CHICK GROWTH, SIBLING RIVALRY, AND CHICK PRODUCTION IN AMERICAN BLACK OYSTERCATCHERS

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ABSTRACT.—I studied chick growth, sibling rivalry, and chick production in a population of American Black Oystercatchers (*Haematopus bachmani*) on Cleland Island, British Columbia from 1975 to 1978. For these birds, survival from hatching until time of first flight is the critical life-history stage. Chick growth varied with brood size, and heavier chicks had higher survival to the time of first flight. Once chicks could fly, however, their survival to 1 and 2 yr of age was not related to brood size or weight at time of first flight. Dominance hierarchies based on weight existed in two-chick broods, and dominant sibs could control access to parental feedings through sibling rivalry. Sibling rivalry probably increases the likelihood of some chick production in years when food is difficult to obtain. *Received 15 March 1983, accepted 12 January 1984.*

GROWTH and survival of young animals are affected by how parental investment is partitioned among offspring (Smith and Fretwell 1974). In most animals, parental investment is limited to the partitioning of energy among eggs. In animals that also feed dependent young, however, the allocation of parental care among individual offspring affects offspring growth and survival (Brockelman 1975). In principle, when offspring are dependent on parental feeding, it should be possible to relate parental foraging performance and chick feeding to chick production, but in practice this is a difficult task. In this study the relationship between parental foraging performance and chick production in American Black Oystercatchers (*Haematopus bachmani*) was examined indirectly by studying: (1) the average chick production from one and two-egg clutches; (2) the relationship between brood size and chick growth; (3) sibling rivalry and factors affecting the establishment and maintenance of weight differences in two-chick broods; and (4) the relationships between chick weight and chick survival.

METHODS

Study area.—Cleland Island (49°10'N, 126°05'W), an Ecological Reserve near Tofino, British Columbia, was the site of this study. Cleland is a low-lying, basalt reef about 7.7 ha in area. The tides are mixed, mainly semi-diurnal, with a mean tidal range of 2.8 m. Low tide exposes an extensive intertidal zone inhabited by a diverse community of marine invertebrates (Campbell and Stirling 1968).

The climate is mild and wet, with an average annual temperature of 9°C and average annual precipitation of 309 cm recorded for Tofino (Climate of British Columbia 1976). Major storms sometimes occur during the summer, resulting in local flooding on the island.

Study animal.—Each year about 35–40 pairs of American Black Oystercatchers breed on Cleland. Nonbreeding oystercatchers and failed breeders (more than 100 birds on some occasions) use the island as a high-tide roost. Birds lay 1–3 eggs in nest cups in basalt crevices lined with bits of broken shell or in scrapes made on beaches of broken shell. Egg laying occurs from mid-May until mid-July. Incubation begins when the clutch is complete and lasts about 26 days. Eggs hatch within a few hours of each other. Chicks hatched first are brooded while the rest of the clutch hatches.

American Black Oystercatcher chicks are precocial but dependent on parental feeding for an extended period (Groves 1982). Parent oystercatchers feed their chicks during low-tide periods. Very young chicks remain near the nest, and parents take turns guarding the chicks and carrying food, item by item, from the intertidal area to the chicks. As they become bigger and more agile, chicks follow their parents into the intertidal zone to be fed. Around the time they begin to fly (35+ days), chicks begin to capture small prey items for themselves, but the most profitable prey items are still provided by their parents (Groves 1982).

Chick growth, survival, and feeding by parents.—De-

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TABLE 1. Clutch size of American Black Oystercatchers over 6 yr, Cleland Island.

Year	Number of clutches			Total clutches	Mean clutch size	SD
	1 egg	2 eggs	3 eggs			
1970[a]	14	38	9	61	1.92	0.61
1971[a]	8	26	14	48	2.13	0.67
1972[a]	11	34	13	58	2.03	0.65
1976	11	25	18	54	2.13	0.73
1977	12	38	10	60	1.97	0.61
1978[b]	5	15	9	29	2.14	0.69
Total	61	176	73	310	2.04	0.66

[a] Data from Hartwick (1974).
[b] Data based on five visits to the island.

tails of nest histories, chick growth, and survival were recorded in 1976 and 1977. Nests were located as clutches were commenced and checked every 3 days to obtain nest histories. After eggs pipped, nests were checked daily to determine the date of hatching. A unique combination of colored plastic leg bands and numbered metal Wildlife Service bands was put on each chick to ensure positive identification. Chick weights and exposed culmen lengths were measured every third day (as weather permitted) until chicks flew or disappeared. All weighings were done within 1.5 h of high tide, when most intertidal feeding areas had been submerged for several hours. This minimized the contribution of recently filled crops to chick weights. Analysis of variance was used to analyze chick weights according to brood-size for 3-day intervals of age. Because not all chicks were weighed during each 3-day interval, each set of chick weights for a 3-day interval of age was treated as a separate sample. No attempt was made to compare growth rates.

Records of parents feeding chicks were made in 1977. Observations were made with a 20× spotting scope during low-tide periods. When a chick was fed, prey type and size, chick identification, parent identification, and time of feeding were recorded. Interactions between siblings were also recorded. The data presented here focus on four oystercatcher families with two-chick broods. They were observed for 43.2 h of active feeding during 14 observation periods. The chicks observed ranged in age from 14 to 53 days (day of hatching is day 0).

RESULTS

Clutch size and chick production.—The clutch size of American Black Oystercatchers ranges from 1 to 3 eggs. Data on 310 clutches gathered in three seasons of this study and three seasons of Hartwick's (1974) study are presented in Table 1. The mean size of all 310 clutches was 2.04 eggs (SD = 0.66). Of the 114 clutches completed in 1976 and 1977, only 23% (26 clutches) survived to hatch chicks, and just 12% (14 clutches) produced flying young.

In 1976 and 1977 1-egg and 2-egg clutches did not consistently produce different numbers of chicks per clutch (Table 2), but these results are tentative because of small sample sizes. The number of chicks surviving to fly did not differ significantly between clutch sizes ($\chi^2 = 0.57$, df = 1, NS). An average of 0.50 (±0.53) chicks per clutch survived to fly from 1-egg clutches, whereas 0.75 (±0.77) chicks per clutch survived to fly from 2-egg clutches. (No comparable data on 3-egg clutches exist because no 3-egg clutches hatched 3 chicks during 1976 and 1977.)

Chick growth and sibling rivalry.—The growth of American Black Oystercatcher chicks from hatching to time of first flight varied with brood size and a chick's rank (based on weight) in the brood (Fig. 1). Weights of chicks in 1-chick and 2-chick broods did not differ significantly until chicks were 14–16 days old. At that age, average weights of chicks in 1-chick broods were greater than weights of chicks in 2-chick broods ($F = 8.89$, df = 1,22, $P < 0.005$), and these dif-

TABLE 2. Chick production by American Black Oystercatchers from 1-egg and 2-egg clutches in 1976 and 1977.

Number of clutches fledging	Clutch size			
	1976		1977	
	1 egg	2 eggs	1 egg	2 eggs
0 chicks	1	4	4	3
1 chick	1	1	4	5
2 chicks	—	2	—	1

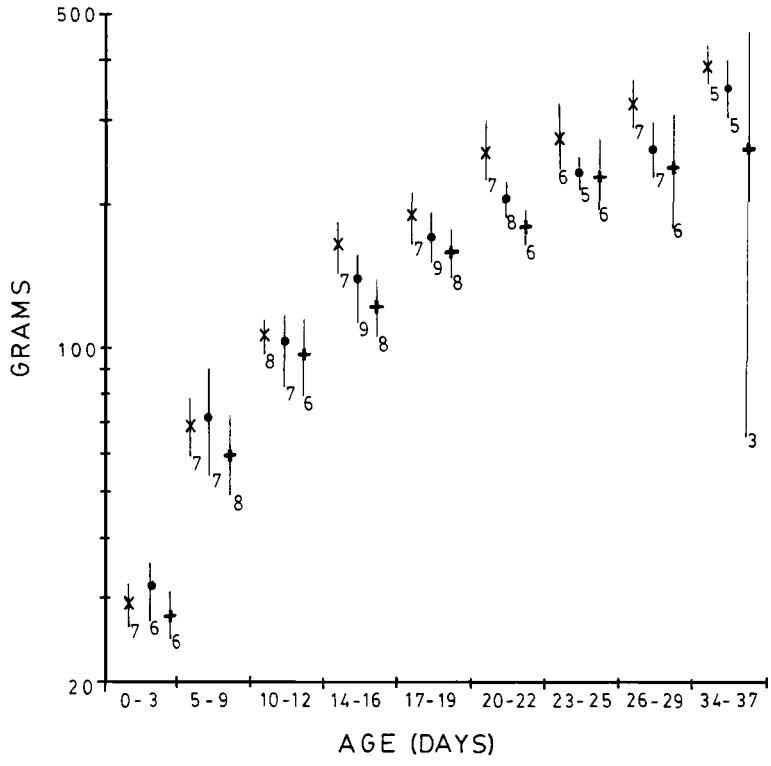

Fig. 1. Average chick weights (log scale) are plotted against chick age in days. Data are plotted according to brood size and chick rank in brood (for 2-chick broods). × = 1-chick brood; ● = big sib in 2-chick brood; + = little sib in 2-chick brood. (Vertical bars are 95% confidence limits.)

ferences persisted until chicks could fly. Average weights of siblings in two-chick broods did not differ statistically, but in some broods, the larger chick weighed up to 48% more when chicks began to fly.

Weight differences between siblings in two-chick broods were possibly affected by dominance relations between sibs and the resulting unequal distribution of food. As a result of chasing and dominance, big sibs could control access to parental feedings. Big sibs initiated 36 of 38 overt chases observed ($\chi^2 = 30.42$, df = 1, $P < 0.005$). During observation sessions when chasing was observed, little sibs were fed much less often than big sibs (Fig. 2, $\chi^2 = 85.78$, df = 1, $P < 0.001$). During sessions when chasing did not occur, however, little sibs were fed more often than big sibs ($\chi^2 = 40.03$, df = 1, $P < 0.005$).

On one occasion, I observed the establishment or reinforcement of dominance between 15 day-old sibs weighing 158 g and 128 g. No conflict between these sibs had been previously observed. Both chicks reached a parent returning with food at the same time. The big sib turned, pecked the little sib on the head and neck, and then chased the little sib for several meters. Afterwards the big sib returned to the parent and took the food. Subsequently, the little sib avoided the big sib or parent with food whenever the big sib exhibited agonistic behavior (overt or merely an approach). In this and other two-chick broods, dominance relations persisted after the chicks were flying and still being fed by their parents (pers. obs.).

Chick survival.—Heavier oystercatcher chicks had a better chance than lighter chicks of surviving to fly. Often the cause of chick mortality could not be determined, but important sources of mortality included storms, crow predation on eggs, and gull predation on chicks. Chicks that survived to fly were heavier at 20 days of

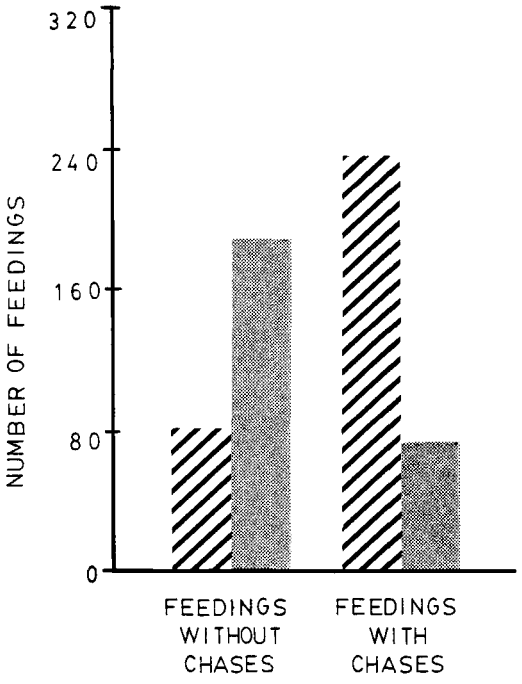

Fig. 2. Frequency of parental feedings and sibling chases in 2-chick broods. Hatched bars are big siblings; open bars are little siblings.

age than chicks that did not fly (Fig. 3, $t = 2.36$, df = 21, $P < 0.05$). All chicks heavier than 200 g at 20 days of age ($n = 15$) eventually flew except one that was probably eaten by a river otter (*Lutra canadensis*) (pers. obs.). Of 10 chicks weighing 200 g or less at 20 days of age only 5 survived to fly ($P = 0.035$, Fisher's Exact Test).

Chick survival from hatching to time of first flight varied with brood size and rank in brood (Fig. 4). Mortality was highest during the first week after hatching. In one-chick broods all of the mortality occurred during this period. In two-chick broods mortality occurred until chicks began flying.

Post-fledging survival.—There was no evidence that survivorship or weights of fledged birds from one- and two-chick broods differed. Similar proportions of color-banded American Black Oystercatchers that had fledged from 1-chick and 2-chick broods in 1976 and 1977 were resighted as 1 and 2 yr olds in the high-tide roost area by September 1978 (1-chick broods = 7 chicks fledged, 3 resighted; 2-chick broods = 10 chicks fledged, 6 resighted; $P = 0.30$, Fisher's Exact Test). Weights at the time of first flight did not differ between birds resighted 1 or 2

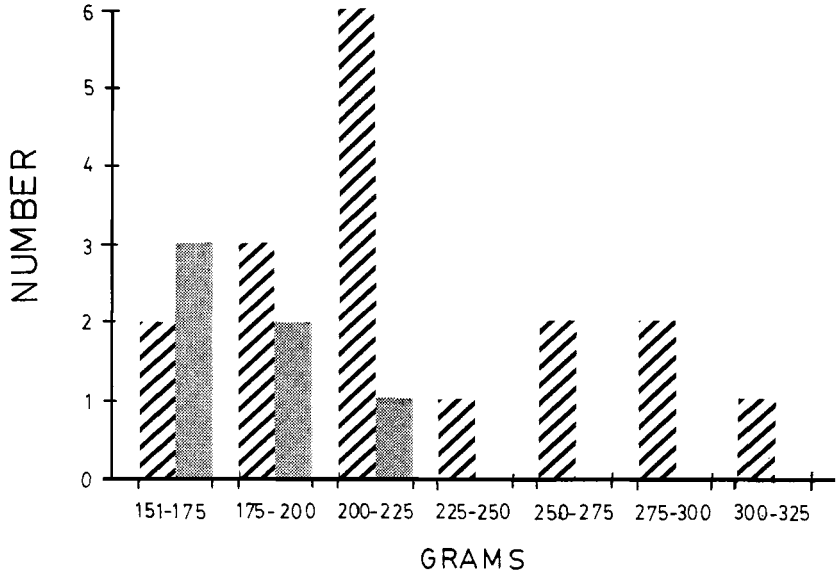

Fig. 3. Chick survival to fly according to weight at 20 days of age. Hatched bars are chicks that survived to fly; open bars are chicks that did not fly.

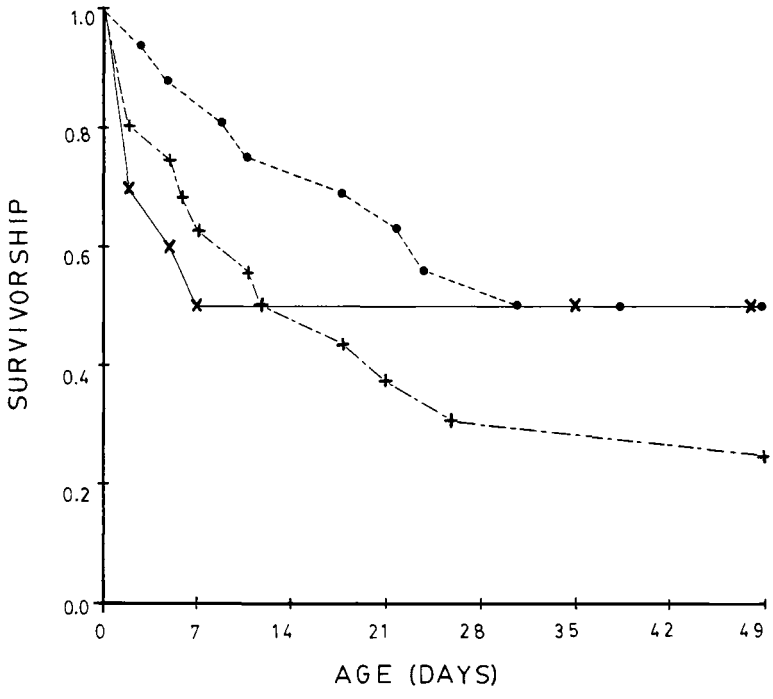

Fig. 4. Chick survivorship, 1976 and 1977 combined. Chick survival from hatching is plotted against chick age in days. × = 1-chick broods; ● = big sibs in 2-chick broods; + = little sibs in 2-chick broods.

yr later and birds not resighted (resighted: $\bar{x}$ = 351 g, SD = 45.1, n = 9; not resighted: $\bar{x}$ = 350 g, SD = 68.7, n = 8; t = 0.32, df = 15).

Discussion

Chick growth and sibling rivalry.—Variations in American Black Oystercatcher chick growth with brood size (Fig. 1) suggest that the ability of parents to provide food limits chick growth. Siblings of different sizes represent different amounts of parental investment (Trivers 1972), and size differences of siblings may facilitate rapid responses to sudden changes in food availability through brood reduction (Ricklefs 1965). Both sibling rivalry (O'Connor 1978) and parental behavior can maintain or increase differences in sizes of siblings.

Two-chick broods are more demanding of parents' time and energy than 1-chick broods, and differences in chick weights related to brood size were established by the time chicks were 2 weeks old. Chick-growth patterns suggest that increased parental investment and increasing brood size are not proportional. A less than proportional increase in parental investment with increasing brood size has been reported in numerous other bird species (for summary, see Klomp 1970), and Norton-Griffiths (1969) has presented an hypothesis that accounts for this phenomenon. He hypothesized that parental feeding of Common Oystercatcher chicks (*H. ostralegus*) is motivated by parental hunger and that chick feeding will occur primarily during periods when parents are motivated to feed themselves. Sibling rivalry also appears to affect chick growth and survival. Safriel (1981) reported a similar situation in Common Oystercatchers in Europe. In both this study and Safriel's, prey availability to chicks was controlled by parental delivery of prey, and chicks, especially large chicks, appeared to be rarely satiated. Hunger and the sight of a parent carrying food are likely stimuli for the occurrence of sibling rivalry.

Hunger alone did not stimulate dominance behavior in American Black Oystercatcher chicks in this study, as siblings that expressed

well-established dominance relations in the presence of a parent with food would spend hours crouched side-by-side in hiding places between feedings. The degree of food limitation, however, may affect dominance behavior. Ingram (1959) found that cannibalism among nestling Short-eared Owls (*Asio flammeus*) was most frequent in years of extreme food shortage, when parents were unable to provision their nest by caching food within reach of bigger chicks. Similarly Procter (1975) demonstrated that the nutritional condition of South Polar Skua chicks (*Catharacta maccormicki*) (measured as percentage of standard weight at a particular age) was positively correlated with the occurrence and intensity of aggression between sibs in naturally and artificially created two-chick broods.

Once established, dominance relations between siblings in this study persisted, and heavier siblings were dominant. Other studies (Ricklefs and Hainsworth 1967, Meyburg 1978) suggest that dominance is quickly and irreversibly decided in one fight. Dominance usually follows weight or age differences attributed to asynchronous hatching (e.g. Bryant 1978, Ingram 1962, Meyburg 1973, Miller 1973, Procter 1975, Safriel 1981), but exceptions have been reported (Ricklefs and Hainsworth 1967, Meyburg 1978).

Chick production and chick survival.—Chick production by American Black Oystercatchers was low and varied between years. Some pairs did not produce any flying chicks in four seasons (Groves 1982). Predation and unpredictable bouts of severe weather, factors unrelated to parental foraging performance, constrained chick production. Breeding success and chick production for Cleland Island American Black Oystercatchers were much lower than Harris (1967) reported for Common Oystercatchers on Skokholm Island, Wales. There, 37% and 59% of eggs produced flying young in two consecutive years. On Cleland Island, Hartwick (1974) reported that 13%, 9%, and 13% of eggs produced flying young in 3 yr (1970–1972), and during this study only 5% of eggs produced flying young in 1976 and 9% in 1977.

During this study, the number of chicks produced from 1- and 2-chick broods did not differ significantly (Table 2). Lower chick growth and the occurrence of sibling rivalry in 2-chick broods suggest that these chicks were not as well provisioned by their parents as chicks in 1-chick broods. In only one brood in this study did these factors apparently contribute to starvation of a chick. In seasons of unusually stormy weather, however, weight differences maintained by sibling rivalry could affect chick production.

Fledging success varied with brood size and chick weight. Higher rates of chick loss in two-chick broods may be due to the behavior of parent oystercatchers. Chicks are frequently brooded by their parents during the first week after hatching, and predators are able to locate chicks by observing the behavior of parents. As chicks grow older and are brooded less, predators are no longer able to locate chicks directly by observing their parents (Y. Yom-Tov pers. comm.). Instead, predators must search for cryptically colored chicks. A predator probably has a better chance of finding a chick on a territory with a 2-chick brood than on a territory with a 1-chick brood. Furthermore, parent oystercatchers may be able to defend 1 chick more effectively than 2, especially as both parents are often needed to drive a gull away from a chick (pers. obs.). Chick behavior may also affect patterns of chick mortality. In experimental enclosures, oystercatcher chicks that lost fights over food often remained in open areas, begged, and ran around, while siblings that won fights and obtained food sat quietly under cover (Safriel 1981). The conspicuous behavior of subordinate, hungry chicks probably makes them more vulnerable to predation.

Heavier chicks had a better chance of surviving to fly (Fig. 3). There were no differences in weight at the time of first flight between birds that were and were not resighted as 1 and 2-yr olds, nor were there any differences related to brood size in the proportion of birds resighted 1 and 2 yr later. This suggests that the critical life-history period for American Black Oystercatchers is survival from hatching to first flight. Once a bird can fly, its prospects for survival are apparently quite good, although no data are available on eventual recruitment of flying young to the breeding population.

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