floater populations generated by local breeding populations at carrying capacity. Predictably, floater numbers at Goukamma were low (30% less than the estimated number of breeders at carrying capacity). However, at De Hoop, there were 3% more floaters than breeders, and at Malgas and Jutten islands floater populations at breeder carrying capacity exceeded breeder numbers by more than 50%.

**Discussion**

The argument developed here to explain changes in densities of breeding oystercatchers following environmental improvement focuses on two hypotheses. First (hypothesis 1), in the face of improved habitat quality, territorial oystercatchers reduce territory size to optimise the cost/benefit ratio of territoriality (Figure 7). As a result, floaters can establish territories in vacancies arising from territory shrinkage. The model interprets this process as an increase in the population threshold ($N'_t$) at which exclusion of sexually mature birds begins, with $N'_t$ reflecting the contribution of habitat quality in determining population densities. An increase in $N'_t$ covers all possible factors (e.g. food availability, nesting habitat and chick-rearing habitat) contributing to improved habitat quality. Simplistic as this interpretation of $N'_t$ is, it may be reasonable for African Black Oystercatchers because the birds are sedentary (Hockey 1996). Second (hypothesis 2), increased floater pressure may force reductions in territory size by exerting density-dependent pressure on breeders. Model simulations very strongly suggest that hypothesis 2 cannot explain patterns of population change observed in the field. By contrast, based on concordance between simulations manipulating $N'_t$ and the patterns of breeder numbers in the field, hypothesis 1 is a much more parsimonious explanation of the underlying process driving changes in breeder numbers. In support of this conclusion, the rapid increase in breeder numbers at Goukamma between 1992 and 1995 tracked very closely a depletion of the adjacent floater population (DL and PARH unpublished data). That so many of these birds were able to obtain territories so quickly can only be explained by shrinkage of existing territories. Resource-linked territory shrinkage should carry no costs, whereas territory shrinkage forced by competitor pressure is predicted to result in suboptimal territories with reduced reproductive success as a necessary corollary (Figure 7). There is no evidence (based on a data set spanning more than a decade) that breeding productivity at Goukamma was compromised following territory shrinkage in the early 1990s, further supporting the conclusions that breeder density is determined by resource density not competitor density.

One puzzling feature of the model simulations is the 3–7 year lag between projected and observed increases in breeder numbers. Although delayed maturity is a seemingly obvious explanation for this lag, improved breeding success alone cannot explain the rapid rate of increase in breeder numbers at any of the sites (Figure 3). Rather, it seems that territorial birds are slow to detect and/or react to changes in habitat quality. Most studies demonstrating territory size adjustment in response to changing resource levels have focused on species that defend short-term territories (e.g. Holmes 1970; Cody and Cody 1972; Gill and Wolf 1975). African Black Oystercatchers not only defend long-term territories, but most defend them year round.

![Figure 7: Schematic representation of how reduction in territory size in response to improved resources (as opposed to conspecific pressure) is viewed in the model, from the perspective of the territory owner. In (a), reduction in optimal territory size is beneficial when resources improve, because net gains ($T_{opt2}$) increase with a decrease in territory size (cf. $T_{opt2}$ and $T_{hyp}$). In (b), territory size is reduced, but not to maximise net gains, because with increasing competitor density the cost increases more rapidly with an increase in territory size. Thus, with adequate conspecific pressure, territory holders reduce territory size to optimise the cost/benefit margin ($T_{opt2}$), but at the cost of reduced net gains (cf. $T_{opt2}$). $T_{hyp}$ represents the net gain to the territory owner if territory size was not reduced in the face of a density-dependent increase in costs of territory defence. Because $T_{hyp} < T_{opt2}$, it pays to reduce territory size to 'make the best of a bad situation'. A $b$-value of unity in the model is viewed as a situation where a change in competitor density has little influence on the gradient of the cost curve for territory holders. Thus, territory size and hence the number of territory holders are not influenced by competitor density (modified from Both and Visser 2003)](image-url)
Studies of species with similar attributes have reported that territory size may vary in different areas and across habitats, but does not vary in response to short-term changes in food abundance, even when those changes are large (e.g. Patterson 1980). Patterson (op. cit.) argued that such stability in territory size may evolve as an adaptation to long-term ‘average’ resource levels. Under these conditions, reducing territory size for short-term gain in response to short-term improvement in resources would be maladaptive because the costs of any subsequent attempt to regain lost ground when conditions deteriorated may be prohibitive. Based on field evidence, it seems likely that African Black Oystercatchers have evolved such a conservative system of territory defence. This conservatism does not preclude adjustment of territory size to track resources, but there is inertia on the part of pairs to do so (territory defence is shared and mostly ritualised; Baker and Hockey 1984). Most studies demonstrating a failure of species with long-term territorial systems to adjust territory size in response to changing resources have only allowed for short response times (e.g. Charles 1972; Gill and Wolf 1975; Hirons 1976; Mares et al. 1982; McNair 1987). Although no experimental resource manipulation has been undertaken for African Black Oystercatchers, the invasion of alien Mytilus, as well as increased protection, have provided natural experiments allowing insight into longer term responses. Such insights would not have been possible had environmental conditions and breeding densities remained stable.

If enhanced protection and food supply influence territory size independently (as seems to be the case), this begs an explanation of how the former may have had this effect. A common benefit of such protection for oystercatchers is reduced disturbance by humans and their dogs (Loewenthal 2007). High disturbance prior to protection may well have artificially increased the total breeding and foraging area defended by resident territorial adults because of the need to be able to ‘escape’ to safe foraging/resting/nesting refuges. Simple measurement of territory resource levels, however, would have led to the conclusion that these territories were unnecessarily large. There is support for this ‘super-territory’ theory from at least one heavily disturbed area on the Cape Peninsula, South Africa. At this site, breeding and feeding territories have become totally disjoint because prime breeding habitat backing the feeding grounds became too heavily disturbed for birds to breed successfully. This situation has strongly compromised the reproductive success of these pairs (Loewenthal 2007).

By changing breeder density in the model, it was possible to estimate the strength of density dependence exerted by competitors. The weakness of this approach is the insensitivity of estimates of the breeding population to changes in $b$ when $b$ is high (>0.6–0.8). These high values of $b$ indicate that competitor density has little influence on territory size and hence on the density of breeding birds: floaters can counteract the effects of breeder mortality, but do not exert a density-dependent effect that forces territory compression.

Because territory size is fixed for a given resource level, and territories are well defended, when breeder vacancies arise through mortality, neighbouring territory holders do not enlarge their territories. Thus, if resource levels vary over the short term, the strength of defence may come at the price of inflexibility. Significant short-term changes in the resource base for African Black Oystercatchers are probably rare: there is little within-site, interannual fluctuation in the standing-stock biomass of rocky shore invertebrates in South Africa (Wieters 2006). A significant exception to this has arisen with the invasion of Mytilus, which has greatly increased invertebrate biomass on the shore (Robinson et al. 2005) and to which there were lagged responses in oystercatcher breeding density (Hockey and van Erkom Schurink 1992).

If floaters have little influence on territory size, there is no reason why $b$ should vary across habitats, although $N^b$ will vary: this forms the model’s description of the contribution of resource levels to population densities in different habitats. Counter to this, however, is a suggestion that the value of $b$ for Eurasian Oystercatchers may differ across different breeding habitats (Goss-Custard et al. 1996a). If these differences are real, can they be explained in the context of $b$ reflecting an evolved system of competitive asymmetry? Unlike African Black Oystercatchers, Eurasian Oystercatchers migrate between winter feeding grounds and summer breeding grounds, and thus have to re-establish a breeding territory every year (Hulscher et al. 1996). Individuals are highly site faithful to both areas (Ens and Cayford 1996; Hulscher et al. 1996) and have fairly stable long-term breeding territories (Harris 1970). However, their diets switch seasonally when they change habitats, demanding a level of behavioural flexibility not required by a resident, territorial species. This behavioural plasticity required by migrants may in turn have resulted in the evolution of more flexible territory defence behaviour (because of repeated exposure to short-term changes in resource type/availability/quality). However, if the strength and flexibility of territory defence are trade-offs, then birds with more flexible defence behaviour are also more vulnerable to territory compression from conspecifics. The magnitude of the competitive asymmetry (between breeders and floaters) would be correspondingly small (and reflect as a lower $b$-value in Equation 1 – see Appendix S1). The act of migration itself may further serve to lessen this asymmetry because all breeders have to establish/re-establish territories when they arrive on the breeding grounds.

Responses of territorial American Pied Oystercatchers Haematopus palliatus to intruders support our contention that competitive asymmetry is not habitat specific. At high breeding densities, the aggressive responses of territory holders are simply truncated versions of the response curves of territory holders at lower breeding densities, the response curves having exactly the same slopes and elevations (Vines 1979).

Among African Black Oystercatchers, changes in breeder densities across habitats could be adequately simulated by manipulating the density at which competitive exclusion began, with no requirement that $b$ must differ between habitats to explain these changes. Indeed, the assumption that $b$ is a species-specific constant (Equation 2, see Appendix S1) precludes the density-dependent relationship itself changing as the total potential breeding population changes. This is contrary to the approach adopted in several studies in which the constraint of a minimum fixed territory size for a given habitat (at which point $b = 1$) is
explicitly incorporated into models of carrying capacity (Brown 1969; Klomp 1972, 1980; Goss-Custard et al. 1996a, 1996b). Our model differs fundamentally in its interpretation of the true meaning of $b = 1$. We argue that in the context of a territorial species, $b = 1$ simply reflects a system of competitive asymmetry where a change in competitor density has no influence on optimal territory size. It does not reflect the endpoint of a process of territory compression brought about by conspecific pressure. The confusion in the interpretation of $b$ is due to the fact that even when $b \ll 1$ (i.e. when conspecific pressure has a relatively large effect), because of the asymptotic nature of the competitive relationship, the proportion of competitors excluded as competitor numbers increase closely approximates a situation where $b = 1$. This is basic to the concept that the very nature of territoriality itself is a logarithmic form of competitive asymmetry, irrespective of the value of $b$, and is reflected in the fundamental model Equation 1 (Appendix S1). Thus, the ‘one in, one out’ rule (Goss-Custard and West 1997) at high population numbers is effectively satisfied for a range of $b$-values when the number of competitors is large. The concept of carrying capacity for a territorial bird must consider the basic territorial nature of the animal itself: in the case of resident African Black Oystercatchers, equilibrium population size is the only realistic definition of carrying capacity. Breeding population densities are almost entirely dependent on breeders (slowly) adjusting territory size in response to habitat quality, with conspecific density having little influence and floaters only being able to enter the breeding population when vacancies become available. This leads to strong regulation of the total population because the net per capita growth rate of the population decreases rapidly as floater numbers increase.

Our model assumes a constant logarithmic relationship between the proportion of competitors prevented from breeding and the total number of individuals competing for breeding territories (Equation 2, Supplementary Figure S1), so it cannot be used to validate the assumption that $b$ is a constant. A behaviour-based model developed for Eurasian Oystercatchers made no a priori assumptions with regard to the nature of the density-dependent function as competitor densities increased. Rather, it was allowed to develop based on individual behaviour (Goss-Custard et al. 1996b). This latter model describes birds competing for food on the non-breeding grounds. However, if (feeding) territoriality is operating and can be described by Equation 1 (Appendix S1), then the density-dependent function should be constant.

The consequences of exclusion are important in population dynamics, but are secondary to the exclusion process itself. In the same study of Eurasian Oystercatchers (Goss-Custard et al. 1996b), whichever set of assumptions (regarding the behaviour of individual competitors) was used, in each case giving rise to a $b$-value $< 1$, it proved impossible to force $b$ to increase to unity, even when entirely unrealistic productivity rates gave rise to very high competitor densities. Furthermore, several curvilinear functions were generated, based on different assumptions about mortality. However, in each of these scenarios the population stabilised at numbers well below the carrying capacity predicted by $b = 1$; in other words, $b$ did not change in response to competitor density (Goss-Custard et al. 1996b). These results were derived using an individual game-theory approach and it is likely that they are fundamental. Further, they strongly suggest that interference competition and not exploitative competition is overwhelmingly important in governing this species’ population dynamics in the non-breeding season (Goss-Custard et al. 1996b; Goss-Custard et al. 2001). Most importantly, however, these behavioural models support our contention that a constant, species-specific value of $b$ may be fundamental to and descriptive of the population dynamics of territorial species.

Territorial systems can collapse under conditions of very high food abundance or when competitors become so locally abundant that territory holders are overwhelmed (Carpenter 1987b). The latter situation may arise (albeit rarely) in local non-breeding populations of Eurasian Oystercatchers (Goss-Custard et al. 1996b). However, these situations, if they occur, reflect a change in individual behaviour at high densities, not the endpoint of territorial compression. When this happens, it becomes very difficult to define carrying capacity, but in a theoretical context it cannot be defined as the point at which $b = 1$.

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