Supplementary Information

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

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Appendix S1: Development of a model describing the putative density-dependent effect of competitors on breeding densities of shorebirds

There are two key components to the model: first, describing how a population is regulated by territorial exclusion of sexually mature adults (floaters); and second, and more specifically, describing the influence of the total potential breeding population on the numbers that actually breed (i.e. the strength of the density-dependent effect).

For African Black Oystercatchers *Haematopus moquini*, population regulation by means of territorial exclusion is suspected (see Introduction). However, although the species' global population size has increased by >40% over the past 25+ years (Loewenthal et al. 2015), the manner in which territorial exclusion varies with local population size has not been documented. In Britain, many breeding populations of Eurasian Oystercatchers *H. ostralegus* have remained fairly stable despite a large increase in the total population (Goss-Custard et al. 1995), suggesting little density dependence but strong territorial regulation of the breeding population. Two other sources of data for the same species suggest that the proportion of adults that are floaters increases as breeder numbers increase (Goss-Custard et al. 1996a), implying density dependence. Whether or not density dependence is operating, if the proportion of floaters increases as the total number of potential breeders increases, then the possibility of population regulation arises because the net *per capita* growth rate of the population will decrease as population size increases (because a smaller proportion of the total population is reproductively active). Population size will stabilise when the floater population reaches a level at which the reduced *per capita* productivity is balanced by mortality. Because of the logarithmic relationship between exclusion and population size, populations should stabilise quickly because the regulatory effect is strong. Time-dependent population models incorporating this relationship show that even populations with high reproductive rates will reach equilibrium fairly quickly (Goss Custard et al. 1996a).

The simplest way in which the proportion of floaters varies as the total potential breeding population increases can be described by a power function (Figure S1):

$$\Delta k \propto \Delta(\ln Nt) \quad (1)$$

where k = the proportion of the potential breeding population excluded and Nt = the total potential breeding population. It is important to emphasise that the proportionality expressed in Equation 1 makes no explicit statement regarding density dependence. It only reflects the way in which exclusion varies with population size and hence provides a powerful mechanism for population regulation. Equation 1 can be expressed as an equality:

$$\Delta k = b \cdot \Delta(\ln Nt) \quad (2)$$

where b = the constant of proportionality. Up to this point, the number of potential breeders excluded has been expressed as a proportion (i.e. k), but k can also be expressed as a 'k-value', in a similar way to which Varley and Gradwell (1960) defined mortality in key-factor analysis (Goss-Custard 1980), i.e.

$$k = \ln Nt - \ln Nb \quad (3)$$

where Nb = the number of birds that breed. Regardless of how k is expressed, the linearity of Equation 2 still holds, but expressing k as in Equation 3 allows density dependence to be modelled on a scale of zero to one (Goss-Custard 1980). Rearranging Equation 2 gives:

$$b = \frac{\Delta k}{\Delta(\ln Nt)} \quad (4)$$

and substituting the value of k (Equation 3) gives:

$$b = \frac{\Delta(\ln Nt - \ln Nb)}{\Delta(\ln Nt)} \quad (5)$$

From Equation 5 it is clear that if the total potential breeding population has no influence on the breeding population, then Nb remains constant and Equation 5 becomes:

$$b = \frac{\Delta(\ln Nt)}{\Delta(\ln Nt)} = 1 \quad (6)$$

However, if every potential breeder becomes a breeder, then the influence of the potential breeding population on the breeding population can be considered infinite or undefined. In this case Nt must equal Nb and hence Equation 5 becomes:

$$b = \frac{0}{\Delta(\ln Nt)} = 0 \quad (7)$$

Any intermediate value of b describes a situation in which the total potential breeding population has some influence on the breeding population through conspecific pressure. However, because of the logarithmic relationship of Equation 1, the proportion of birds excluded will always reach an asymptote unless $b = 0$. The asymptotic nature of the relationship when competitor numbers are high means that as the total number of competitors (Nt) increases, the proportion of competitors excluded (k) very nearly approximates a constant, even when there is great variation in Nt . Values of b have been used extensively to describe the strength of density-dependent effects in Eurasian Oystercatcher populations, not only in the context of floaters influencing breeder numbers, but also to describe the possible influence of conspecific pressure on densities on the non-breeding grounds (Goss-Custard et al. 1996a, 1986b).

A subtly different conceptualisation of b is advanced here (cf. Goss-Custard 1980; Goss-Custard et al. 1996a, 1986b). This stems from the need to distinguish between density dependence and population regulation. The two concepts are frequently confused, possibly because traditional studies of density-dependent effects (e.g. the influence of conspecific density on reproductive output) have focused on processes that *also* act in a regulatory fashion, i.e. density-dependent effects that also involve negative feedbacks. However, the two processes are not necessarily linked (Rodenhouse et al. 1997). Because birds compete for territories, the density-dependent effect can be viewed as the possible influence of the potential breeding population on the realised breeding population.

Viewed in this context, conspecific pressure influencing breeding population density provides a perfect example of a situation where the density-dependent effect acts in exactly the *opposite* way to the regulatory process. Nonetheless, the population can be regulated over time purely by territorial exclusion, because the nature of territoriality itself is such that birds which are prevented from breeding accumulate at a much faster rate than the number of breeders, even if the breeding population increases rapidly (i.e. $b \ll 1$).

At this stage, the model describes only a change in the degree of exclusion (k) with a change in the number of potential breeders (Nt) (Equation 2). However integrating the differential form of Equation 2, i.e.:

$$\int dk = b^* \int d(\ln Nt) \quad (8)$$

gives:

$$k = b^* \ln Nt + C \quad (9)$$

Note that Equation 9 takes the form $y = bx + c$. Therefore C in Equation 9 is the x -intercept, making $k = 0$ solves for C . Thus Equation 9 becomes:

$$k = b^* \ln Nt - b^* \ln Nt' \quad (10)$$

where Nt' reflects the population size at which exclusion begins. Substituting for k in Equation 3 and rearranging gives:

$$\ln Nb = \ln Nt - b^* \ln Nt + b^* \ln Nt' \quad (11)$$

The degree of exclusion (k) is thus dependent on the potential breeding population size at which exclusion begins (Nt'), the total potential breeding population (Nt) and b (Figure S2).

There are a few important points regarding the model's assumptions and explanatory power as it is developed in this paper. First, b is a constant reflecting an evolved system of competitive asymmetry; it is thus independent of both population size (as reflected in Equation 8) and habitat quality. It is important to point out that the model

does not ignore aspects of habitat quality (e.g. food availability) as influencing territorial aggression, and hence exclusion. Rather (from Equation 10), N_t reflects the 'contribution' of habitat attributes to territorial aggression and hence exclusion, and it is this, rather than b , that varies with habitat quality. The term $b \ln N_t$ thus describes territoriality in a particular environment. Besides changing basic demographic rates, the effects of changes in habitat quality on territoriality can also be modelled by varying N_t , assuming that improved habitat results in smaller territories and an increase in N_t (Figure S3). Escalating aggression as population density and the proportion of floaters increase is described by the term $b \ln N_t$. Thus, the degree of exclusion, k , is dependent not only on b , but also on both N_t and N_t .

The model assumes that prey depletion does not play an important regulatory role in African Black Oystercatcher population dynamics, i.e. N_t is assumed to be independent of local oystercatcher density. On rocky shores, the birds eat mostly mussels (primarily *Perna perna* and *Mytilus galloprovincialis*) and limpets (primarily *Scutellastra granularis*) (Hockey and Underhill 1984). Oystercatchers may heavily impact limpet densities (Hockey and Branch 1984), but if limpets become locally depleted, the birds switch to mussels as a primary food source (Loewenthal 2007). Intertidal mussels occur at very high densities and stocks are regulated by self-thinning rather than by predation, even when predator densities are high (Griffiths and Hockey 1987). On sandy shores, white mussels *Donax serra* are the main prey (Hockey 1981), but oystercatchers have a negligible impact on the abundance of this species (Ward 1990).

The model does not consider the possible regulatory function of density-dependent mortality. A study of Eurasian Oystercatchers incorporating both empirical evidence and game-theoretic models of foraging behaviour concluded that interference competition led to density-dependent starvation over a large range of population sizes without prey depletion having a significant effect (Goss-Custard et al. 2001). This further supports the contention that exploitative competition is unlikely to limit oystercatcher populations at high densities.

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Figure S1: An asymptotic function illustrating how the proportion of mature birds excluded varies with the number of potential breeders in the model. k = Proportion excluded, N_t = total potential breeding population, N_t^* = potential breeding population size at which exclusion begins. Modified from Goss-Custard (1980)

Figure S2: Graphical representation of the way in which density dependence can be modeled. Where $b = 1$, the number of birds breeding does not depend on the total number available to breed. However, when $b < 1$, the number breeding depends both on N_t^* and on the slope, b . Modified from Goss-Custard (1980)

Figure S3: Diagram illustrating the way in which improvement in habitat quality was modelled. The change in habitat quality is hypothesised to lead to a reduction in optimal territory size and is reflected by an increase in N_t^* (population size at which exclusion begins) in the model, with b remaining constant. k = Degree of exclusion