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THE RIDDLE OF THE SANDS: WHY ARE SHOREBIRD DENSITIES SO HIGH IN SOUTHERN ESTUARIES?

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Abstract.—Population data for migratory waders (*Aves*: Charadrii) during the middle of the nonbreeding season at 31 coastal wetlands in the western Palearctic and Ethiopian regions were analyzed to examine the relationships between bird density and energy intake, intertidal foraging area, and latitude. Wader density is closely linked to population energy intake at individual sites during the nonbreeding season and increases from northern to southern latitudes independently of wetland size. A simple mathematical model linking the variations in the seasonalities of invertebrate production and bird predation is used to provide a mechanistic explanation of the observed variation in bird density with latitude. Results are discussed in the light of current competition- and survival-based models of wader distribution, and, contrary to predictions of some models, we conclude that wader populations track the carrying capacities of coastal wetlands across a wide latitudinal range.

During the boreal summer, many millions of waders (*Aves*: Charadriiformes: Charadrii) breed at high arctic and subarctic latitudes. During the boreal winter these birds migrate southward to occupy a latitudinal range of more than 100°, extending from the Arctic Circle to Australasia and the southern limits of the continental land masses (Hayman et al. 1986). There is a tendency for the most northerly breeding species and populations to spend the nonbreeding season to the south of the more southerly breeders, a pattern known as leapfrog migration (Swarth 1920; Boland 1990).

Four models have been proposed that may explain large-scale patterns of wader distribution during the nonbreeding season. The “time allocation” model, originally developed for Nearctic passerines, proposes a payoff between breeding season length and survival between breeding attempts (Greenberg 1980). Migration to a climatically benign nonbreeding site should be selected in compensation for a short breeding season among species or populations that breed at high latitude and/or altitude. Survival of these individuals during the nonbreeding season should be concomitantly high. The “physiological tolerance” model, based on Bergmann’s rule, predicts that selection pressure for choosing a climatically benign nonbreeding site should be greater for small than for large birds. Available evidence does not support this model as an explanation for the nonbreeding distri-

bution of waders (Pienkowski and Evans 1985; Boland 1988), and it will not be considered further.

Two models identify competition as the proximate mechanism shaping wader dispersion patterns. These models have as a basic tenet that some or all birds should try to minimize the distance between their breeding and nonbreeding grounds, but they invoke different reasons for this. The "breeding resources" model (Alerstam and Hogstedt 1980) assumes a greater predictability in the timing of the onset of spring at high northern latitudes than at low northern latitudes and hypothesizes that low-latitude breeders should remain close to the breeding grounds in order to monitor the onset of spring and thus ensure timely arrival on the breeding grounds. High-latitude breeders, by contrast, can time their northward migration using a circannual clock. As an extension of this hypothesis, Alerstam and Hogstedt (1980) propose that low-latitude breeders will tolerate heavy competition to be close to their breeding grounds whereas Arctic breeders will obviate overt competition (with low-latitude breeders) by migrating farther away. Evidence presented by Slagsvold (1982) casts doubt on the validity of the assumption that the timing of spring is less predictable at low latitudes, and this model also will not be considered further.

The final model is the most recent and is based on competition for resources during the nonbreeding season (Pienkowski and Evans 1984, 1985; Pienkowski et al. 1985). In this "winter competition" model, the high risk of migration, particularly for juvenile birds, is viewed as a selective force promoting short-distance migration (Pienkowski and Evans 1985). Pienkowski and Evans (1985, p. 332) propose that "shorebirds in the eastern Atlantic settle in (boreal) autumn as near to the breeding grounds as possible, but some are prevented from doing so by competition." Three predictions stemming from this model require validation. (1) Competition is most severe close to the breeding grounds; that is, pressure on food resources is greater at more northerly wintering latitudes than at more southerly ones, providing latitude equates with distance traveled. (2) Interannual fluctuations in breeding success will result in greater interannual variability in wader numbers at sites farthest from the breeding grounds; that is, sites nearest the breeding grounds should always be close to carrying capacity. (3) The costs of long-distance migration exceed the survival benefits of spending the nonbreeding season in ostensibly benign environments farther south; that is, birds spending the nonbreeding season at North Temperate latitudes close to the breeding grounds should have a higher survival during the nonbreeding season than birds that migrate farther to tropical, subtropical, and warm temperate latitudes.

A key issue underpinning predictions 1 and 2 above is that of defining and determining the carrying capacity of a habitat for waders. This study concentrates on estuaries and coastal lagoons: these are discrete habitat units where large numbers of migratory waders gather. We define the carrying capacity of a coastal wetland for waders as being the number of waders that can occupy that wetland without removing prey at a rate that, when combined with rates of prey mortality from other sources, exceeds prey production on a long-term basis. Piersma (1987) has offered essentially the same definition.

The aims of this study are to test the predictions of the winter competition

model using data from a wider range of latitudes than that used by Pienkowski and Evans (1985) in formulating the model, to determine how the carrying capacities of coastal wetlands vary for waders in relation to latitude and to seasonal variations in the intensity of predation and invertebrate production, and to assess whether wader populations at coastal wetlands near the breeding grounds are closer to carrying capacity than are wader populations at more distant wetlands.

METHODS

Wader Distribution and Survival

Data on the location, intertidal area, and wader numbers were gathered from 31 estuaries, coastal lagoons, and mud flats spanning the full latitudinal range of the Palearctic-Ethiopian flyway. These data were examined with simple and partial regression analyses (Dixon et al. 1988) to determine the relationship between migrant wader density (D , in birds per hectare) in the middle of the nonbreeding season (December–February) and wetland area (A , in hectares) and latitude (L). Latitude was linearized as $60^{\circ}\text{N} = 1$, $50^{\circ}\text{N} = 2$, and so on. The data used are summarized in Appendix A.

Although there was no correlation between wetland size and latitude ($r = 0.19$, $df = 29$, $P = .31$), all wetlands south of 10°N were relatively small (App. A). Consequently, analyses performed on the entire data set were repeated for the subset ($n = 17$) of small sites (intertidal area $< 3,000$ ha). This procedure was done to ensure against detecting an inadvertent area effect, but it also has the virtue that use of small wetlands alone should ensure maximal accuracy of count data.

It is not known how closely differences in wader density are linked to differences in energy intake rates of wader populations at different sites. Variations in species composition and the relative abundance of species at different sites could strongly influence the population energy intake rate if some communities were dominated by large species and others by small species. Major variations in the size structure of wader communities could thus negate the use of bird density alone as a basis for comparing energy requirements of different populations. The relationship between wader density and population energy intake rate per unit intertidal area was calculated for six sites in the United Kingdom and three sites in South Africa for which multiple counts exist. All sites were less than 2,000 ha in extent. Energy intake rates of individuals of different species were calculated from Nagy's (1987) equation for field metabolic rate ($\text{FMR} = 10.90 W^{0.640}$, where W is wet body mass in grams), corrected for a 75% assimilation efficiency. Daily energy intake of the midwinter population of each species at each site was calculated from the median of between four and 14 midwinter counts. These values were summed to obtain a total population energy intake rate (E , in $\text{kJ} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$).

Published coefficients of variation (CVs) from regional wader counts made in Britain and France over several years (Pienkowski and Evans 1985) were compared with similar data from Walvis Bay Lagoon (23°S) and Langebaan Lagoon

(33°S), South Africa, to test the prediction that variability in wader numbers increases with increasing distance from the breeding grounds.

The putative inverse relationship between the survival rate (S) of a species and the latitude of its nonbreeding site (Pienkowski and Evans 1985) was reevaluated with an all-possible-subsets regression analysis (Dixon et al. 1988) that incorporated the additional parameters of (mean wader body mass)^{0.33} and mean clutch size (C). Mallory's C_p statistic, in conjunction with an adjusted r^2 value, was used to identify which combination of variables best explained observed patterns of variation in survival rate. Survival rate data were normalized by an arcsine transformation. Data used in this analysis, and their sources and related assumptions, are summarized in Appendix B.

Prey Availability and Estuarine Carrying Capacity

Waders that spend the nonbreeding season north of the equator are resident during the cool period of the year, when invertebrate production is lowest. South of the equator the birds' residence period coincides with the peak period of invertebrate production. The manner in which the biomass of invertebrate prey available to birds is influenced by asynchrony (north of the equator) or synchrony (south of the equator) in periods of peak production and predation was investigated with a simple mathematical model. This model is designed to provide a mechanistic (qualitative) investigation of changes in carrying capacity with latitude. Invertebrate production in estuaries decreases with increasing distance from the equator, concomitantly with decreasing mean annual ambient temperature (Kalejta and Hockey 1991). To keep the model as simple as possible, no correction factor for these changes was incorporated. Rather, the latitude effect was examined by comparing the interaction between production and predation at sites equidistant north and south of the equator, where annual invertebrate productivity is assumed to be equal. In the model, Ba_t and Bu_t are the prey biomasses respectively available and unavailable to birds in month t . The ratio $Ba_t:Bu_t$ was held constant at 70:30. This ratio approximates the biomass stratification of intertidal benthic invertebrates respectively above and below a depth of 50 mm in the substratum at the Berg River estuary, South Africa (33°S) (Kalejta 1991). Values of Ba_{t+1} and Bu_{t+1} were obtained month by month from the recursive relationships

$$Ba_{t+1} = 0.7 \{ [Ba_t P_t + Ba_t(1 - Mx_t) - Ba_t Mb_t] + [Bu_t P_t + Bu_t(1 - Mx_t)] \} \quad (1)$$

and

$$Bu_{t+1} = 0.43 (Ba_{t+1}), \quad (2)$$

where P_t is the production-biomass ratio, including somatic production and reproduction; Mx_t is the prey mortality rate from sources other than predation by waders; and Mb_t is the prey mortality due to predation by waders.

The terms in braces in equation (1) calculate total prey biomass at time $t + 1$, and the values of 0.7 and 0.43 in equations (1) and (2), respectively, retain a 70:30 ratio between available and unavailable invertebrate biomass. Predation by birds

was held constant in the 6 mo of the boreal winter and was reduced to a lower constant for the remainder of the year. The background prey mortality rate was assumed to be density-dependent because it incorporates processes such as senescence, competition, and predation among invertebrates. Bird-induced mortality is assumed to be density-independent. Thus, in the calculation of Ba_{t+2} , the term $Ba_t Mb_t$ (from eq. [1]) becomes $Ba_t Mb_{t+1}$. The pattern of avian predation used in the model is simplistic because it assumes that migrant birds arrive at and depart from all estuaries simultaneously. This clearly ignores the use of estuaries as staging areas and takes no account of variations in the residence periods of different species and populations at different latitudes. Although some of these data are available for some sites, no overall pattern is sufficiently clear at present to warrant inclusion of such variation in the model. Likewise, background prey mortality rate (Mx) was held constant in the absence of data indicating an alternative treatment.

The ways in which differences in the relative seasonality of production and predation influence the availability of prey to birds were assessed qualitatively for three hypothetical estuaries, one equatorial, one north of the equator, and one an equal distance south of the equator. The purpose of this assessment was not to define empirically a real-world situation but to illustrate how prey availability is influenced by variation in the degree of synchrony between production and predation. In all three estuaries, the initial prey biomass, the annual invertebrate production-biomass ratio, and the annual predation by birds were the same: only the seasonalities of the production and predation were varied. Background prey mortality rate was held constant. Parameters of equation (1) were set initially to represent an equatorial estuary in which invertebrate production was assumed to be aseasonal and the monthly production-predation ratio was held constant at 0.1575. The summer and winter predation rates by birds were then adjusted to produce a stable, cyclical fluctuation in the available prey biomass. With all other parameters held constant, the monthly production-biomass ratio was then seasonalized to simulate a South Temperate estuary with a maximal production-biomass ratio (0.2) during the main 6-mo wader residence period and minimum production-biomass ratio (0.1) during the 6 mo of the austral winter. The annual production-biomass ratio remained the same as in the equatorial estuary. To simulate a North Temperate estuary, the seasonality of production was reversed. The effects of varying the seasonality of production were assessed in terms of their influence on available prey biomass over a 5-yr period. The robustness of the model was tested by increasing and decreasing the annual production-biomass ratio in each hypothetical estuary by 10% and comparing the effects of this on available prey biomass. The overall sensitivity of the model to changes in its component parameters was assessed with parameter values from the tropical estuary simulation as a base run. Each parameter was changed, individually, at intervals of 5%, from -45% to +45% (per annum) of the original value, and the effects on predicted total prey biomass after 5 yr were calculated. Initial values in equation (1) were $Ba_0 = 70$, $Bu_0 = 30$, $Mx = 0.095$, Mb (boreal summer) = 0.036, Mb (winter) = 0.146, and $P = 0.1575$: these values provide a stable, cyclical fluctuation in available prey biomass. The long-term consequences of

changing the ratio of available to unavailable prey biomass were also calculated by using the stable fluctuation in available prey at a ratio of 70:30 as a starting point and then decreasing and increasing this ratio while holding all other parameters constant. It must be emphasized that this model is designed to provide a mechanistic (qualitative) investigation of changes in carrying capacity with latitude. It cannot be used to predict absolute carrying capacity because of the unknown properties of the background prey mortality rate.

The same model was used in a slightly different way to examine the relative carrying capacities of a South Temperate and a North Temperate estuary equidistant from the equator. Data from the Berg River estuary, South Africa, were used to set values for the seasonal production-biomass ratios and bird-induced mortalities (Kalejta 1991; Kalejta and Hockey 1991). The background prey mortality rate was adjusted to produce a stable annual cycle in available prey biomass at the Berg River estuary. Bird-induced mortalities alone were then adjusted, all by the same proportion, to establish the same stable cycle in a North Temperate (33°N) estuary in which the seasonality of production was reversed. The proportional difference in bird-induced mortality required to generate the same stable cycle in available prey biomass at the two estuaries was equated with the proportional difference in the carrying capacity of the two estuaries for waders.

RESULTS

Spatial and Temporal Patterns of Wader Distribution

Wader density increased significantly from north to south when all sites were included (fig. 1A). Although a linear regression of density on latitude gave a highly significant result ($r = 0.70$, $df = 29$, $P < .0001$), the distribution of residuals indicated that an exponential model was a more parsimonious explanation of the data. The form of the model was $D = 3.39 \times 10^{0.09L}$ ($r = 0.63$, $df = 29$, $P < .0001$). There was a negative relationship between wetland area and wader density ($r = -0.49$, $df = 29$, $P < .01$; fig. 2). Both latitude and wetland area had a significant influence on wader density when the other independent variable was held constant (partial correlation: latitude $r = 0.59$, $df = 29$, $P < .01$; area $r = 0.42$, $df = 29$, $P < .05$). The relationship between wader density, latitude, and wetland area was described by the equation

$$\log D = 1.21 + 0.08L - 0.17 \log A$$

($F = 14.32$, $df = 2,28$, $r = 0.71$, $P < .001$).

Forty percent of the variance of wader density was explained by latitude and 10% was explained by wetland area.

The pattern of increasing wader density with increasing distance from the breeding grounds was reinforced when only small sites (<3,000 ha) were used in the analysis. Wader density at these sites increased with increasing distance from the breeding grounds ($D = 5.19 \times 10^{0.08L}$, $r = 0.80$, $df = 15$, $P < .0001$; fig. 1B) but was independent of wetland size ($P = .55$).

Wader density was strongly and linearly correlated with population energy

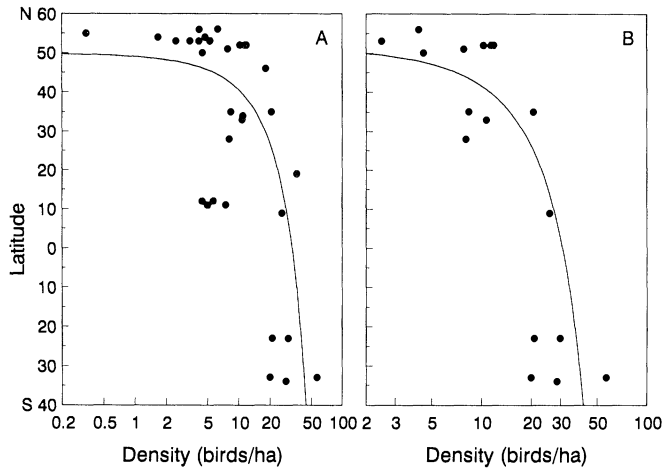


FIG. 1.—The relationship of wader density to latitude for (A) all sites and (B) wetlands of more than 3,000 ha on the east Atlantic seaboard. The dependent variable is plotted on the X-axis for illustrative purposes.

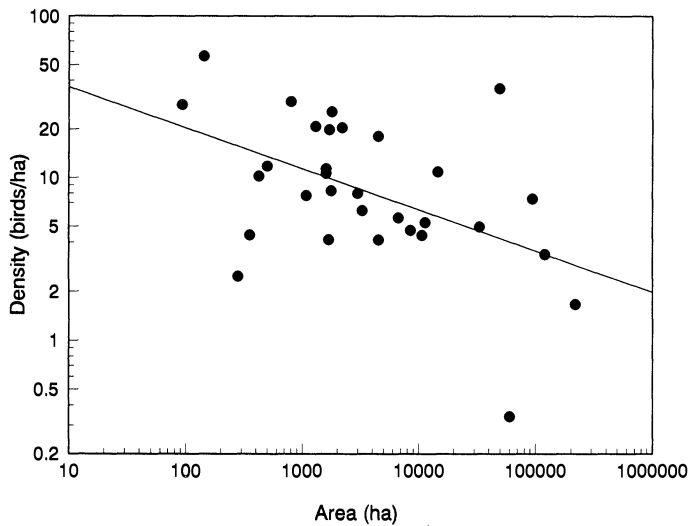


FIG. 2.—The relationship between wader density and wetland area at 31 sites on the east Atlantic seaboard.

intake rate ($E = 1070.3 + 207.2D$, $r = 0.96$, $df = 7$, $P < .001$; table 1). Population energy intake rate at five British estuaries was approximately 27% of that at two South African estuaries. These values do not take into account temperature-linked variation in metabolic rate, which would have the effect of increasing energy intake rate at cold, northern sites (Kersten and Piersma 1987).

Although the interannual coefficients of variation in numbers of gray plovers,

TABLE 1
POPULATION ENERGY INTAKE AND DENSITY OF WADERS AT NINE
SITES IN THE UNITED KINGDOM AND SOUTH AFRICA

Site	Density (birds · ha ⁻¹)	Energy Intake (kJ · ha ⁻¹ · d ⁻¹)
United Kingdom:		
Estuarine:		
Inner Clyde	4.1	2,382
Deben	10.2	3,329
Stour	11.4	3,293
Exe	7.8	3,936
Kingsbridge	4.4	1,799
Mean ± SD		2,948 ± 849
Nonestuarine:		
Foryd Bay	2.5	1,650
South Africa:		
Estuarine:		
Berg	56.6	12,316
Swartkops	28.4	9,725
Nonestuarine:		
Langebaan	19.8	5,254

TABLE 2
COEFFICIENTS OF VARIATION IN WADER NUMBERS DURING THE MIDDLE OF THE NONBREEDING SEASON IN
FOUR REGIONS OF THE EAST ATLANTIC SEABOARD

	Britain and Ireland	France	Walvis Bay	Langebaan Lagoon
Gray plover (<i>Pluvialis squatarola</i>)	.21	.24	.32	.32
Knot (<i>Calidris canutus</i>)	.21	.35	.96	.38
Bar-tailed godwit (<i>Limosa lapponica</i>)	.34	.58	.18	1.01
Dunlin (<i>Calidris alpina</i>)	.19	.29
Curlew sandpiper (<i>Calidris ferruginea</i>)22	.17

NOTE.—Data bases from Europe span 1973–1981 (from Pienkowski and Evans 1985), and data from Langebaan Lagoon span 1976–1985 (from Underhill 1985). Data from Walvis Bay (22°58'S, 14°27'E) were collected between 1986 and 1990 (A. J. Williams, unpublished data; $n = 4$ counts for all species except bar-tailed godwit, for which $n = 3$).

Pluvialis squatarola, increased slightly with increasing distance from the breeding grounds, there was no consistent trend among species of increasing CVs from north to south (table 2). The CV of curlew sandpipers, *Calidris ferruginea*, at the southern limit of their nonbreeding range was less than that of the similarly sized and morphologically comparable dunlin, *Calidris alpina*, at the northern limit of its range. Furthermore, Northern Hemisphere data are integrated from several sites, which should have the effect of reducing CVs, whereas Southern Hemisphere data are site specific.

TABLE 3
RESULTS OF ALL-POSSIBLE-SUBSETS REGRESSION ANALYSIS
OF PIENKOWSKI AND EVANS'S (1985) SURVIVAL DATA

Independent Variables*	df	Mallory's Cp	Adjusted r^2	P (two-tailed)
1	16	4.02	.37	< .01
2	16	4.92	.34	< .02
3	16	11.13	.12	NS
1, 2	15	2.61	.46	< .005
1, 3	15	5.64	.34	< .02
2, 3	15	4.10	.40	< .01
1, 2, 3	14	4.00	.44	< .01

* 1, Mean body mass^{0.33}; 2, mean clutch size; 3, midlatitude of the nonbreeding range.

Survival Rate

A critical element of the winter competition model is that survival rate decreases with increasing migration distance. The analysis presented by Pienkowski and Evans (1985) suggests a marginal negative correlation between percent annual survival (arcsine transformed) and migration distance. (Note that two different types of survival rate data are included in their analysis; see App. B.)

We reanalyzed Pienkowski and Evans's (1985) data, excluding golden plover, *Pluvialis apricaria*, a predominantly terrestrial species during the nonbreeding season. Of the three independent variables, body mass, clutch size, and latitude, a combination of body mass and clutch size best explained variations in survival rate. The form of the best model was $S = 70.89 + 1.28W^{0.33} - 3.62C$ (table 3).

Prey Availability and Estuarine Carrying Capacity

The model for calculating temporal patterns of available prey biomass was most sensitive to changes in the invertebrate production-biomass ratio and the background mortality rate of prey, the latter being the variable most difficult to determine empirically (fig. 3A). A 40% increase in the annual production-biomass ratio resulted in an approximate trebling of the total invertebrate biomass after 5 yr (fig. 3A). The prey biomass available to birds over time was also influenced by the ratio of available to unavailable prey biomass. As this ratio increased, with other parameters held constant, available biomass, and hence estuarine carrying capacity for waders, decreased (fig. 3B).

The model showed that the seasonality of invertebrate production, relative to the period of maximum predation by waders, strongly influenced estuarine carrying capacity for waders at three hypothetical estuaries (North Temperate, equatorial, and South Temperate). When predation by birds was equal at all sites, the level of invertebrate productivity required to maintain a stable, cyclical pattern of available prey biomass was greatest at the North Temperate estuary and least at the South Temperate estuary (fig. 4B). The carrying capacity of a southern estuary is thus greater than that of a northern estuary of equal size and equidistant from the equator simply because of differences in the seasonality of prey production. This pattern of higher carrying capacity in southern estuaries persisted when

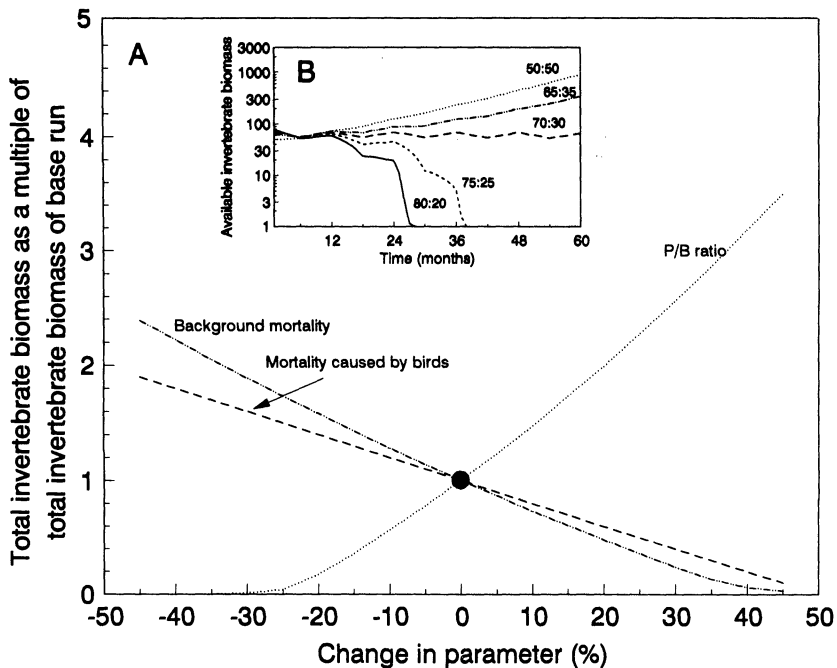


FIG. 3.—Sensitivity analysis of the model used to calculate prey biomass. *A*, The effect on total invertebrate biomass after 5 yr of changing one parameter at a time at intervals of 5%. *B*, The effects on the available prey biomass of changing the ratio of available to unavailable prey biomass.

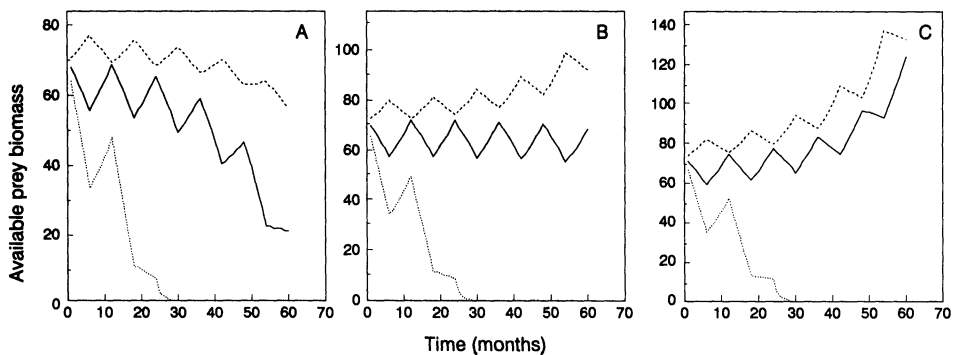


FIG. 4.—Changes in available prey biomass (B_a) over time at North Temperate (*dotted lines*), tropical (*solid lines*), and South Temperate (*dashed lines*) estuaries. Total predation and prey production are equal at the three sites: differences in B_a indicate the effects of seasonally variable production. In *B*, parameters were set to achieve stable, cyclic fluctuations in B_a at the tropical estuary. In *A* and *C*, the annual production-biomass ratio was decreased and increased, respectively, by 10% per annum to test the qualitative robustness of the model. All iterations start at the beginning of a wader residence period.

the production-biomass ratio was decreased or increased (figs. 4A and C), supporting the qualitative robustness of the model (fig. 3).

To determine the proportional difference in carrying capacity of two estuaries of equal size and equidistant north and south of the equator, available prey biomass at the Berg River estuary was set in long-term equilibrium with parameters (eq. [1]) $Ba_0 = 70$, $Bu_0 = 30$, $Mx = 0.096$, Mb (boreal winter) = 0.146, Mb (summer) = 0.036, monthly P (winter) = 0.2, (summer) = 0.1. To achieve the same equilibrium cycle of Ba in an estuary at 33°N, reversing the seasonality of P , Mb had to be reduced by 27%, although total invertebrate production was the same in both instances. The regression relating wader density to latitude at wetlands of less than 3,000 ha predicts that the density of waders at an estuary at 33°N will be only 30% of the density at 33°S.

The empirical relationship between wader density and latitude demonstrates that wader densities at wetlands on the Palearctic-Ethiopian flyway increase from north to south. The model provides a mechanistic explanation for a concomitantly increasing carrying capacity, determined by seasonal differences in prey productivity.

DISCUSSION

Evans (1984) has criticized the applicability of the term "carrying capacity" to wader populations in the nonbreeding season. He argues that there is no reason why the net result of all individuals in a population maximizing their nonbreeding fitness would be for prey populations to be cropped at the maximum sustainable rate. This argument can be accepted if density-dependent behavior of the birds, such as interference, regulates predator density below the level that prey populations could support (Goss-Custard 1985) or if population numbers are regulated on the breeding grounds at a level below the carrying capacity of the nonbreeding grounds.

There is evidence that interference increases with increasing bird density and that this interference is more pronounced among visual than among tactile foragers (Goss-Custard 1980). It has also been shown that wader abundance is linked to prey abundance (Goss-Custard et al. 1977). What is not known is whether interference imposes an upper limit on wader density when prey availability is high.

There is circumstantial evidence that this is not the case. Aggregations of waders feeding on temporarily superabundant prey, such as stranded fish eggs, achieve densities that far exceed the average density recorded at any wetland or estuary. This was illustrated by an experiment at the Berg River in which we artificially increased prey availability by lowering the water level in a commercial salt pan, thus allowing waders access to very high densities of chironomid fly larvae and amphipods. In this experiment, the prey capture rate of curlew sandpipers increased as the density of foraging conspecifics increased; this pattern persisted at foraging densities far higher than those that occur naturally on estuarine mud flats (fig. 5).

The empirical determination of carrying capacity is problematic (Piersma 1987),

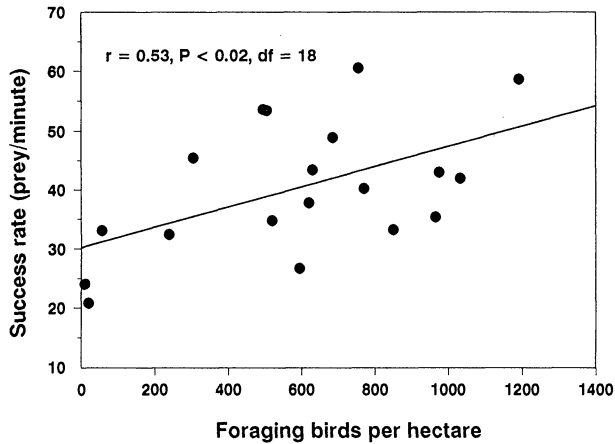


FIG. 5.—The prey capture rate of curlew sandpipers in relation to their foraging density under conditions of experimentally enhanced prey availability at the Berg River estuary, South Africa.

but the latitude-related differences in wader density at wetlands along the Palearctic-Ethiopian flyway strongly suggest that interference does not limit wader density independently of the prey supply, given that interference occurs on northern estuaries (Goss-Custard 1980) where wader densities are relatively low. If differences in wader density can be tied to long-term differences in prey availability, then wader density can be assumed to track carrying capacity, even if it does not equal carrying capacity. This is an important concept in terms of the predictions of the winter competition model. The model requires that the ratio of actual predator take (APT) to maximum sustainable yield (MSY) be highest at sites close to the breeding grounds. If APT is less than MSY, this could be due either to interference or to wader populations' not being regulated by food supply during the nonbreeding season.

In temperate and subtropical estuaries there is a negative relationship between estuarine invertebrate production and distance from the equator and a positive relationship between production and mean annual ambient temperature (Kalejta and Hockey 1991). This study has further established that carrying capacity is not linked solely to production per se but is influenced by the seasonality of that production relative to the seasonality of predation.

In the context of the winter competition model, carrying capacity should not be confused with habitat availability. Considering the numbers of birds alone, the winter competition model has some superficial attraction. Along the east Atlantic seaboard there are many more shorebirds at estuaries in western Europe and equatorial Africa than in southern Africa; but there are relatively few estuaries in the south. In regional terms, the carrying capacity of western Europe is greater than that of southern Africa, but the carrying capacity per unit estuary area is much less. Southern African estuaries are few—there are only four estuaries and

three coastal lagoons on more than 2,000 km of coast between southern Angola (17°S) and the Cape of Good Hope (34°S). These sites are isolated and far from the breeding grounds. If the risks of long-distance migration outweigh the benefits of migrating to a climatically benign nonbreeding site, as assumed in the winter competition model, why are wader densities at these sites consistently high, and why do juvenile birds reach these distant sites even in years following low breeding success (see, e.g., Underhill 1987)?

The validity of using wader density alone as an indicator of population energy intake rate was tested for nine sites, and a strong linear correlation between the variables existed ($r = 0.96$, $df = 7$). The slope of this regression (207) is thus equivalent to the daily energy intake (kJ) of an "average" wader. Relative to the other eight sites in the analysis, waders at the Swartkops estuary have a high individual daily energy intake (343 kJ). The benthic invertebrate fauna at this site is dominated (82% of standing crop biomass; Hanekom et al. 1988) by the large thalassinid mudprawn *Upogebia africana*. Consequently, large waders, mainly gray plovers and whimbrels (*Numenius phaeopus*), are common (Martin and Baird 1987).

If the values calculated for population energy intake rate in this study are compared with predicted values for estuarine invertebrate production (Kalejta and Hockey 1991), this provides further, albeit tentative, support for a link between wader density and estuarine carrying capacity across the full latitudinal range of the east Atlantic seaboard. Population daily energy intake rate at British estuaries is about 27% of that at South African estuaries (table 1). Kalejta and Hockey's (1991) regression predicts that invertebrate production in British estuaries is approximately $20\text{--}30 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. Production at the three South African sites ranges from 78 to $95 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (mean, $89 \pm 9 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) (Kalejta and Hockey 1991). Production in British estuaries is thus about 21%–38% of production in South African estuaries.

The proportions of annual invertebrate production consumed by waders at estuaries at the northern and southern limits of the Palearctic-Ethiopian flyway are similar. However, the paucity of site-specific data linking energy demands of waders directly to invertebrate production militates against overinterpreting this observation. Other factors must be considered if data are to be evaluated quantitatively rather than qualitatively. These include residence time, migratory pulses, the predatory impact of nonwader species, the influence of temperature on metabolic rate, and the proportion of their daily energy requirement that some species, such as the Eurasian oystercatcher (*Haematopus ostralegus*) and Eurasian curlew (*Numenius arquata*), derive from nonestuarine habitats, such as coastal meadows (see, e.g., Heppleston 1971).

On the basis of the information available to date and the results of our own analyses, we argue that three basic tenets of the winter competition model related to competition, population variability, and survival rate cannot be substantiated when tested with data from the full latitudinal range of the Palearctic-Ethiopian flyway. We also suggest, on the basis of our model, the relationship between wader density and latitude, and crude ratios of production to consumption, that the proportion of the maximum sustainable yield of invertebrates that is con-

sumed annually by waders may well be approximately constant at sites spanning a wide latitudinal range.

If the dispersion patterns of waders during the nonbreeding season are not structured proximally by competition, it can be predicted from evolutionary principles that the energetic costs of long-distance migration will be counterbalanced by energetic benefits that make the risk of mortality among individuals migrating to southerly nonbreeding sites equal to or less than the risk among shorter-distance migrants. The Palearctic-Ethiopian flyway does not extend south of 34°S, at the southern tip of Africa. Integration of our model with data on invertebrate production from Kalejta and Hockey (1991), if we assume the same background prey mortality rate at all sites, suggests that 59° from the equator is the point at which estuarine carrying capacity for waders is close to zero in both hemispheres. On the east Atlantic seaboard, some purple sandpipers (*Calidris maritima*) spend the nonbreeding season north of the Arctic Circle, but these birds feed on rocky shores, not in estuaries (Summers 1990). Although the continental land masses do not extend south to 60°S, large numbers of waders do spend the nonbreeding season in the Magellan regions of Argentina, Chile, and Tierra del Fuego, in the low 50s latitudes (Morrison and Ross 1989). An important contribution to our understanding of wader dispersion in relation to characteristics of the prey base could be made by a study of estuarine productivity, in relation to shorebird density and foraging behavior, in the Magellan region.

As more site-specific, empirical studies of interactions between waders and their food supplies become available, it should be possible to extend our analyses to test whether wader density not only tracks wetland carrying capacity but also approximates it. If shorebird populations are regulated by density-dependent processes—an assumption that has been questioned by Evans and Pienkowski (1984)—establishing the existence or nonexistence of an empirical link between bird density and wetland carrying capacity is an essential prerequisite for resolving the debate on whether population regulation occurs on the breeding or the nonbreeding grounds.

SUMMARY

The winter competition model predicts that, during the nonbreeding season, waders should compete to occupy those nonbreeding sites that are closest to their arctic and subarctic breeding grounds. The rationale for this prediction is the assumption that the risks of long-distance migration, especially for juvenile birds, override the benefits to be derived from spending the nonbreeding season at climatically benign sites far from the breeding grounds. As a corollary, the intensity of competition for food should decrease in proportion to distance from the breeding grounds. However, densities of waders at estuaries and coastal wetlands along the Palearctic-Ethiopian flyway during the nonbreeding season increase with increasing distance from the breeding grounds, although interannual variability in numbers does not increase concomitantly. In addition, there is no evidence that survival rate either decreases or increases with increasing migration distance. A simple mathematical model is used to examine the relationship of estuarine

carrying capacity to the intensity and seasonality of predation by waders and to production by invertebrates. The model indicates that carrying capacity is not a simple function of invertebrate production. The carrying capacity of Southern Hemisphere estuaries, where peaks of production and predation coincide, is higher than that of their Northern Hemisphere counterparts, where production and predation peak asynchronously. The predictions of the model, the empirical relationship between wader density and latitude, and a more tentative empirical link between invertebrate production and its consumption by waders suggest that wader populations at coastal wetlands throughout the nonbreeding range occur at densities that closely track carrying capacity.

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APPENDIX A

TABLE A1

LOCATIONS AND ATTRIBUTES OF THE 31 COASTAL WETLANDS USED IN ANALYSES

Site	Latitude	Area (ha)	Number of Waders*
Inner Clyde, U.K.	56°N	1,693†	7,008†
Lindisfarne, U.K.	56°N	3,278†	20,496†
Danish Wadden Sea	55°N	60,000‡	20,404§
German Wadden Sea	54°N	220,000‡	364,647§
Ribble estuary, U.K.	54°N	8,520†	40,246†
Dutch Wadden Sea	53°N	120,000‡	405,220§
Dee estuary, U.K.	53°N	11,420†	60,128†
Mersey estuary, U.K.	53°N	4,540†	18,748†
Foryd Bay, U.K.	53°N	280†	694†
Deben estuary, U.K.	52°N	424†	4,339†
Stour estuary, U.K.	52°N	1,600†	18,212†
Ventjager, Netherlands	52°N	500‡	5,900‡
Exe estuary, U.K.	51°N	1,080†	8,394†
Kingsbridge estuary, U.K.	50°N	355†	1,574†
Vendée, France	46°N	4,500‡	81,000‡
Thyna/Ras Onga, Tunisia	35°N	1,780	14,773
Merja Zerga, Morocco	35°N	2,200 [#]	45,000 [#]
Kneiss, Tunisia	34°N	14,600	158,298
Gourine, Tunisia	33°N	1,600	17,056
Puerto Cansado, Morocco	28°N	3,000 [#]	24,000 [#]
Banc d'Arguin, Mauritania	19°N	49,100 ^{**}	1,936,550 ^{††}
Gêba, Guinea-Bissau	12°N	6,690‡	37,670‡
Bolama, Guinea-Bissau	12°N	10,670‡	46,970‡
"South," Guinea-Bissau	11°N	33,205‡	164,790‡
Bijagos, Guinea-Bissau	11°N	94,232‡	699,120‡
Sierra Leone River	9°N	1,800‡‡	46,200‡‡
Walvis Bay, Namibia	23°S	800§§	23,754§§
Sandwich Harbour, Namibia	23°S	1,300‡	27,000§§
Berg estuary, South Africa	33°S	143	8,088
Langebaan Lagoon, South Africa	33°S	1,700‡	33,707 ^{##}
Swartkops estuary, South Africa	34°S	93 ^{***}	2,638 ^{***}

* Golden plovers (*Pluvialis apricaria*) and lapwings (*Vanellus vanellus*) were omitted because they are predominantly terrestrial foragers; snipes (*Gallinago* and *Lymnocyptes* spp.) and purple sandpipers (*Calidris maritima*) were omitted because they rarely forage on intertidal soft-sediment flats.

† Data supplied by British Trust for Ornithology (from Birds of Estuaries Enquiry data bank). Total is the sum of species medians from five January high tide counts, 1986–1990. Areas exclude salt marsh.

‡ Zwarts 1988.

§ Smit 1982, January counts.

^{||} van Dijk et al. 1986. Kneiss counts, February; others, January.

[#] Kersten and Smit 1984.

^{**} Wolff and Smit 1990.

^{††} Trotignon et al. 1980. These counts were used in preference to Altenburg et al.'s (1982) counts because of their timing (December–January vs. January–March).

^{‡‡} Tye and Tye 1987.

^{§§} Whitelaw et al. 1978. Area excludes salt marsh. Counts were made on intertidal mud flats only, at low tide.

^{|||} Velasquez et al. 1991. Counts were made on intertidal mud flats at low tide. Total is the sum of species medians from eight counts in January and February, 1988 and 1989.

^{##} Data were supplied by the Western Cape Wader Study Group. Total is the sum of species medians from 14 midsummer (usually January) high tide counts, 1976–1989.

^{***} Martin and Baird 1987. Area excludes salt marsh. Total is the sum of species medians from five January low tide counts, 1983–1985.

APPENDIX B

TABLE B1

DETAILS OF ANNUAL SURVIVAL RATES, NONBREEDING LATITUDE, BODY MASS^{0.33}, AND MEAN CLUTCH SIZES USED IN THE SURVIVAL ANALYSIS

Species and Survival*	Latitude*	Mass ^{0.33} †	Clutch Size‡
European oystercatcher (<i>Haematopus ostralegus</i>):			
.94‡	50	7.98	2.78
.89‡	45	7.98	2.78
Gray plover (<i>Pluvialis squatarola</i>):			
.86§	52	6.17	4.00
Ringed plover (<i>Charadrius hiaticula</i>):			
.72‡	45	3.93	3.79
.85‡	53	3.93	3.79
Kentish plover (<i>Charadrius alexandrinus</i>):			
.75‡	20	3.48	3.00
Bar-tailed godwit (<i>Limosa lapponica</i>):			
.88§	52	6.63	2.00
Eurasian curlew (<i>Numenius arquata</i>):			
.81§	52	9.13	3.78
Redshank (<i>Tringa totanus</i>):			
.78‡	44	5.04	3.95
.72‡	40	5.04	3.95
Common sandpiper (<i>Actitis hypoleucos</i>):			
.76‡	27	3.55	4.00
Ruddy turnstone (<i>Arenaria interpres</i>):			
.85§	52	4.84	3.90
.78‡	10	4.84	3.90
Sanderling (<i>Calidris alba</i>):			
.83§	52	3.71	3.93
Temminck's stint (<i>Calidris temminckii</i>):			
.81‡	10	2.85	3.98
Dunlin (<i>Calidris alpina</i>):			
.73‡	30	3.56	3.82

* From Evans and Pienkowski (1984) and Pienkowski and Evans (1985).

† Calculated from Cramp and Simmons (1983).

‡ Species whose survival was monitored by returns to the breeding site (Pienkowski and Evans 1985): a midlatitude of the nonbreeding range was used. The latter presumably was determined on the basis of ringing returns, as intraspecific differences were recognized dependent on breeding locality.

§ Species whose survival was determined by monitoring the return of individually marked birds to wintering sites (Pienkowski and Evans 1985): the latitude of the wintering site was equated to the midlatitude of the nonbreeding range.

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