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 ter-

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

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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. **emished tvalue.199PROC MIXED: two T*Of**

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.

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 h218 kJ h

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 $\pm$ 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). M0Tng rates

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

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 posthatch, 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).

REFERENCES

Andres B.A. 1996. Consequences of the Exxon Valdez spill on Black Oystercatchers. Ph.D.-thesis, Ohio State Univ., Columbus.

Andres B.A. 1998. Shoreline habitat use of Black Oystercatchers in Prince William Sound, Alaska. J. Fld. Ornithol. 69: 626-634.

Andres B.A. & G.A. Falxa 1995. Black Oystercatcher. In: Poole A. & F. Gill (eds) The Birds of North America, no.155. Academy Nat. Sc., Philadelphia; American Ornithologists' Union, Washington, D.C.

Emms S.K., & N.A.M. Verbeek 1991. Brood size, food provisioning and chick growth in the Pigeon Guillemot *Cepphus Columbia*. Condor 93: 943-951.

Ens B.J., M. Kersten, A. Brenninkmeijer & J.B. Hulscher 1992. Territory quality, parental effort, and reproductive success of Black Oystercatchers

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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 reproductie-ve activiteiten afstemmen op de kwaliteit van het terri-torium.