TERRITORY STRUCTURE, PARENTAL PROVISIONING, AND CHICK GROWTH IN THE AMERICAN BLACK OYSTERCATCHER *HAEMATOPUS BACHMANI*

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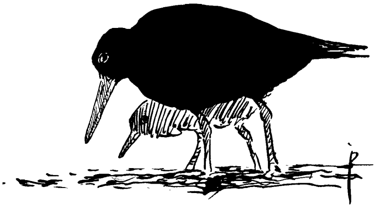
Hazlitt S.L., R.C. Ydenberg, & D.B. Lank 2002. Territory structure, parental provisioning, and chick growth in the American Black Oystercatcher *Haematopus bachmani*. Ardea 90(2): 219-227.

We investigate parental food provisioning and chick growth to better understand how parental effort and territory structure relate to reproductive success in the American Black Oystercatcher. American Black Oystercatcher chick diet was comprised mainly of limpets. Most prey items were 20 mm or shorter in length. Provisioning rates (kJ h^{-1}) were significantly correlated with mean delivery rates rather than mean prey size, and higher provisioning rates resulted from a greater number of deliveries of small prey items. Provisioning rates were extremely variable among pairs but increased significantly with brood size and brood age. Larger brood sizes occurred more frequently on shallow sloped territories, therefore provisioning rates were significantly higher on shallow sloped than steep sloped territories. Provisioning rates appeared to decrease with increasing intertidal slope, a trend significantly supported by the growth patterns of the slow-growing chick in multi-chick broods. The effect of intertidal slope became more important when chicks were older and demand was higher, with parents occupying shallow territories achieving higher provisioning rates to older chicks relative to parents on steep territories. We discuss the hypothesis that American Black Oystercatcher parents adjust parental effort with respect to territory quality and propose possible parental adjustment mechanisms.



Key words: *Haematopus bachmani* - American Black Oystercatchers - provisioning rates - chick growth - territory structure

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INTRODUCTION

The reproductive performance of species provisioning offspring depends on both the availability of prey and the parental effort required to capture and deliver it. For example, in the strongly territorial breeding system of the Eurasian Oystercatcher *Haematopus ostralegus*, shoreline breeding territories are located adjacent to mudflats, where prey are captured, allowing offspring to accompany both foraging parents on the mudflat (Ens *et al.* 1992). But for interior territories not adjacent to mudflats, each prey item must be transported back to the breeding territory. Although parental effort is higher in the interior territories, reproductive performance is higher in shoreline territories (Ens *et al.* 1992; Kersten 1996).

American Black Oystercatchers *Haematopus bachmani* are territorial, open nesting shorebirds, less well-studied than their European congeners. Each pair defends a breeding and feeding territory along rocky shorelines, usually laying three eggs but very rarely raising three young to independence (Andres & Falxa 1995). Parents feed their young marine invertebrates obtained from the adjacent intertidal area, and young are totally dependent on parents for food for up to four months (Andres & Falxa 1995). American Black Oystercatchers prefer shallow sloping shoreline sites for breeding and breeding success is higher on shallow sloping than on steep sloping shoreline territories (Andres 1998; Hazlitt *in press*). However, there is no relationship between the size of the monopolized shoreline territory and slope of the intertidal area or the reproductive success of breeding pairs (Hazlitt *in press*).

We investigate parental food provisioning and chick growth to better understand how parental effort and territory structure relate to reproductive success in the American Black Oystercatcher. Three mechanisms may contribute to an effect of territory slope on the provisioning and growth of American Black Oystercatchers: (1) Breeding territories with shallow sloped intertidal areas may have larger prey items. Invertebrate biomass is greater in the lower sections of the intertidal shelf, and large prey species are available only in these regions (Groves 1982). (2) Shallow sloped intertidal areas may have more food available because they have more total area available during the tidal cycle, and thus access to some prey types and larger size classes may be greater than on steep sloped territories (Kozloff 1993; Andres 1996). Finally, (3) shallow sloped territories may facilitate higher delivery rates because chicks are able to accompany parents along the moving tide line, decreasing the travel cost for each delivery, analogous to the contrast between shoreline and interior territories in Eurasian Oystercatchers (Ens *et al.* 1992).

In this paper we investigate in more detail the effect of territory structure (i.e. slope of the intertidal feeding area) on the reproductive success of American Black Oystercatchers by examining the provisioning and growth of young. In the discussion, we consider the hypothesis that American Black Oystercatcher parents adjust parental effort to territory quality and propose possible parental adjustment mechanisms.

METHODS

The study was conducted in the southern Gulf Island archipelago, Strait of Georgia, British Columbia (48°35’N, 123°15’W) in May - August 1996 and 1997. Over the two years of the study 34 American Black Oystercatcher breeding pairs occupying territories on 21 islands or islets were monitored. Breeding territories were visited by boat approximately every five days throughout the breeding season. Behavioural observations were conducted using 7x42 binoculars to determine territory boundaries, reproductive status of a pair, and whereabouts of the brood. For each territory we measured the length of the shoreline (m) at high tide using a 50m measuring tape. The slope of the littoral zone was measured with a clinometer at high, mid and low points along transects perpendicular to the shoreline at 5 m intervals throughout the territory (details in Hazlitt *in press*).

Provisioning observations

Observations of American Black Oystercatcher parents provisioning offspring were made during the linear phase of chick growth (Groves 1984). Three to five observation periods on each of 11 territories were made using a spotting scope from nearby vantage points. Observation sessions lasted 4 h, centred on the lowest tide of the day (Groves 1982). A total of 49 observation sessions were made, in which 2156 deliveries were recorded. An event recorder was used to record: (1) the time of each prey delivery by each parent to the brood; (2) the prey species; (3) the length of the prey item; (4) times when the brood was out of the sight of the observer. Prey species were categorized as limpet *Lottia* spp., chiton *Katherina tunicata*, crab *Hemigrapsus* spp., polychaete *Nereis* spp., isopod *Idotea* spp., cockle *Clinocardium nuttalli*, mussel *Mytilus trossulus*, barnacle *Balanus* spp., unidentified flesh, or unknown items. Prey size was estimated as an increment of the parent bill length (1/6, 1/5, 1/4, 1/3, 1/2, 2/3 and 1 bill length). This method may be inaccurate as an estimate of the actual prey size, but it should not result in systematic biases within the data (Goss-Custard *et al.* 1987; Emms & Verbeek 1991). We used a mean bill length for the American Black Oystercatcher of 73.5 mm (Andres & Falxa 1995). For the purposes of estimating energy delivery, unidentified flesh and unknown items were assumed to be limpets (they were the most common prey item) of average size captured (mean ± SD, 1.77 ± 0.42 cm, $n = 1135$).

Length-dry weight regressions and energy estimates were obtained for prey species from the literature (summarized in Hazlitt 1999). If no conversion regression was available, we used 20.16 kJ g^{-1} (dry weight) to estimate the energetic value (Menge 1972). For each observation period, the number of deliveries and the total energy (kJ) delivered to the brood was calculated. The delivery rate was the number of deliveries divided by the time the brood was in sight of the observer. The provisioning rate was the total amount of energy (kJ) delivered divided by the time the brood was in sight of the observer (kJ h^{-1}).

Chick growth

Chicks were measured approximately every five days from 5 to 35 d of age, which corresponds with the linear phase of growth (Groves 1984). American Black Oystercatcher chicks are capable of short flights at 35 to 40 d, but remain with the parents on the territory (Andres & Falxa 1995). Excessive human disturbance can prolong the time until independent flight (Nysewander 1977), or cause chicks to flee the territory (Hazlitt 1999), and we therefore ceased attempts to find or catch young when they reached 35 days of age, or as soon as chicks became capable of flight. Chicks were located on the territory by following the movements of the parents. Captured chicks were weighed to the nearest gram using Pesola® spring balances.

A regression line was fitted to the 3 - 7 weights (mean ± SD, 4.3 ± 1.3) obtained for each chick, and the slope of the regression used as the measure of individual growth rate (Nisbet *et al.* 1995). An average growth rate was calculated for each brood. A total of 47 chicks from 32 broods were measured over the two seasons. There is a single statistical outlier (studentized outlier criteria; Freund & Littell 1991), which was a chick raised on a territory occupied in one season only. The outlier was excluded from analyses reported below.

Chicks were classified as singletons, and in multi-chick broods as the fast-growing sibling(s) and the slow-growing sibling (Groves 1984). Of the 31 broods, 17 were singletons, 12 were 2-chick broods and only two were 3-chick broods. There were four cases of chick loss during the linear phase of growth. We estimated the growth rate of the surviving chick before and after the loss of its sibling. For comparative purposes, we selected four chicks from intact broods matched for rank and territory slope, and calculated their growth rate during the first 15 days of the linear growth phase.

Statistical analyses

Statistical analyses were conducted using SAS 6.12 for Windows. The effects of brood size and brood age on the provisioning rate were investigated using repeated measures analysis of variance. F-statistics were calculated using maximum likelihood estimates from an unstructured covariance model with missing values (PROC MIXED: SAS Institute 1990). F-statistics were based on type III SS, controlling for other effects in the model. Analyses of effect of both brood size and intertidal slope excluded territories with intertidal slopes greater than 25 degrees, because no pairs on steeper sloped territories raised more than 1 chick. A mean provisioning rate (based on residuals from regressions on brood size and age), mean number of deliveries and mean prey size delivered was calculated from the 3 to 5 observation sessions for each pair. A multiple regression model was used to determine the relative contributions of the number of deliveries and mean prey size delivered to the rate of provisioning (kJ h^{-1}).

Analysis of variance was used to examine the effect of brood size on average brood growth rate and the effect of brood size and intertidal slope of the territory on individual chick growth rate. F-statistics were based on type III SS, controlling for other effects in the model. Custom hypothesis tests were conducted using the analysis of variance contrast statement in SAS to test for predicted differences in chick growth rates with brood size. The comparison between chick growth rates prior to and after sibling loss were done using pairwise *t*-tests. Each territory was used as a single observation in analyses of territory structure. Average values for chick growth and brood size were used for the 10 territories that were followed in both years.

RESULTS

Chick diet

Of the 2156 deliveries observed, 1620 prey items (75%) were identified and their size estimated (Table 1). Limpets were the most frequently delivered item (70%), followed by chitons (12%) and barnacles (13%). Limpets comprised 70% of the total energy (kJ) delivered, followed by chitons (20%) and barnacles (9%). All other prey types together comprised only 5% of the chick diet, and less than 2% of the total energy delivered. Most items (73%) delivered were less than 20 mm in length, and few large items (2/3 to 1 bill length) were observed (7%). The size distribution of limpets and barnacles delivered was skewed towards small size classes relative to other prey species (Table 1). The only large prey in the chick diet were chitons, which compromised 12% of the items delivered and 20% of energy provided.

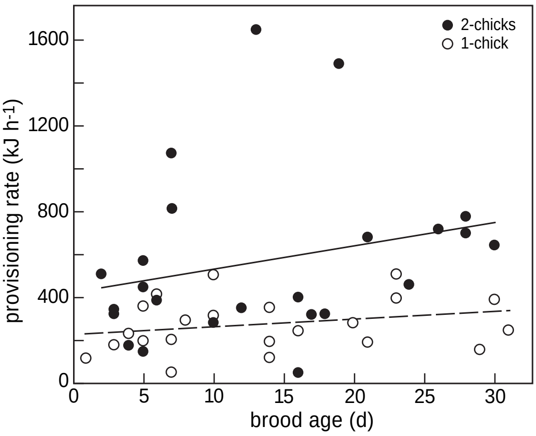

Fig. 1 Parental provisioning rates (kJ h^{-1}) in relation to age and size of the brood. Open circles (dashed line) represent broods of one and closed circles (solid line) represent 2-chick broods. Repeated measures analysis of variance: Brood age $F_{1,9} = 17.9$, $P = 0.002$; Brood size $F_{1,9} = 16.7$, $P = 0.003$; Brood age * Brood size $F_{1,9} = 2.95$, $P = 0.12$.

Provisioning

Of the 11 American Black Oystercatcher pairs observed provisioning broods, six pairs raised a single chick and five pairs raised 2-chick broods to fledging. Provisioning rates increased significantly with brood age ($F_{1,9} = 17.9$, $P = 0.002$) (Fig. 1), and provisioning rates to 2-chick broods were significantly higher than provisioning rates to a single chick ($F_{1,9} = 16.7$, $P = 0.003$) (Fig. 1). Provisioning rates to single chicks ranged from 218 kJ h^{-1} at day 5 to 325 kJ h^{-1} when chicks were

Table 1. Frequencies (%), by type and size (increment of bill length), of prey items delivered to 11 Oystercatcher broods in 1996 and 1997 (*n* = 1620). ‘Other prey types’ include crab, mussels, cockles, and worms.

Prey Size	1/6	1/5	1/4	1/3	1/2	2/3	1	All
Prey Type								
Limpet	23%	13%	21%	10%	2%	0%	0%	70%
Chiton	0%	0%	1%	2%	5%	3%	1%	12%
Barnacle	6%	4%	2%	1%	0%	0%	0%	13%
Other	0%	0%	1%	2%	1%	0%	0%	5%
All	30%	18%	24%	15%	8%	4%	2%	100%

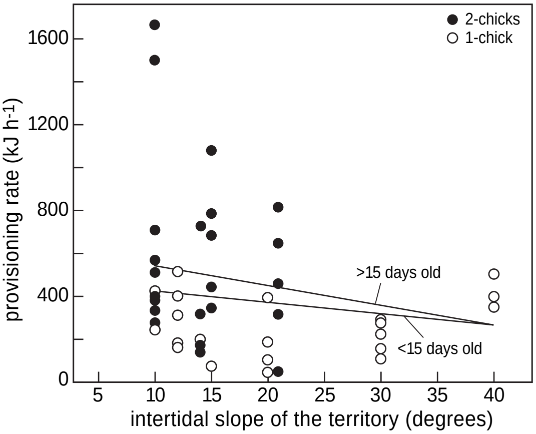

Fig. 2. Parental provisioning rates (kJ h^{-1}) in relation to slope of the intertidal feeding area and age of the brood. Regression lines represent provisioning rates to broods less than 15 days old and broods greater than 15 days old. Repeated measures analysis of variance: Brood age $F_{1,8} = 28.5$, $P = 0.0007$; Intertidal slope $F_{1,8} = 25.5$, $P = 0.0007$; Brood age * Intertidal slope $F_{1,8} = 5.1$, $P = 0.05$.

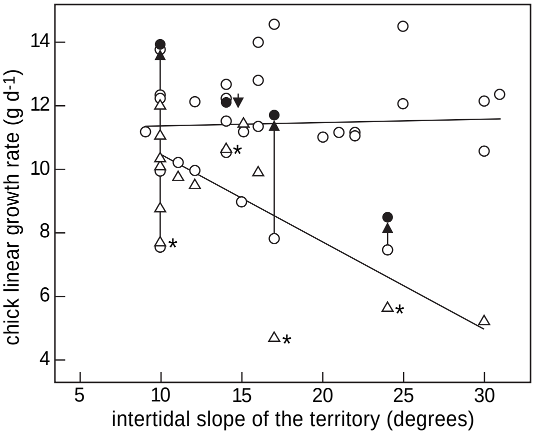

Fig. 3. Growth rates of single chicks and the fast-growing and slow-growing chicks in multi-chick broods compared to intertidal slope of the territory ($n = 46$). Open circles represent the singletons and fast-growing chicks. Triangles represent the slow-growing chicks. Triangles accompanied with an asterisk denote that the chick was lost during the linear phase of growth ($n = 4$). Closed circles and arrows represent the change in growth rate of surviving siblings in the 4 cases of sibling loss. Analysis of variance: Chick rank $F_{1,44} = 0.32$ $P = 0.72$; Territory slope $F_{1,44} = 10.3$, $P = 0.003$; Chick rank * Territory slope $F_{1,44} = 4.41$ $P = 0.02$.

35 days old. Rates to 2-chick broods ranged from 420 kJ h^{-1} and increased to 800 kJ h^{-1} (Fig. 1).

We could not demonstrate a difference in the slopes of territories on which single and 2-chick broods were raised (t-test; $t = 1.2$, $P = 0.2$), although the data suggest that single chick territories (mean ± SE, 21 ± 3.8) were steeper than 2-chick territories (14 ± 4.2). But as the chicks aged, the provisioning rates on steeper beaches did not increase as rapidly compared to provisioning rates on shallow sloped beaches (Fig. 2). Most prey items were small, and so delivery (items h^{-1}) and provisioning (kJ h^{-1}) rates were strongly correlated on each territory ($r^2 = 0.64$, $F_{1,9} = 16.38$, $P = 0.003$). Variation in the mean size of delivered prey did not explain a significant amount of the variation in the mean provisioning rate ($r^2 = 0.24$, $F_{1,9} = 2.86$, $P = 0.13$). If anything, parents provisioning single chicks delivered slightly larger items (mean ± SD, 2.34 ± 0.27 cm) than those provisioning 2-chick broods (2.06 ± 0.19 cm), but the difference was not significant (Wilcoxon test: $Z = -1.55$, $P = 0.12$).

Chick growth

The average growth rate of two and three chick broods did not differ ($F_{1,29} = 1.29$, $P = 0.27$) but single chick broods grew significantly faster than multi-chick broods ($F_{1,29} = 11.0$, $P = 0.002$). The difference is attributable to the decline in growth rate with the slowest growing chick in multi-chick broods ($F_{1,44} = 10.0$, $P = 0.0003$). Single chicks and the fast growing sibling in a multi-chick brood did not differ in growth rate ($F_{1,44} = 1.94$, $P = 0.17$), however both had significantly faster growth rates than the slower growing siblings in multi-chick broods ($F_{1,44} = 16.8$, $P = 0.0002$).

We recorded four cases of chick loss during the linear phase of growth, and in each instance the slow-growing brood member was lost (Fig. 4). The growth rate of the fast-growing chick prior to sibling loss was not significantly slower than the early period of the fast-growing chick growth from intact broods on similar sloped territories (pairwise *t*-test: $n = 4$, $t = -2.6$, $P = 0.08$). We could detect no significant change in the growth rate of the surviving chick after sibling loss (pairwise *t*-test: $n = 4$, $t = -1.9$, $P = 0.15$), however growth rates did increase in 3 of the 4 cases (Fig. 4). Neither average brood growth rate ($r^2 = 0.11$, $F_{1,19} = 2.38$, $P = 0.14$) nor growth of single and fast-growing chicks varied significantly with intertidal slope of the territory ($r^2 = 0.003$, $F_{1,29} = 0.077$, $P = 0.78$) (Fig. 4). However, the growth rates of slow-growing chicks in multi-chick broods significantly decreased with steeper sloped intertidal areas ($r^2 = 0.43$, $F_{1,13} = 9.98$, $P = 0.008$) (Fig. 4).

DISCUSSION

American Black Oystercatchers provision benthic marine invertebrates captured in the intertidal area to their offspring. Consistent with other studies (Hartwick 1976; Groves 1982), limpets were the major food item, accounting for most of the energy provided to young. The largest prey item delivered, chitons, comprised only 12% of items delivered but 20% of the energy provided. Most items delivered to the young were only 20 mm in length.

Based on our provisioning rate estimates, each parent of a single 35 day old chick must provision one average-sized limpet (approximately 21 kJ) about every eight minutes during the low tide cycle. This increases to every 4 min per parent in a 2-chick brood, and every 2.6 min in a 3-chick brood. We therefore estimate the delivery rate to a 3-chick brood to be about 630 kJ h^{-1} for young chicks, rising to over than 1000kJ h^{-1} for 35 day old chicks (Fig. 1). The American Black Oystercatcher pair with the highest provisioning rate (> 1000kJ h^{-1} measured in 1996) raised a 3-chick brood in 1997. This was the first record of a pair raising three young to independence in British Columbia (Hartwick 1974; Groves 1984; Hazlitt 1999).

Pairs occupying shallow-sloped territories delivered more food compared to pairs breeding on steep-sloped territories, but they did not deliver significantly larger prey items. Instead, the main factor contributing to higher provisioning rates (kJ h^{-1}) was that more items were delivered per hour. Although single chicks and the fast-growing chicks in multi-chick broods had similar rates of growth across all territories, the rate of growth of the slow-growing chick in multi-chick broods declined markedly on steeper sloped territories. In four cases these slow-growing chicks disappeared during the linear phase of growth.

We suggest that parents on shallow-sloped territories were able to achieve higher delivery rates because their territories allow offspring to accompany provisioning parents on feeding excursions into the intertidal area. Nol (1989) found that the area and location of the intertidal feeding area relative to the nest site was more important than the density of prey during the chick-rearing period in American Oystercatchers *Haematopus palliatas*. This is analogous to the pattern observed in the European Oystercatcher where breeding pairs that nest in shoreline territories adjacent to feeding areas raise more offspring than those nesting inland because travel time for each food delivery is greatly decreased (Ens *et al.* 1992; Kersten 1996). We also observed that on steep-sloped territories, in contrast to the European system, one parent remains with the young in the rocks above the tide to provide protection, while the other parent provisions, which would also reduce the rate of provisioning (Purdy & Miller 1988).

Parental adjustment of reproductive effort?

Variation in quality is high among American Black Oystercatcher territories (Groves 1984; Hartwick 1974; Hazlitt 1999). During our study, pairs on most territories failed to produce any fledglings in either year, some produced young in one season, and only a few pairs were able to fledge young in both seasons (Hazlitt & Butler 2001). As American Black Oystercatchers are long-lived, monogamous shorebirds with strong territory and mate fidelity, established pairs undoubtedly have good information about the quality of the breeding territory. Hatching success and subsequent brood size are correlated with the slope of the intertidal feeding area (an index of chick food delivery capacity) on American Black Oystercatcher breeding territories (Hazlitt *in press*), suggesting that parents produce a brood size appropriate to their territory, which in most cases is less than three.

In spite of this, American Black Oystercatchers produce many more eggs than young raised on the territory (Groves 1984; Hazlitt & Butler 2001). Of the 23 clutches that fledged any young during our study, only 6 (1 brood of 3 and 5 broods of 2) produced more than one independent offspring. During hatching, single eggs frequently disappeared, were abandoned or were damaged (Hazlitt & Butler 2001). Oystercatcher eggs are small relative to female body mass (Nol *et al.* 1984) and presumably relatively inexpensive, and we hypothesize that the third and perhaps even the second eggs are ‘insurance’ eggs, giving protection against unpredictable egg loss (Mock & Forbes 1995). Should all three eggs survive incubation, a strong adjustment occurs just at hatch when the rate of egg mortality is 4 times higher than incurred throughout the incubation (Hazlitt & Butler 2001).

On some territories, sibling competition promotes further brood reduction. Sibling hierarchies develop quickly, with dominant offspring already heavier than subordinate chicks at the beginning of the linear growth phase (Groves 1984). Sibling rivalry for food and starvation is well-documented in oystercatchers (Safriel 1981; Groves 1984; Andres 1996; Kersten & Brenninkmeijer 1995). The greatest incidence of American Black Oystercatcher chick loss occurs in the first week post-hatch, prior to the peak demand period (Groves 1984; Hazlitt & Butler 2001). In this study, poor growth of the slow-growing chick in multi-chick broods occurred primarily on steeper or poor quality territories.

The results of this study show that the rate of parental provisioning to offspring and growth rates of the slower-growing chick in multi-chick broods is related to the structure of an American Black Oystercatcher territory. We suggest that shallow-sloping shoreline territories allow offspring to accompany provisioning parents on feeding excursions into the intertidal area, somewhat analogous to the European Oystercatcher (Ens *et al*. 1992). We also suggest that American Black Oystercatchers make use of both egg overproduction and offspring handicapping as tactics in a brood reduction strategy (Mock & Forbes 1995).

ACKNOWLEDGEMENTS

We thank D. Lissimore and J.E. Cotter for their help with the fieldwork, and M.J.F. Lemon, T.M. Sullivan, L.F. Keller, C.M. Smith, and B. Sherman for help with various aspects of the research. Permission to establish a field camp on Sidney Island was granted by the British Columbia Ministry of Environment, Lands and Parks. We thank R.W. Butler for comments on previous drafts of this paper. L. Bruinzeel and an anonymous reviewer provided valuable comments on the manuscript. We thank Dick Dekker for his help with the Dutch summary. Financial support was provided by the Canadian Wildlife Service, Pacific and Yukon Region, the Center for Wildlife Ecology at Simon Fraser University, and the John K. Cooper Foundation.

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SAMENVATTING

Het leefgebied van de Amerikaanse Zwarte Scholekster *Haematopus bachmani* is de rotsachtige kust van de Stille Oceaan in Noord-Amerika. Gepaarde vogels verblijven vrijwel het gehele jaar in hun territorium, waar zij tussen mei en augustus hun jongen grootbrengen. Wij bestudeerden de relatie tussen de kwaliteit van het territorium (de hoeveelheid voedsel die de ouders aanbrachten) met de groei van de kuikens en het reproductieve succes van het paar. Gedurende twee jaar (1996-97) observeerden wij 34 territoria. Broedparen foerageerden in de kuststrook tussen hoog- en laagwater en brachten voor hun jongen schelpdieren aan, waarvan de meeste 20 mm lang waren of kleiner. De energieopbrengst (kJ u^{-1}) van het voedsel voor de jongen was sterk afhankelijk van het aantal voedingen per uur, maar onafhankelijk van de grootte van de prooien. De kwaliteit van het territorium, met name de steilheid van de ruwe met rotsblokken bezaaide kuststrook, bleek bepalend voor de overlevingskansen van de kuikens. Op minder steile oevers was de voedselaanvoer groter en kwamen vaker grotere broedsels tot ontwikkeling. De kuikens groeiden langzaam. In broedsels met meer dan één jong vertoonde hun groei een negatieve correlatie met de hellingshoek van het territorium. Dat was niet het geval in broedsels met één jong of voor het snelst groeiende jong in een groter broedsel. In drie van de vier waargenomen gevallen dat er een jong verdwaald raakte en verdween, nam de groei van het overgebleven jong toe. Het belang van territoriumkwaliteit werd duidelijker naarmate de jongen groter werden en meer voedsel nodig hadden. Dit zou als volgt verklaard kunnen worden. Op vlakkere oevers konden de jongen hun ouders vergezellen bij het foerageren in de getijdenzone, hetgeen op steile terreinen niet mogelijk was. Daar moest een van de ouders bij de jongen blijven, terwijl de ander het voedsel aanbracht. Een gelijkwaardige

situatie werd bij de Europese Scholekster *Haematopus ostralegus* geconstateerd. Paren die hun territorium vlakbij het wad hadden (‘hokkers’), deden het beter dan ‘wippers’ die verder van het wad huisden en heen en weer moesten vliegen. Als hypothese stellen wij voor dat ouders van de Zwarte Scholekster hun reproductieve activiteiten afstemmen op de kwaliteit van het territorium.

Received 23 March 2001, accepted 5 March 2002
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