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BROOD REDUCTION IN BLACK-LEGGED KITTIWAKES

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ABSTRACT.—In 1978 and 1979 we studied brood reduction in Black-legged Kittiwakes (*Rissa tridactyla*) on St. Paul Island, Alaska. In two-egg clutches, first-laid eggs were largest; they were incubated before second eggs were laid and consequently hatched first. Chicks from first-laid eggs begged more frequently, fed more frequently, grew faster, and were more aggressive than their sibs. These sibling differences frequently facilitated the ejection of younger siblings from the nest by first-hatched young. Lower feeding and growth rates and higher aggression levels occurred in broods in which the second chicks subsequently died than in broods in which both chicks fledged. Chick loss was most frequent during inclement weather. These data are consistent with the hypothesis that brood reduction is related to the amount of food that chicks receive. *Received 5 September 1981, resubmitted 26 March 1982, accepted 10 December 1982.*

WHEN birds breed in regions where nestling food supplies are unpredictable at the time of oviposition, brood reduction provides a mechanism that adjusts brood size to food resources during the nestling period (Lack 1954, Howe 1976, Stearns 1976). Females lay clutches of a size appropriate for years of high nestling food availability. If food is plentiful, all young can be reared, but, if food subsequent to oviposition is in short supply the brood may be reduced by the appropriate number (Lack 1954, 1966). An alternative hypothesis is that extra eggs are produced as insurance against the loss of first-laid eggs during incubation or the early death of oldest chicks (Nisbet and Cohen 1975, Stinson 1979). These hypotheses are not mutually exclusive.

Brood reduction occurs through a number of mechanisms, including the starvation of weaker chicks unable to compete for food (Nisbet and Cohen 1975, Parsons 1975, Lundberg and Väisänen 1979) and aggressive activities between siblings that result in the weaker chick either being denied access to required resources or being killed (Gargett 1970, Meyburg 1974, Stinson 1979). Although brood reduction always involves the death of some chicks, chick mortality and sib fighting can be minimized by producing chicks of unequal competitive ability. Species in which brood reduction is common exhibit reproductive characteristics that produce chicks of unequal competitive ability: egg size (and hence hatchling size) varies within a clutch (Ricklefs et al. 1978, O'Connor 1979), and eggs hatch asynchronously (Nisbet and Cohen 1975, Parsons 1975, Howe

1976, Hahn 1981). The inequality of chicks permits the sequential demise of weaker chicks, while reducing the risk of harm to the larger, healthier chicks (Lack 1947, 1954; Nisbet and Cohen 1975; Parsons 1975; Bryant 1978; Stinson 1979). Brood reduction will result in lower energetic waste if it occurs soon after hatching, because minimal care is invested in doomed chicks.

In this study we examined brood reduction in Black-legged Kittiwakes (*Rissa tridactyla*) nesting on St. Paul Island, Alaska. Previously, Hunt et al. (1978) found that this population of Black-legged Kittiwakes rarely raised more than one young per nest although almost half of the nests initially contained two eggs. Our objectives were to determine the frequency and circumstances under which two-chick broods failed to fledge both chicks and the mechanism by which brood size was reduced. In particular, we sought evidence concerning mortality patterns within broods, timing of mortality, first chick priority, and interactions between sibs and between chicks and parents, including the interplay of feeding and growth rates and sibling aggression with brood reduction. Because the net reproductive success of a pair ultimately depends on the number of young successfully raised, we compared the production of young per nest for pairs laying one- and two-egg clutches.

METHODS

This study was conducted during 1978–1979 on St. Paul Island, Pribilof Islands, Alaska (57°08'N,

170°20'W), where one of over 50 Black-legged Kitti-wake colonies in the Bering Sea (Sowls et al. 1978) is located. The estimated marine bird population of St. Paul Island is 253,800; 31,000 are Black-legged Kittiwakes (Hickey and Craighead 1977). Ten other seabird species also nest on the island.

In order to determine chick mortality patterns, the timing of mortality, and fledging success, we monitored the contents of 82 and 50 completed nests in 1978 and 1979, respectively. During the egg-laying and early incubation periods in 1978 and during the early incubation period in 1979, we noted nest contents every 4–7 days. Beginning during late incubation, we inspected nest contents at least once daily in 1978 and twice daily in 1979. This schedule was maintained throughout the entire nestling period in 1978 and through three-fourths of the nestling period in 1979.

In order to learn whether or not first chicks have a size advantage at hatching, we determined the volume of eggs in 13 nests that hatched two chicks. We measured egg dimensions using calipers and calculated egg volume (cc) using Maunder and Threlfall's (1972) equation:

$$\text{Vol (cc)} = 0.4866(\text{egg breadth}^2)(\text{egg length}).$$

In order to follow chick-growth patterns, we banded newly hatched chicks and monitored their growth in 22 different two-egg nests. First weights were usually taken within 24 h of hatching. Using 300-g, 500-g, and 1-kg capacity Pesola spring scales, we measured chick weight every 2 days until just before first flight (approximately 43 days) in 1978. In 1979, weights were measured daily until chicks were 3 weeks of age. We calculated growth rates (g/day) for two time periods, between day 1 and 5 (the period during which most brood reduction occurred) and between day 3 and 23 (the period of linear growth).

To develop methods for quantifying sibling and parent behavior, we observed seven nests for 154.4 nest hours in 1978. Using these pilot observations, we determined a coding system for recording behavioral repertoires and applied this system to 163.6 nest hours of observation in 1979. We began our observations the day the second chick hatched in 7 nests and on the second and fourth day of the second chick's life in the remaining 2 nests. Observations ended when the second-hatched chick died. In the three nests that were accessible, first-hatched chicks were marked with picric acid and both chicks were banded with plastic leg bands. We were able to identify chicks from the six inaccessible nests by size differences, because older chicks average about 25% heavier than younger chicks at the time younger chicks hatch (Braun 1981). We viewed nests from distances ranging between 5 and 15 m with 7× and 8× power binoculars and 20–40× power spotting scopes. All behavior was recorded on tape. Stop watches were used to monitor time to the nearest second. Obser-

vation periods were continuous, varying in length from 4 min to 12.9 h. Mean observation length was 2.0 ± 2.0 h ($n = 80$).

Using these observations, we compiled the following information for each nest: presence and expression of sibling dominance, feeding rates, begging rates, which chick was fed first after a parent returned to a nest with food, number of distinct aggressive bouts and the initiator of each bout, chick behaviors during each aggressive bout, and the response of younger chicks to aggression (older chicks were not attacked). A chick was classified as dominant when it demonstrated the vast majority of aggressive behaviors (pecks, bites, pushes) and its sibling demonstrated virtually all submissive behaviors (crouches, puts head down, turns away, hides, flees). There were no intermediate cases in which dominance relations were ambiguous. Feeding rates were defined as the number of feedings/h of observation. Begging rates were defined as the number of 30-s intervals of observation in which a chick begged per hour of observation. Aggressive bouts were defined as any attack series with pauses of less than 2 min. During each bout any change in younger chick behavior was noted. These behaviors were later categorized as either submissive (previously defined) or not submissive (no apparent response, holds ground, fights back).

To determine the interplay of sibling aggression with actual or potential parental feeding, we examined nest activities occurring during the 10-min period before aggression occurred. Activities were categorized as either related to feeding events (begging or feeding by either chick, parent returns to nest with food) or not related to feeding events.

To determine whether or not brood reduction was correlated with inclement weather, we recorded the daily sea state, precipitation, wind speed, and temperature in 1979. Any day on which either white caps, moderate to heavy rainfall, or winds greater than 27 mps prevailed were considered to be days of adverse weather. Because temperature fluctuated little, it was excluded as a criterion for adverse weather.

RESULTS

Nestling mortality and reproductive success in relation to brood size.—More chicks fledged from two-egg clutches than from single-egg clutches, even though mortality occurred in a greater proportion of the nests containing two chicks (Table 1). Nestling mortality was concentrated within the first 8 days of the nestling period (Fig. 1) and was primarily accounted for by the death of the younger chick in two-chick broods. Second-hatched chicks suffered significantly greater mortality than their older siblings or

TABLE 1. Nestling mortality and reproductive success in one- and two-chick broods.

	One-chick broods		Two-chick broods	
	1978	1979	1978	1979
Number of young fledged/nest from known one- or two-egg clutch (n)	0.48 (42)	0.48 (25)	0.87 (39)[a]	1.08 (25)[b]
Proportion of nests in which one or more young died (n)	0.17 (24)	0.25 (16)	0.62 (16)[c]	0.63 (19)[d]
Nestling mortality, number to die/number to hatch (n)				
Single chicks	0.17 (24)	0.25 (16)	—	—
First-hatched chicks	—	—	0.06 (16)	0.11 (19)
Second-hatched chicks	—	—	0.56 (16)[e,f]	0.63 (19)[e,f]
Mean age of death, second-hatched chicks, $\bar{x} \pm SD$ (n)	—	—	3.8 ± 2.6 (5)	4.5 ± 3.3 (12)

[a] Significantly different from one-chick broods: $t = -2.98$, $P < 0.01$, df = 79.
[b] Significantly different from one-chick broods: $t = -3.46$, $P < 0.01$, df = 48.
[c] Significantly different from one-chick broods: $\chi^2 = 8.86$, $P < 0.01$, $n = 40$.
[d] Significantly different from one-chick broods: $\chi^2 = 5.05$, $P < 0.025$, $n = 35$.
[e] Significantly greater than chicks from one-chick broods; 1978: $\chi^2 = 6.86$, $P < 0.01$, $n = 40$; 1979: $\chi^2 = 5.05$, $P < 0.025$, $n = 35$.
[f] Significantly greater than first-hatched chicks; 1978: $\chi^2 = 9.31$, $P < 0.005$, $n = 32$; 1979: $\chi^2 = 11.31$, $P < 0.005$, $n = 38$.

chicks from single-chick broods and died early in the nestling period (Table 1).

Second-hatched chicks were pushed out of their nests by their older siblings. Severe harassment by the dominant older chick typically preceded ejections. Intimidation, monopolization of parental feedings, and beatings (all from the older chick) typified harassment. This dominance was established usually within 24 h of the hatching of the second chick and was maintained throughout the second chick's life. Younger chicks were pecked on the nape of the neck, head, and axilla; they were shaken, dragged, and pushed about the nest. Although not all younger chicks were severely beaten, they were all harassed in some manner. When younger chicks were ejected, they were weak but still alive. No sibling victim died in the nest. Of the 16 nests hatching two young in 1978, sibling ejection occurred in 9 (≈56%). In only one nest did the older chick die and the younger chick live. This older chick died of a congenital heart malformation (M. Roelke, pers. comm.). In 1979, sibling ejection occurred in 12 of the 19 nests known to hatch two young (≈63%). In none of these nests was the older chick ejected by its younger sibling, but in two nests the older chick subsequently died more than 24 h after the younger chick was ejected.

Most nests completely covered the rock surface upon which they were built, and the expelled chicks fell to the cliff bottom and subsequently died. In the small number of cases where a ledge existed behind or to the side of the nest, the ejected siblings sought refuge there. While outside of their nest, however, they were exposed and were not fed. Unless these chicks re-entered their nest, they died on the ledge a few centimeters from their nest. Chicks were infrequently permitted to re-enter their nests, but only for short periods.

Sibling ejection was correlated with inclement weather. Significantly more second sibs were ejected within 24 h of adverse weather than were ejected during milder weather [$\chi^2 = 3.95$, $P < 0.05$, $n = 19$; the sample includes seven nests from a separate supplemental feeding experiment (Braun 1981)].

Comparison of chicks from first- and second-laid eggs.—Several factors may have contributed to the higher survival of first-hatched chicks and their dominance over younger siblings. First-laid eggs were larger than second eggs, and they hatched earlier (Table 2). Therefore, at the time the second chick hatched, it weighed less than the first chick (Table 2). The magnitude of difference was correlated with hatching interval ($r = 0.71$, $P < 0.05$, $n = 13$).

The initial advantages of the older chicks in terms of weight, size, and dominance were correlated with subsequent advantages in growth, feeding, and aggressiveness. Within nests with two young, the growth rate of the second chick was consistently lower than that of its older sibling during the first 5 days of life (Table 3). The magnitude of difference
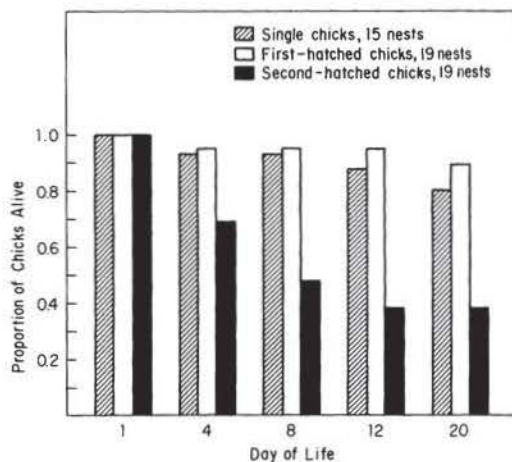
Fig. 1. Proportion of Black-legged Kittiwake young alive throughout their first 20 days of life in 1979.

ranged between 0.5 and 14.2 g/day. Although there was a trend for the older chick to have a higher growth rate during the first 3 weeks of life in the nests that fledged both young, these data were not statistically significant. In 1978, peak weights of first- and second-hatched nestlings were not different (Table 3).

Black-legged Kittiwake parents trade duties; while parent A tends the nest, parent B is at sea foraging and collecting food. When parent B returns to the nest, the adults exchange duties, and within the next few minutes the young usually begin feeding from the food parent B has gathered. Older chicks fed first from this new supply of food, and they also begged more frequently than their younger sibs (Table 3). Presumably these differences contributed to the higher feeding rates of first-hatched chicks during the first 5 days of life (Table 3).

First-hatched chicks initiated 118 of 120 aggressive bouts between siblings. In only two bouts initiated by the first-hatched chick did the younger chick fight back; most of the time it behaved submissively. Second chick response to aggression was recorded during 78 aggressive bouts. In the 123 changes observed in younger chick behavior during these periods, 104 were toward more submissive behavior and 19 were toward less submissive behavior. Most aggressive bouts were initiated following the occurrence of a feeding-related event (one-tailed Mann-Whitney U-Test: $U = 5$, $P = 0.006$, $n = 7,7$).

Another mechanism that favored the survival of the older chick was selective parental allocation of food. Two modes of selective feeding were observed in Black-legged Kittiwakes. The first was unsolicited feeding (no solicitation occurred for 2 min prior to feeding), and the second was redirected feeding (only one sibling solicited food, but the parent offered food to and fed the other chick). Unsolicited feedings were observed in 7 of 9 nests, and it was the older chick that was the beneficiary in 59 of 61 occurrences. Redirection of feeding was observed in only three nests, and in 9 of the 11 occurrences the second-hatched chick begged, but the older sibling was fed.

Comparison of two-chick broods with and without brood reduction.—To determine whether or not chicks from nests in which brood reduction occurred behaved differently from chicks from nests in which brood reduction did not occur, we compared a variety of aspects between the respective groups. Differences were found only in feeding rates, sibling aggression, and early chick-growth rates between nests in which brood reduction did and did not occur. In other behaviors compared, no significant differences were found between the two classes of nests (Table 4).

Older chicks had higher feeding rates than did younger chicks in all nests examined, but chicks fed more frequently in the nests in which

TABLE 2. Initial characteristics of eggs and chicks.

	1978 $\bar{x} \pm SD$ (n)	1979 $\bar{x} \pm SD$ (n)
Egg volume, first laid egg (cc)	49.5 ± 3.7 (13)[a]	—
Egg volume, second laid egg (cc)	47.2 ± 3.2 (13)[a]	—
Sibling age difference (days)	1.3 ± 0.49 (16)	1.2 ± 0.72 (29)
Sibling weight difference (g)	12.7 ± 9.0 (4)	9.3 ± 9.4 (9)[b]

[a] Paired Sign Test between volume of first- and second-laid egg (one-tailed, $x = 2$, $P = 0.011$, $n = 13$).
[b] Paired Sign Test between sibling weights when second chick hatched, 1979 (one-tailed, $x = 1$, $P = 0.02$, $n = 9$).

TABLE 3. Comparision of first- and second-hatched young in two-chick broods.

	Year	First young $\bar{x} \pm$ SD (n)	Second young $\bar{x} \pm$ SD (n)	Test
Early chick growth, days 1–5 (g/day)	1978	15.7 ± 1.9 (7)	10.9 ± 3.5 (6)	One-tailed sign[a]: $x = 0, P = 0.016, n = 6$
	1979	14.7 ± 2.5 (7)	8.5 ± 6.1 (6)	One-tailed sign[a]: $x = 0, P = 0.016, n = 6$
Linear growth, days 3–23 (g/day)	1978	17.2 ± 1.0 (5)	14.8 ± 2.3 (5)	One-tailed sign[a]: $x = 1, P = 0.188, n = 5$
	1979	17.7 (2)	13.9 (2)	—[b]
Peak weights (g)	1978	492 ± 52 (7)	453 ± 31 (4)	Two-tailed MWU: $U = 8, P = 0.316, n = 4, 7$
Proportion fed first	1979	0.91 ± 0.13 (8)	0.09 ± 0.13 (8)	One-tailed sign[a]: $x = 0, P = 0.004, n = 8$
Begging rate[c]	1979	1.96 ± 1.07 (9)	1.30 ± 1.32 (9)	One-tailed sign[a]: $x = 1, P = 0.02, n = 9$
Feeding rate (number/h)	1979	2.32 ± 1.44 (9)	0.88 ± 0.62 (9)	One-tailed sign[a]: $x = 1, P = 0.02, n = 9$

[a] Paired Sign test based on between sib comparison.
[b] Insufficient sample size for statistical analysis.
[c] Defined in methods section.

brood reduction did not occur (Table 5). Older chicks from nests in which brood reduction did not occur had significantly higher feeding rates than did older chicks from nests in which brood reduction occurred. Likewise, younger chicks from nests in which brood reduction did not occur had significantly higher feeding rates than did younger chicks from nests in which brood reduction occurred (Table 5). In nests in which the second-hatched chick lived, all second-hatched chicks fed, on average, more often than once/hour; in contrast, only one second chick fed this often among nests in which second-hatched chicks were ejected.

Aggression (min/h, number of bouts/h) was lower in nests in which both chicks fledged than in nests in which the second chick died, although the differences are not statistically significant, because in one nest no aggression was witnessed before the second chick was

TABLE 4. Similarities between nests in which brood reduction did and did not occur.

Event	Conclusion	Test
Dominance hierarchy	Established in all nests, established first day of second chick's life	—
Proportion of fights initiated by the first chick	First chick is the aggressor (>94% in all nests)	One-tailed Mann-Whitney U: $U = 7, P = 0.50, n = 3, 5$
Proportion of time that the second chick responds submissively	Second chick responds submissively most of the time	One-tailed Mann-Whitney U: $U = 4, P = 0.196, n = 3, 5$
Proportion of fights initiated in concurrence with an event related to feeding	Most aggression occurs in concurrence with some event related to feeding	One-tailed Mann-Whitney U: $U = 2, P = 0.114, n = 3, 4$
Proportion of time the first chick fed first after a parental exchange	First chick feeds first after a parental exchange (>70% in all nests)	One-tailed Mann-Whitney U: $U = 3, P = 0.125, n = 3, 5$
Proportion of begging by the second chick	Second chick's begging is suppressed in all nests by similar amounts	One-tailed Mann-Whitney U: $U = 5, P = 0.385, n = 3, 5$

TABLE 5. Differences between nests in which brood reduction did and did not occur.

	Nests that fledged two young	Nests in which the second young died	Test
Feeding rate, both chicks (number/h) $\bar{x} \pm$ SD (n)	2.56 ± 1.75 (6)	1.13 ± 0.70 (12)	One-tailed Mann-Whitney U: $U = 14, P = 0.025, n = 6, 12$
Feeding rate, older chick (number/h) $\bar{x} \pm$ SD (n)	3.55 ± 2.11 (3)	1.70 ± 0.40 (6)	One-tailed Mann-Whitney U: $U = 2, P = 0.048, n = 3, 6$
Feeding rate, younger chick (number/h) $\bar{x} \pm$ SD (n)	1.56 ± 0.47 (3)	0.55 ± 0.35 (6)	One-tailed Mann-Whitney U: $U = 0, P = 0.012, n = 3, 6$
Aggression, min/h $\bar{x} \pm$ SD (n)	0.33 ± 0.21 (3)	2.02 ± 1.48 (6)	One-tailed Mann-Whitney U: $U = 5, P = 0.19, n = 3, 6$
Aggression, number of bouts/h $\bar{x} \pm$ SD (n)	0.37 ± 0.06 (3)	1.05 ± 0.78 (6)	One-tailed Mann-Whitney U: $U = 3, P = 0.083, n = 3, 6$
Proportion of short bouts (<10 s in length)	0.54 ± 0.04 (3)	0.18 ± 0.18 (6)	One-tailed Mann-Whitney U: $U = 0, P = 0.012, n = 3, 6$

ejected (Table 5). Longer aggressive bouts occurred in the nests in which the second-hatched young died (Table 5).

Early chick growth appeared to differ between the nests in which brood reduction did and did not occur. Second chicks from nests in which brood reduction occurred generally had lower growth rates than did second chicks from nests in which brood reduction did not occur in both years, although the differences are not statistically significant due to the small number of nests we were able to measure (Table 6).

Older chick growth rates among the nests in which brood reduction did and did not occur were similar in both years. These data suggest that in both groups of nests, food requirements of older chicks were met first. Variation in growth occurred primarily in the second chick.

Discussion

Brood reduction in the Black-legged Kittiwake is facilitated by the superior competitive ability of the first-hatched chick resulting from

TABLE 6. Early chick growth (g/day) in nests in which brood reduction did and did not occur.

	1978			1979		
	Nest	First chick	Second chick[a]	Nest	First chick	Second chick[b]
Second chick dies	105	17.0	—[c]	235	12.2	−2.0
	307	16.0	6.5	313	12.6	6.6
	439	15.5	7.3	314	17.8	14.8[d]
				436	17.5	8.5
				442	13.3	—[c]
	($\bar{x} \pm$ SD)	(16.2 ± 0.8)	(6.9)	($\bar{x} \pm$ SD)	(14.7 ± 2.7)	(7.0 ± 6.9)
Second chick lives	304	15.6	10.5	201	13.0	9.0
	306	13.5	13.0	508	16.8	14.3
	434	18.8	15.8			
	443	13.3	12.3			
	($\bar{x} \pm$ SD)	(15.3 ± 2.6)	(12.9 ± 2.2)	($\bar{x} \pm$ SD)	(14.9)	(11.7)

[a] Comparison of growth rates between second chicks from nests in which brood reduction did and did not occur, one-tailed Mann-Whitney U-Test: $U = 0, P = 0.067, n = 2, 4$.

[b] Comparison of growth rates between second chicks from nests in which brood reduction did and did not occur, one-tailed Mann-Whitney U-Test: $U = 2, P = 0.267, n = 2, 4$.

[c] Chick was ejected before two weights were obtained.

[d] Second chick from nest 313 (age 7 days) entered nest 314; the first chick of nest 314 ejected both younger chicks within 24 h. (We believe the second chick from nest 314 would have fledged had not an extra chick entered; growth rates indicate a large quantity of food was delivered to the young. Including this nest in the group in which brood reduction occurred accounts for the data not reaching significance.)

differences between siblings in age and size when the second chick hatches. The first chick is able to dominate the second chick's access to food, with the result that the second chick gets to feed only after the first chick is replete. Thus, initial differences in size between the chicks are rapidly accentuated.

The mortality of second chicks does not directly result from reduced access to food within the nest. Rather, the smaller, weaker chick is forced from the nest by its more aggressive sibling. Exposure and starvation resulting from exclusion from the nest are the causes of death. Parents do little to aid the second chick directly, although their preferential feeding of the first chick may result in a temporary reduction in its aggressiveness. Replete chicks appeared less aggressive after feeding, but our data are inadequate to demonstrate this conclusively.

In Black-legged Kittiwakes, as in other species (Rowe 1947, Lockie 1955, Proctor 1975), the availability of food probably determines the level of sibling aggressive behavior and, hence, the probability of brood reduction. Within the breeding season, foraging success of seabirds is diminished during periods of inclement weather (Kazama 1968, Salt and Willard 1971, Dunn 1973, Birkhead 1976), and brood reduction predominated within these periods. This pattern of within-season fluctuation of chick expulsion with food availability also occured between years. No second chicks survived at the Pribilofs in 1975 and 1976 (Hunt et al. 1981), cold, stormy years (Niebauer 1981) with a lower abundance of young pollock (Smith 1979), an important kittiwake food (Hunt et al. 1982). In contrast, in 1977 through 1979 the weather was milder (Niebauer 1981), in 1977 and 1978 young pollock were more available (Smith 1979), and in 1977–1979 small numbers of Black-legged Kittiwakes fledged two young. On the basis of our observations and these seasonal and yearly fluctuations in chick expulsion, we hypothesize that the dominant chick will expel its sibling during periods in which the dominant chick remains hungry. Thus, only if the parents are able to keep the first chick well fed will the second chick have a chance to survive.

Finally, we know of four nests in which two eggs were laid but only the second-laid hatched and two nests in which the first-hatched chick died very early in life and the second-hatched subsequently fledged. These observations provide support for the hypothesis that the production of two eggs is useful insurance against the loss of the first-laid egg. The higher reproductive success of birds that lay two-egg clutches may, therefore, be attributed both to the birds that successfully rear two young and to those that benefit from the insurance value of the second-laid egg.

LITERATURE CITED

BIRKHEAD, T. R. 1976. Effects of sea conditions on rates at which Guillemots feed chicks. British Birds 69: 490–492.

BRAUN, B. M. 1981. Siblicide, the mechanism of brood reduction in the Black-legged Kittiwake, *Rissa tridactyla*. Unpublished M.S. thesis, Irvine, California, Univ. California.

BRYANT, D. M. 1978. Establishment of weight hierarchies in the broods of house martins (*Delichon urbica*). Ibis 120: 16–26.

DUNN, E. K. 1973. Changes in fishing ability of terns associated with windspeed and sea surface conditions. Nature 244: 520–521.

GARGETT, V. 1970. Black Eagle experiment No. 2. Bokmakierie 22: 32–35.

HAHN, D. C. 1981. Asynchronous hatching in the

Laughing Gull: cutting losses and reducing ri-
valry. Anim. Behav. 29: 421–427.

HICKEY, J. J., & F. L. CRAIGHEAD. 1977. A census
of seabirds on the Pribilof Islands. Environmen-
tal assessment of the Alaskan Continental Shelf.
Annual reports of principal investigators. Boul-
der, Colorado, NOAA Environ. Res. Lab. 2: 96–
195.

HOWE, A. F. 1976. Egg size, hatching asynchrony,
sex and brood reduction in the Common Grack-
le. Ecology 57: 1195–1207.

HUNT, G. L., JR., B. MAYER, W. RODSTROM, & R.
SQUIBB. 1978. Reproductive ecology, foods and
foraging areas of seabirds nesting on the Pribilof
Islands. Environmental assessment of the Alas-
kan Continental Shelf. Annual reports of prin-
cipal investigators. Boulder, Colorado, NOAA
Environ. Res. Lab. 1: 570–775.

———, Z. EPPLEY, B. BURGESON, & R. SQUIBB. 1982.
Reproductive ecology, foods and foraging areas
of seabirds nesting on the Pribilof Islands, 1975–
1979. Environmental assessment of the Alaskan
Continental Shelf. Final reports of principal in-
vestigators. Boulder, Colorado, NOAA Environ.
Res. Lab. 12 Biol. Studies: 1–258.

KAZAMA, T. 1968. On the mass destruction of Rissa
tridactyla and Calonectris leucomelas and their
migration at Kashiwazaki, Niigata Prefecture.
Tori 18(84): 260–266.

LACK, D. 1947. The significance of clutch size. Ibis
89: 302–352.

———. 1954. The natural regulation of animal
numbers. Oxford, Oxford Univ. Press.

———. 1966. Population studies of birds. Oxford,
Clarendon Press.

LOCKIE, J. D. 1955. The breeding and feeding of
jackdaws and rooks with notes on carrion crows
and other Corvidae. Ibis 97: 341–369.

LUNDBERG, C. A., & R. A. VÄISÄNEN. 1979. Selec-
tive correlation of egg size with chick mortality
in the Black-headed Gull (Larus ridibundus).
Condor 81: 146–156.

MAUNDER, J. E., & W. THRELFALL. 1972. The

breeding biology of the Black-legged Kittiwake
in Newfoundland. Auk 89: 789–816.

MEYBURG, B. 1974. Sibling aggression and mortal-
ity among nestling eagles. Ibis 116: 224–228.

NIEBAUER, H. J. 1981. Recent fluctuations in sea
ice distribution in the eastern Bering Sea. Pp.
133–140 in The eastern Bering Sea shelf: ocean-
ography and resources, Vol. 1 (D. W. Hood and
J. A. Calder, Eds.). Washington, D.C., U.S. Dept.
Commerce.

NISBET, I. C. T., & M. E. COHEN. 1975. Asynchro-
nous hatching in common and roseate terns,
Sterna hirundo and S. dougallii. Ibis 117: 374–379.

O'CONNOR, R. J. 1979. Egg weights and brood re-
duction in the European Swift (Apus apus). Con-
dor 81: 133–145.

PARSONS, J. 1975. Asynchronous hatching and chick
mortality in the herring gull Larus argentatus. Ibis
117: 517–520.

PROCTER, D. L. C. 1975. The problem of chick loss
in the south polar skua Catharacta maccormicki.
Ibis 117: 452–459.

RICKLEFS, R. E., D. C. HAHN, & W. A. MONTEREC-
CHI. 1978. The relationship between egg size
and chick size in the Laughing Gull and Jap-
anese Quail. Auk 95: 135–144.

ROWE, E. G. 1947. The breeding biology of Aquila
verreauxi Lesson. Ibis 89: 576–606.

SALT, G. W., & D. E. WILLARD. 1971. The hunting
behavior and success of Forster's Tern. Ecology
52: 989–998.

SMITH, G. B. 1979. The biology of walleye pollock.
Seattle, Washington, Natl. Mar. Fish. Serv.,
Northwest and Alaska Fish Cent., Processed
Rept.

SOWLS, A. L., S. A. HATCH, & C. L. LENSINK. 1978.
Catalog of Alaskan Seabird Colonies. U.S. Dept.
Interior, Fish Wildl. Serv. FWS/OBS 78/78.

STEARNS, S. C. 1976. Life history tactics: a review
of the ideas. Quart. Rev. Biol. 51: 3–47.

STINSON, C. H. 1979. On the selective advantage
of fratricide in raptors. Evol. 33: 1219–1225.