Open access • Journal Article • DOI:10.1093/AUK/103.2.401

Proximate and Ultimate Causation of Egg Size and the "Third-chick Disadvantage" in the Western Gull — Source link

Raymond Pierotti, Cheryl A. Bellrose

Institutions: University of California, Berkeley, San Jose State University

Published on: 01 Apr 1986 - The Auk (University of California Press)

Topics: Proximate and ultimate causation

PROXIMATE AND ULTIMATE CAUSATION OF EGG SIZE AND THE "THIRD-CHICK DISADVANTAGE" IN THE WESTERN GULL

RAYMOND PIEROTTI[1] AND CHERYL A. BELLROSE[2,3]

[1]*Department of Psychology, University of California, Berkeley, California 94720 USA, and*
[2]*Department of Biological Sciences, San Jose State University, San Jose, California 95192 USA*

ABSTRACT.—It is generally observed in gulls (*Larus* spp.) that produce a typical clutch of three that the third- or last-laid egg is smaller and lighter than its earlier-laid counterparts. This typically results in the third chick hatching later, growing at a slower rate, and having a higher rate of mortality. This suite of factors has been described as the "third-chick disadvantage," and various functional interpretations have been suggested to explain its adaptive basis. We report on egg size, chick growth, and survival in a population of Western Gulls (*Larus occidentalis*) where the third-chick disadvantage appeared to be nonexistent. We suggest that functional interpretations of this phenomenon may be premature and that variation in egg size in gulls may simply be due to variation in female energy reserves, and that in colonies where food is abundant and nest density low, the third-chick disadvantage may be reduced or absent. *Received 10 May 1985, accepted 5 December 1985.*

BIRDS typically lay their eggs about one day apart (Murton and Westwood 1977), and most species initiate incubation only after the clutch has been completed, which synchronizes the time of hatching (Lack 1968). In some species, however, incubation begins before the clutch is complete. This causes the eggs to hatch asynchronously, with the result that later-hatching offspring have a competitive disadvantage relative to their older siblings. This disadvantage often translates into reduced survival of later-hatching offspring, and reduced reproductive output. As a result, considerable speculation has been generated as to the adaptive function of asynchronous hatching in birds (e.g. Lack 1968; Parsons 1970, 1975; Hussell 1972; Davis 1975; Howe 1976; O'Connor 1978; Hahn 1981; Gould 1982; Mock 1984; Slagsvold et al. 1984).

The primary hypothesis proposed to explain the mortality of offspring associated with asynchronous hatching has been that asynchronous hatching increases parental reproductive output by reducing the chances of total reproductive failure when food is scarce and the parents cannot provide adequately for the entire brood (Lack 1968, Hussell 1972, Hahn 1981, Gould 1982). This implies that more food is provided to early-hatching offspring, and that late-hatching offspring survive only when food supplies are plentiful (Hahn 1981, Graves et al. 1984).

In gulls, brood asynchrony generally is referred to as the "third-chick disadvantage" (Parsons 1972, Coulter 1977) because the typical clutch size in this group is three (Winkler and Walters 1983), and the third, or last-laid, egg is typically significantly smaller in length and width, weighs less, and hatches last (Parsons 1970, 1972, 1975; Briggs 1977; Coulter 1977; Mills 1979; Schreiber et al. 1979; Hahn 1981; Pierotti 1982; Slagsvold et al. 1984). As a result, gull chicks hatched from third-laid eggs are smaller at hatching, usually grow more slowly, and have reduced survival rates compared with their siblings. Hahn (1981) argued that the third-chick disadvantage is an adaptive response that benefits parent gulls by reducing sibling rivalry over parental investments and by minimizing "wasteful" competition within the brood. Similarly, Slagsvold et al. (1984) argued that this "intraclutch variation in egg size has an ultimate, adaptive value."

In contrast, Schreiber et al. (1979) found variation in egg sizes within clutches between years and suggested that caution be used when attributing functional attributes to variation in egg size. Similarly, Mills (1979) found variation between breeding seasons in egg size patterns and presented evidence that the most efficient foragers could produce the largest eggs. Wink-

[3] Present address: Department of Wildlife and Fisheries, University of California, Davis, California 95616 USA.

ler and Walters (1983) reviewed clutch size in larids and found that both egg size and clutch size appeared to be increased when food was abundant.

In this paper we expand upon this point and argue that the third-chick disadvantage is largely a result of diminished energy reserves in female gulls. We present evidence to demonstrate that if breeding gulls have adequate food supplies, the third-chick disadvantage is almost nonexistent. Our data come from a population of Western Gulls (*Larus occidentalis*) where the food supply was abundant and competition for breeding space was minimal (Bellrose 1983).

METHODS

Study site.—The colony of Western Gulls nested on abandoned salt ponds of the Monterey Bay Salt Company, adjacent to Elkhorn Slough in the town of Moss Landing, Monterey Co., California. The shallow waters in and around Elkhorn Slough are breeding grounds for several species of marine fishes, including jacksmelt (*Atherinopsis californiensis*), northern anchovy (*Engraulis mordax*), plainfin midshipman (*Porichthys notatus*), and several species of surfperches (Embiotocidae) (Kukowski 1972, Cailliet et al. 1977). Many other species of fishes and marine invertebrates are abundant both in Elkhorn Slough and the adjacent Monterey submarine canyon.

This population of Western Gulls has been monitored since 1973 (Pierotti 1976, Harvey 1983, Bellrose 1983). With the exception of the El Niño year of 1983, the food supply for the colony has been superabundant. Food was so abundant during most years, including 1981 and 1982, that entire fish and marine invertebrates, e.g. squid (*Loligo opalescens*), were found uneaten around gull nests on days when the colony was visited.

Nests in the colony were arranged linearly along dikes in the salt ponds and typically were spaced well apart. During the 1981 breeding season 53 nests with a mean internest distance of 23.7 m were monitored, and during the 1982 breeding season 59 nests with a mean internest distance of 24.7 m were monitored (Bellrose 1983). Possibly as a result of this wide spacing, rates of aggressive interaction were the lowest of any Western Gull colony yet monitored (Pierotti 1976, 1981; cf. Bellrose 1983).

Breeding biology.—During May–August 1981 and May 1983 the colony was visited at 2-day intervals; during May–July 1982 the colony was visited daily. Each nest was marked with a wooden stake labeled for subsequent identification. Upon discovery, each egg was marked with a black marker pen, egg length and width were measured using Vernier calipers, and eggs were weighed using a 100- or 300-g Pesola scale. The date of laying (accurate within one day) also was recorded, and sequence of laying was determined.

When chicks hatched, the date and the hatching weight were recorded. Chicks were banded initially with rubber bands with nest number and position in hatch sequence written in indelible ink, and with U.S. Fish and Wildlife Service aluminum bands after the chicks attained a weight of 100 g. This allowed identification of individual chicks on subsequent visits. Chicks were weighed until the age of 15 days during the 1981 and 1982 breeding seasons. All chick deaths were noted, and cause of death determined when possible. The terrain was flat and open, so dead chicks were easily found. Chicks that survived past 15 days of age and attained a weight of 500 g were presumed to have fledged, unless found dead after that point.

RESULTS

Clutch size.—The modal clutch size of Moss Landing Western Gulls was three. Mean clutch size in this colony was comparable to the largest average clutch sizes recorded for Western Gulls (Schreiber 1970, Briggs 1977, Coulter 1977, Pierotti 1981), with a mean of 2.86 ± 0.54 eggs/nest in 1981 ($n = 56$) and a mean of 2.71 ± 0.72 eggs/nest in 1982 ($n = 60$). There was no difference in the distribution of clutch sizes between the two years. During the 1983 breeding season the salt ponds where the gulls nested were drained. As a result, terrestrial predators were able to enter the colony and all of the eggs were eaten. We were unable to obtain data on clutch sizes during that year, but we identified, weighed, and measured a limited sample of eggs (see below).

Egg dimensions.—There were no differences in either length or width among eggs in relation to hatching sequence during any of the three breeding seasons (Table 1). Weights also were not different among eggs during the 1981 breeding season (ANOVA, $F = 1.144$, $P > 0.5$), but there was a small difference among eggs during the 1982 breeding season (ANOVA, $F = 3.920$, $0.01 < P < 0.05$). This difference was not observed, however, during the 1983 reproductive period ($F = 0.432$, $P > 0.5$). In addition, eggs laid during the 1981 breeding season were lighter than those laid during the 1982 breeding season (ANOVA, $F = 75.80$, $P < 0.001$; Table 1). Weights obtained from the limited sample of eggs available in 1983 were similar to those from 1982.

TABLE 1. Egg-size parameters of Western Gull eggs measured during three breeding seasons in the Moss Landing colony. Variables are presented as $\bar{x} \pm$ SD.

	Egg length (mm)	Egg width (mm)	Egg weight (g)
1981			
First-laid egg (n = 53)	72.7 ± 2.41[a]	50.3 ± 1.31[a]	93.3 ± 6.6[a,c]
Second-laid egg (n = 50)	72.2 ± 2.41	50.6 ± 1.24	92.5 ± 6.9
Third-laid egg (n = 49)	72.4 ± 2.82	49.8 ± 1.24	92.5 ± 6.5
1982			
First-laid egg (n = 59)	72.2 ± 2.50[a]	50.3 ± 1.40[a]	99.0 ± 6.7[b,c]
Second-laid egg (n = 56)	73.0 ± 2.20	50.4 ± 1.20	100.5 ± 6.1
Third-laid egg (n = 48)	71.6 ± 2.40	49.8 ± 0.92	97.0 ± 5.2
1983			
First-laid egg (n = 26)	72.4 ± 2.39[a]	50.2 ± 1.34[a]	100.9 ± 6.7[a]
Second-laid egg (n = 22)	72.9 ± 2.58	49.9 ± 1.18	100.2 ± 6.7
Third-laid egg (n = 6)	72.9 ± 3.00	48.9 ± 1.04	98.2 ± 7.7

[a] Differences among eggs by laying sequence not significant by ANOVA.
[b] Differences among eggs by laying sequence significant at 0.05 level by ANOVA.
[c] Differences among eggs between 1981 and 1982, 1983 seasons significant at 0.001 level by ANOVA.

Eggs laid by Western Gulls in the Moss Landing colony were the heaviest ever reported for this species (R. Pierotti unpubl. data). In the Moss Landing colony third-laid eggs were as large as first- and second-laid eggs. In other colonies third-laid eggs were significantly smaller than first- and second-laid eggs (Briggs 1977, Coulter 1977). This means that, on average, third-laid eggs from the Moss Landing colony were comparable to first- and second-laid eggs from other colonies of Western Gulls.

Laying and incubation intervals.—During the 1982 breeding season female Western Gulls laid three-egg clutches over a 2–5-day period ($\bar{x}$ = 3.9 ± 1.30 days). This is a shorter interval than was reported from Southeast Farallon (Coulter 1977; 3–5-day interval, $\bar{x}$ = 4.3 days) and Año Nuevo islands (Briggs 1977; 3–6-day interval, $\bar{x}$ = 4.3 days). Presumably, females at Moss Landing had less difficulty acquiring the energy necessary for rapid egg formation.

At Moss Landing the length of incubation (time from laying of first egg to hatching of last egg) was 25.7 ± 1.6 days (range = 23–27 days, n = 19). In contrast, the incubation period for Western Gulls from Southeast Farallon Island was significantly longer ($\bar{x}$ = 28.2 days, Coulter 1977; $P < 0.001$ by t-test, 37 df). Similarly, the incubation period of Western Gulls at Año Nuevo Island, the nearest large colony to Moss Landing, was also significantly longer than that of Moss Landing gulls ($\bar{x}$ = 26.6 days, Briggs 1977; $P < 0.05$ by t-test, 35 df). In 1981 50%, and in 1982 54%, of the nests hatched all three eggs within a one-day interval. This is unusual among *Larus* gulls, where there is typically a 2–3-day interval between hatching of the first- and third-laid eggs (Schreiber 1970, Briggs 1977, Coulter 1977, Schreiber et al. 1979, Hahn 1981, R. Pierotti pers. obs.).

Chick growth and survival.—During the first two years of this study, a number of eggs were taken by terrestrial mammalian predators, e.g. striped skunk (*Mephitis mephitis*) and raccoon (*Procyon lotor*). In 1981, 55 (32.9%) of 167 eggs laid in initial clutches were eaten. In 1982, 85 eggs (53.5%) were eaten. Of the eggs that were not eaten by predators, 87% (91) hatched successfully in 1981 and 93% (55) hatched successfully in 1982. In undisturbed nests there were no significant differences in hatching success among eggs by laying sequence in either year (Table 2). In 1983 all eggs in the colony were taken by predators (see above).

There were no significant differences in hatching weights among first-, second-, and third-hatched chicks either within or between years (Table 3). When weights of chicks at 5 and 10 days of age were compared, in 1981 there was a significant difference among weights of 5-day-old chicks, with third-hatched chicks showing the lightest weights overall (Table 3).This difference disappeared by the age of 10 days, when third-hatched chicks were as heavy as first-hatched chicks. During 1982, there were no significant differences among chick weights by laying sequence at either 5 or 10 days of age. In fact, on day 5 third-hatched chicks had

TABLE 2. Breeding performance in Western Gulls producing three-egg clutches undisturbed by mammalian predators.

Egg or chick	No. of nests	No. hatched (%)[a]	No. fledged (%)[b]
First-laid			
1981	34	34 (100)	21 (62)
1982	20	19 (95)	14 (70)
Second-laid			
1981	34	32 (94)	21 (62)
1982	20	20 (100)	13 (65)
Third-laid			
1981	34	28 (82)	21 (62)
1982	20	16 (80)	12 (60)

[a] Difference in distribution of hatching success insignificant by G test during both breeding seasons ($G = 4.58$ in 1981 and $G = 3.21$ in 1982 with 2 df).
[b] Difference in distribution of fledging success insignificant by χ^2 test during both breeding seasons ($\chi^2 = 0.105$ in 1981 and $\chi^2 = 0.570$ in 1982 with 2 df).

the heaviest mean weight (Table 3). There was, however, a significant difference in weights of all chicks combined between years at both 5 and 10 days of age. Chicks in 1982 were significantly lighter on average than their 1981 counterparts.

Chicks in the Moss Landing colony typically reached a weight of 500 g within two weeks of hatching. This is much faster than in the Southeast Farallon colony, where chicks typically did not reach 500 g until they were at least three weeks old (Coulter 1977).

There were no significant differences in the percentages or numbers of first-, second-, and third-hatched chicks that successfully fledged from the Moss Landing colony (Table 2). Overall, third-hatched chicks had the highest survival rates from hatching to fledging during both the 1981 and 1982 breeding seasons. Despite the difference in chick weights, there was no significant difference in the chick survival rate between years.

DISCUSSION

The size and number of eggs laid as well as the typical laying interval usually are considered to be strongly correlated with food supply (Lack 1968, Murton and Westwood 1977). In species such as *Larus* gulls that have a relatively fixed upper limit on clutch size (Winkler and Walters 1983), an increase in the availability of food should be expressed as an increase in egg size or a decrease in laying interval, or both. The Western Gulls nesting at Moss Landing appear to have had such an abundant food supply that they laid unusually large eggs over a relatively short period of time.

What is perhaps most interesting about this

TABLE 3. Weights of Western Gull chicks at hatching, 5 days, and 10 days of age during the 1981 and 1982 breeding seasons. Data are presented as $\bar{x} \pm$ SD.

Chick	Weight (g)		
	Hatching day	5 days old[a]	10 days old[a]
1981			
First-hatched	70.4 ± 5.8^b ($n = 19$)	135.7 ± 21.0^c ($n = 23$)	266.4 ± 52.7^b ($n = 17$)
Second-hatched	71.0 ± 6.0 ($n = 23$)	137.8 ± 24.8 ($n = 19$)	280.2 ± 46.5 ($n = 19$)
Third-hatched	70.8 ± 4.2 ($n = 19$)	119.1 ± 20.8 ($n = 20$)	258.4 ± 40.4 ($n = 19$)
1982			
First-hatched	71.6 ± 6.2^b ($n = 16$)	121.2 ± 19.4^b ($n = 15$)	254.5 ± 49.3^b ($n = 12$)
Second-hatched	72.6 ± 6.1 ($n = 14$)	115.0 ± 18.4 ($n = 15$)	254.2 ± 49.3 ($n = 13$)
Third-hatched	71.6 ± 5.1 ($n = 15$)	128.5 ± 30.2 ($n = 13$)	232.5 ± 31.4 ($n = 10$)

[a] Differences in weight among chicks not significant by ANOVA.
[b] Differences in weight among chicks between years significant at 0.05 level by ANOVA ($F = 4.281$ on day 5, $F = 4.873$ on day 10).
[c] Differences in weight among chicks significant at 0.05 level by ANOVA.

colony, however, is that there were no significant differences among the eggs in a clutch according to order of laying. Every investigation of gull breeding in which eggs were measured or weighed has found that first- and second-laid eggs tend to be significantly larger than third-laid eggs (see reviews in Parsons 1975, Mills 1979, Schreiber et al. 1979, Hahn 1981, Pierotti 1982). The absence of such a difference suggests that instead of being an adaptive response of adult gulls to reduce the sibling rivalry or minimize "wasteful" competition, it may be most parsimonious to treat variation in egg size among gulls as a facultative response to variation in food abundance as reflected in the magnitude of the energy reserves available to females for reproduction (Pierotti 1979, 1982; Houston et al. 1983; Pierotti and Annett in press).

There is evidence from other species of gulls that supports this option. Schreiber et al. (1979) found no significant difference in size between first- and second-laid eggs in three-egg clutches in one year of their study on Laughing Gulls (*Larus atricilla*). During a second year, nest density on the colony increased, and a significant difference in size occurred between first- and second-laid eggs. This implies that increased costs of territorial defense led to a change in energy partitioning among eggs. In the Herring Gull (*Larus argentatus*) a reduction in nest density led to an increase in both adult body weight and egg size (Coulson et al. 1982). This indicates that reduced costs of territoriality led to greater energy reserves, presumably responsible for the increase in egg size. Houston et al. (1983) showed that egg quality (as measured by size) was correlated with female body condition in the Lesser Black-backed Gull (*Larus fuscus*). Winkler (1982; cited in Winkler and Walters 1983) showed correlations in the California Gull (*Larus californicus*) between food supply, adult body weight, egg size, and clutch size. Finally, Pierotti (1979, 1982) and Pierotti and Annett (in press) found that female Herring Gulls feeding on superior food supplies laid larger and heavier clutches, and were capable of laying many eggs without interruption. The results of these studies suggest that egg size is flexible within clutches and is related to food supply and female body condition, and that egg production and female body condition are related to nest density.

The Moss Landing colony has a very low nest density and an abundant food supply. This creates conditions under which female gulls can produce very large eggs. Given the apparent phylogenetic constraint on gulls of a clutch of three, as evidenced by the presence of only three incubation patches (Drent 1970, Pierotti 1981), it is not surprising that the three eggs produced are of equal size.

The increase in the size of the individual eggs and, commensurately, in the total clutch volume may allow the chicks to develop faster within the egg and hatch within a shorter time (Parsons 1972). Larger eggs also may allow for a disproportionately larger yolk, which is important to the development of the chick (Murton and Westwood 1972, Parsons 1976). The eggs laid by Moss Landing Western Gulls were much larger on average than those of the Herring Gull, which is comparable in size (cf. Table 1 with table 1 of Parsons 1970 and table 4 of Pierotti 1982). In fact, many eggs laid at Moss Landing are comparable in size to those laid by Great Black-backed Gulls (*Larus marinus*), a bird that is 50% heavier on average than Western Gulls (R. Pierotti unpubl. data).

At Moss Landing all three eggs are large, there is a tendency for the chicks to hatch over a short time interval, and there are no differences in hatching weight of chicks in relation to hatch order. This combination of factors probably reduces or eliminates the dominance hierarchy observed in gull broods where third eggs are smaller and asynchronous hatching is more pronounced (Briggs 1977, Hahn 1981). Thus, last-hatched chicks compete equally for food and grow at rates comparable to their elder siblings.

Placing daily food supplements beside the nests of Herring Gulls produces increased weight gain of all three chicks and improved chances of survival, especially in the third chick (Graves et al. 1984). This suggests that the presence of a third surviving chick greatly increases the cost of reproduction, and that the third- or last-laid egg functions primarily as insurance against the loss of first- or second-laid eggs. In the Moss Landing colony the abundant food supply appears to function in the same manner as a food supplement. Hence, in colonies where the food supply is abundant and the nest density is low, it is likely that (1) the third egg (and chick) will be used to maximize parental fitness rather than act as insurance, and (2) in such colonies, the third-chick disadvantage and its associated phenomena should be either reduced or eliminated altogether.

ACKNOWLEDGMENTS

We thank the Monterey Bay Salt Co. for permission to work on their property and Moss Landing Marine Laboratory for logistic support. We thank G. Cailliet for information on fish population biology and abundance in and around Elkhorn Slough. We also thank L. R. Mewaldt, R. Schreiber, D. Winkler, B. Würsig, and an anonymous reviewer for their comments. C. Bellrose was partially supported by a grant from the Packard Foundation.

LITERATURE CITED

BELLROSE, C. A. 1983. The breeding biology and ecology of a small mainland colony of Western Gulls (*Larus occidentalis*). Unpublished M.A. thesis, San Jose, California State Univ.

BRIGGS, K. T. 1977. Social dominance in young Western Gulls: its importance in survival and dispersal. Unpublished Ph.D. dissertation, Santa Cruz, Univ. California.

CAILLIET, G., J. NYBAKKEN, & W. BROENKOW. 1977. Ecologic and hydrographic studies of Elkhorn Slough, Moss Landing harbor, and nearshore coastal waters. Moss Landing Marine Lab., Spec. Publ.

COULSON, J. C., N. DUNCAN, & C. THOMAS. 1982. Changes in the breeding biology of the Herring Gull (*Larus argentatus*) induced by reduction in size and density of the colony. J. Anim. Ecol. 51: 739–756.

COULTER, M. C. 1977. Growth, mortality, and the third-chick disadvantage in the Western Gull, *Larus occidentalis.* Unpublished Ph.D. dissertation, Philadelphia, Univ. Pennsylvania.

DAVIS, J. W. F. 1975. Age, egg size, and breeding success in the Herring Gull, *Larus argentatus.* Ibis 117: 460–473.

DRENT, R. H. 1970. Functional aspects of incubation in the Herring Gull. Pp. 1–312 *in* The Herring Gull and its egg (G. P. Baerends and R. H. Drent, Eds.). Behaviour, Suppl. 17.

GOULD, S. J. 1982. The ring of guano. Nat. Hist. 91: 12–19.

GRAVES J., A. WHITEN, & P. HENZI. 1984. Why does the Herring Gull lay three eggs? Anim. Behav. 32: 798–805.

HAHN, D. C. 1981. Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. Anim. Behav. 29: 421–427.

HARVEY, T. 1983. The breeding biology of three species of larids in Elkhorn Slough. Unpublished M.A. thesis, San Francisco, California State Univ.

HOUSTON, D. C., P. J. JONES, & R. M. SIBLY. 1983. The effect of female body condition on egg-laying in the Lesser Black-backed Gull *Larus fuscus.* J. Zool., London 200: 509–520.

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

HUSSELL, D. J. R. 1972. Factors influencing clutch size in arctic passerines. Ecol. Monogr. 42: 317–364.

KUKOWSKI, G. E. 1972. A checklist of the fishes of the Monterey Bay area including Elkhorn Slough, the San Lorenzo, Pajaro, and Salinas rivers. Moss Landing Marine Lab. Tech. Rept. 72-2. Annual Rept., 2.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Chapman and Hall.

MILLS, J. A. 1979. Factors affecting the egg size of Red-billed Gulls *Larus novaehollandiae.* Ibis 121: 53–67.

MOCK, D. 1984. Infanticide, siblicide, and avian nestling mortality. Pp. 3–30 *in* Infanticide: comparative and evolutionary perspectives (G. Hausfater and S. B. Hrdy, Eds.). New York, Aldine Press.

MURTON, R. K., & N. J. WESTWOOD. 1977. Avian breeding cycles. Oxford, Clarendon Press.

O'CONNOR, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide, and suicide? Anim. Behav. 26: 79–96.

PARSONS, J. 1970. Relation between egg-size and post-hatch chick mortality in the Herring Gull, *L. argentatus.* Nature 228: 1221–1222.

———. 1972. Egg-size, laying date, and incubation period in the Herring Gull. Ibis 114: 536–541.

———. 1975. Asynchronous hatching and chick mortality in the Herring Gull, *Larus argentatus.* Ibis 117: 517–520.

———. 1976. Factors determining the number and size of eggs laid in the Herring Gull. Condor 78: 481–492.

PIEROTTI, R. 1976. Sex roles, social structure, and the role of the environment in the Western Gull. Unpublished M.S. thesis, Sacramento, California State Univ.

———. 1979. The reproductive behaviour and ecology of the Herring Gull in Newfoundland. Unpublished Ph.D. dissertation, Halifax, Nova Scotia, Dalhousie Univ.

———. 1981. Male and female parental roles in the Western Gull under different environmental conditions. Auk 98: 532–549.

———. 1982. Habitat selection and its effect on reproductive output in the Herring Gull in Newfoundland. Ecology 63: 854–868.

———, & C. A. ANNETT. In press. Specialization and switching in an ecological generalist: diet and reproductive output in the Herring Gull. *In* Foraging behavior (A. C. Kamil, J. R. Krebs, and H. R. Pulliam, Eds.). New York, Plenum Press.

SCHREIBER, E. A., R. W. SCHREIBER, & J. J. DINSMORE. 1979. Breeding biology of Laughing Gulls in Florida. Part I: Nesting, egg, and incubation parameters. Bird-Banding 50: 304–321.

SCHREIBER, R. W. 1970. Breeding biology of Western Gulls (*Larus occidentalis*) on San Nicolas Island, California. Condor 72: 133–140.

SLAGSVOLD,T., J. SANDVIK, G. ROFSTAD, O. LORENTSEN, & M. HUSBY. 1984. On the adaptive value of intraclutch egg size variation in birds. Auk 101: 685–697.

WINKLER, D. W., & J. R. WALTERS. 1983. The determination of clutch size in precocial birds. Current Ornithol. 1: 33–68.