

## SHORT COMMUNICATIONS

### Brood Reduction and Parental Infanticide in Heermann's Gull

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Some gull species (Laridae) apparently practice facultative brood reduction (Lack 1954). They lay eggs that are raised to fledging only if feeding conditions turn out to be favorable. The last egg laid (i.e. the second or third egg) typically is small and, more importantly, it hatches after the others. The last chick is therefore younger and smaller than its siblings, and is easily outcompeted by them when begging for parental food (e.g. Parsons 1975, Hahn 1981, but see Pierotti and Bellrose 1986). In the Black-legged Kittiwake (*Rissa tridactyla*), death can be precipitated by sibling aggression (siblicide), when elder chicks peck the victim and evict it from the cliff nest (Braun and Hunt 1983).

The roles of family members in brood reduction are currently unresolved and the focus of much research. Lack (1954) and most later authors (e.g. Magrath 1989) consider that in diverse avian taxa, parental fitness benefits from selective chick loss when food is scarce. Consistent with this, parents typically promote the competitive inequality and differential survival of their chicks by creating initial age/size differences. Then parents allow differential feeding and sibling aggression (e.g. Drummond et al. 1986, but see Clark and Wilson 1981). O'Connor (1978) proposed that brood reduction is sometimes imposed on parents by elder chicks that are winning parent-offspring conflict over brood size. The role of parents in selective chick loss is open to alternate interpretations (e.g. Drummond 1987) because parental behavioral contribution is largely passive (Mock 1984). In no species—except the Eurasian Coot (*Fulica atra*), which has been seen to shake chicks to death (Horsfall 1984)—do parents kill the victim by attacking or ejecting it. The White Stork (*Ciconia ciconia*) is another possible example, but cannibalism is also involved (Schuz 1957 in Lack 1966). Death by neglect occurs in the Hooded Grebe (*Podiceps gallardoi*), which abandons its second egg after the first hatches (Nuechterlein and Johnson 1981).

We have evidence from a single season for an active parental role in chick deaths in Heermann's Gull (*Larus heermanni*), a poorly known species that breeds exclusively on islands in and near Mexico's Sea of Cortez. Our study to detect possible brood reduction showed that parents not only created competitive asymmetry between their chicks, but also sometimes

precipitated the death of the last egg/chick by neglect or aggression.

Observations were made on Isla Rasa (28°49'N, 112°59'W), a small (0.55 km<sup>2</sup>), arid island located in a zone of high marine productivity. The island harbors approximately 95% of the worldwide population of Heermann's Gull (Vidal 1976, Velarde González 1989). In the sandy, rock-free area where nests are most dense, we marked (1984) with numbered wooden pegs two samples of nests at the edge of the colony.

To analyze clutch size and nest success, a sample of 61 nests was selected at random in April, before laying began. We recorded nest contents (1) during the laying period by entering the colony daily, (2) during the hatching period by daily visual inspection (through binoculars from 10–30 m), and (3) subsequently by visual inspection every 2–4 days until chicks were 30 days old. Mortality is minimal after this age, but flying does not occur until 45 days. In 8 three-egg clutches each egg was weighed and identified with a pencil mark within 1 day of laying.

To analyze egg and chick mortality in three-egg clutches, a subsample of 40 three-egg nests was selected shortly after laying. In half of them, the 20 randomly assigned *handled nests*, chicks were weighed (within a day of hatching) on a 100-g spring balance and marked on the head with one of three colors of paint according to hatching order. The colors lasted approximately 2.5 weeks. The remaining 20 *control nests* were not handled. We recorded the contents of all 40 nests by visual inspection, daily during the hatching period and then every 2 days until chicks were 30 days old. Because handled and control nests did not differ significantly for any variable examined, they were pooled subsequently.

Aggressive interactions were scrutinized during direct observation of the broods in the subsample, from 10–30 m through binoculars. Between May 10 and June 16, the handled and control groups were watched on alternate days from hatching until chicks were ca. 30 days old. From 0600–1900 in 2-h sessions alternating with rest periods (2 h), an observer watched each brood in succession for 30 min and scanned all other broods in the group every 10 min.

The most common clutch size in the large sample was two eggs (68.3%). Three-egg clutches (18.3%) and one-egg clutches (13.3%) made up the remainder ( $\bar{x}$  = 2.05, SD = 0.56,  $n$  = 61). These values represent colony clutch size near the edge of the main nesting area. The larger the clutch, the more fledglings pro-

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TABLE 1. Number of fledglings produced by different clutch sizes. Data are pooled from a large sample ( $n = 61$ ) and a small sample ( $n = 40$ ).

Clutch size	$n$	Per nest $\bar{x} \pm SD$	Per egg $\bar{x} \pm SD$
1	8	$0.38 \pm 0.51$	$0.38 \pm 0.51$
2	42	$0.67 \pm 0.65$	$0.33 \pm 0.47$
3	51	$0.88 \pm 0.68$	$0.29 \pm 0.46$

duced (Table 1; one-way ANOVA,  $F = 3.33$ ,  $df = 2$ ,  $98$ ,  $P < 0.05$ ), and the mean number of fledglings produced per egg was similar in all three clutch sizes (Table 1). This suggests that an extra egg contributed to a clutch of two produced an average increment in productivity, but the mean number of fledglings from three-egg clutches was still less than one.

There were nonsignificant tendencies for egg weight to decline progressively with laying order and for third-hatched chicks to weigh slightly less than first and second-hatched chicks (Table 2; planned comparisons of first vs. second and second vs. third, using tests derived from Friedman and Kruskal-Wallis tests at overall significance level of 0.10, Gibbons 1976). Larger samples might have revealed significant differences. Third chicks hatched an average 1.86 days (SD = 0.74) after second chicks, which themselves hatched 1.60 days (SD = 0.50) after first chicks ( $n = 14$  broods of three). Hence, as in some gull species thought to practice brood reduction, the third chick potentially experienced a substantial age/size disadvantage in competition with its siblings because of hatching schedule and possibly a slight size disadvantage because of egg size.

We determined comparative survivorship of first, second, and third chicks in the 14 three-egg clutches in the small sample that hatched completely. In six clutches the chicks were not paint-marked, but most deaths occurred in the first few days after hatching, when seniority could be inferred from relative size. Third chicks suffered substantially higher mortality than either first chicks ( $\chi^2 = 9.9$ ,  $df = 1$ ,  $P < 0.01$ ) or second chicks ( $\chi^2 = 8.0$ ,  $df = 1$ ,  $P < 0.01$ ), most of which fledged (Fig. 1). A single third chick fledged (along with both siblings); most died within 1-4 days of hatching.

Deaths of first and second chicks occurred outside observation periods, and the causes were not identified. Of the 13 third chicks in the subsample that died, in seven cases the parent (sex unknown) was observed to peck at the still-live chick. Both begging and quiescent chicks were attacked. Standing chicks were pecked on the head, prone chicks were pecked all over the head and body. Pecks were violent but less violent than pecks sometimes given to alien chicks. After death, chicks were pecked, pushed, and tossed away from the nest. In two other cases parents left

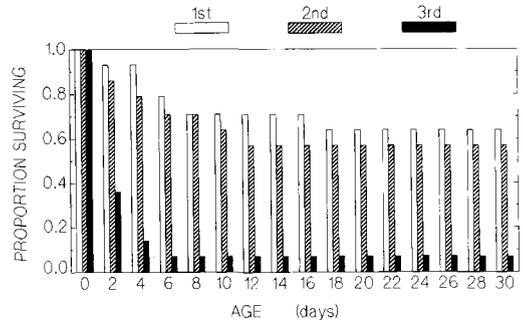


Fig. 1. Survivorship of first-, second-, and third-hatched chicks in 14 broods of three.

the third chick unbrooded and exposed shortly after hatching. Parental pecks to hatchling third chicks did not result in fatal lesions, but probably inhibited begging and led to weakening. Death was probably due to starvation or thermal stress.

There was also neglect during incubation. In 19 clutches in the subsample, two eggs hatched and the last (third?) egg never hatched. Five of the unhatched eggs were left unincubated by parents after they had pipped.

It is unlikely that the observer confused attacks by neighbors or intruders with attacks by parents. Chicks 1-2 weeks of age were sometimes severely attacked by nonparents when they wandered from the nest or were left unbrooded in the nest. In contrast, during the first few days after hatching, at least one parent was almost always on the nest to provide shade, so hatchlings were seldom vulnerable to attack and would be quickly defended by a parent at the nest. Furthermore, in subsequent years a different observer frequently observed parents pecking their own individually marked offspring (including older, ambulatory chicks) on the head and nape. Death sometimes followed, perhaps due to starvation or even more severe attacks by neighbors when chicks fled from their home nests (L. G. Peralta pers. comm.).

Heermann's Gull appears to practice facultative brood reduction similar in most respects to that in other gull species. A third egg is laid, but late hatch-

TABLE 2. Weight of eggs (from 8 three-egg clutches) and chicks (hatched from another 20 three-egg clutches) according to laying or hatching order.

Order	Egg (g) <sup>a</sup>		Chick (g) <sup>a</sup>	
	$n$	$\bar{x} \pm SD$	$n$	$\bar{x} \pm SD$
First	8	$58.6 \pm 3.8$	16	$37.6 \pm 3.5$
Second	8	$55.4 \pm 5.6$	13	$39.5 \pm 3.6$
Third	8	$51.6 \pm 4.3$	5	$34.8 \pm 6.0$

<sup>a</sup> Four clutches produced no chicks, and data missing from the remaining 16 clutches represent eggs that failed to hatch or chicks that disappeared within one day of hatching.

ing and, possibly, small size prejudice its chances of producing a fledgling. Clearly the third egg represents a potential extra unit of parental fitness (Mock and Parker 1986), because one third-hatched chick fledged in addition to its two siblings. In addition, it may serve as insurance against hatching failure of the first two eggs. The risk of such failure could not be assessed because the laying order of eggs was not generally known, and some hatching failure may have been due to parents suspending incubation.

We provide only a partial account of the circumstances in which brood reduction occurs. The high frequency of third chick losses in 1984—a year when fish may have been scarce due to a recent “El Niño” oceanographic event—could have been a response to food shortage. The observed frequency of third-chick losses at the colony edge in a single season and their association with hatching order may not be representative of losses in other conditions.

Neglect of piped eggs and hatchlings constitutes parental infanticide within Mock’s (1984) definition. The pecking of third hatchlings is infanticide, provided pecking contributed significantly to their deaths. It is not necessary for attacks to cause death directly; it is sufficient if they result indirectly in death by other means. Although there is no experimental evidence, pecks and neglect probably caused death indirectly through starvation, heat stress, and attacks by nonparents. If so, then in Heermann’s Gull the parental role in facultative brood reduction is sometimes an active one. This implies that the death benefits parental fitness (cf. Nuechterlein and Johnson 1981).

Active parental elimination of the third egg/chick is atypical and puzzling. Parents that kill so promptly may run some risk of dispensing with a viable chick in favor of a sickly elder sibling. This may be why even parents of obligate brood reduction species allow death to occur through sibling conflict during the first few days after completion of hatching (Drummond 1987). When death occurs through sibling competition, the vigor of elder offspring is tested rather than assumed.

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#### LITERATURE CITED

- BRAUN, B. M., & G. L. HUNT. 1983. Brood reduction in Black-legged Kittiwakes. *Auk* 100: 469–476.
- CLARK, A. B., & D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. *Q. Rev. Biol.* 56: 253–277.
- DRUMMOND, H. 1987. A review of parent-offspring conflict and brood reduction in the Pelecaniformes. *Colon. Waterbirds* 10: 1–15.
- , E. GONZALEZ, & J. L. OSORNO. 1986. Parent-offspring cooperation in the Blue-footed Booby (*Sula nebouxi*). *Behav. Ecol. Sociobiol.* 19: 365–372.
- GIBBONS, J. D. 1976. *Nonparametric methods for quantitative analysis*. New York, Holt, Rinehart & Winston.
- HAHN, D. C. 1981. Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. *Anim. Behav.* 29: 421–427.
- HORSFALL, J. A. 1984. Brood reduction and brood division in coots. *Anim. Behav.* 32: 216–225.
- LACK, D. 1954. *The natural regulation of animal numbers*. Oxford, Clarendon Press.
- . 1966. *Population studies of birds*. Oxford, Clarendon Press.
- MAGRATH, R. D. 1989. Hatching synchrony and reproductive success in the blackbird. *Nature* 339: 536–538.
- MOCK, D. W. 1984. Infanticide, siblicide and avian nestling mortality. Pp. 3–30 in *Infanticide: comparative and evolutionary perspectives* (G. Hausfater and S. B. Blaffer Hrdy, Eds.). New York, Aldine.
- , & G. A. PARKER. 1986. Advantages and disadvantages of ardeid brood reduction. *Evolution* 40: 459–470.
- NUECHTERLEIN, G. L., & A. JOHNSON. 1981. The downy young of the Hooded Grebe. *Living Bird* 19: 69–71.
- O’CONNOR, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide, and suicide? *Anim. Behav.* 26: 79–96.
- PARSONS, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull, *Larus argentatus*. *Ibis* 117: 517–520.
- PIEROTTI, R., & C. A. BELLROSE. 1986. Proximate and ultimate causation of egg size and the “third chick disadvantage” in the Western Gull. *Auk* 103: 401–407.
- SCHUZ, E. 1957. Das Verschlingen eigener Junger (‘Kronismus’) bei Vögeln und seine Bedeutung. *Vogelwarte* 19: 1–15.
- VELARDE GONZÁLEZ, M. E. 1989. *Conducta y ecología de la reproducción de la Gaviota Parda (Larus heermanni) en Isla Rasa, Baja California*. Ph.D. dissertation, Fac. Ciencias, Univ. Nacl. Autónoma México.
- VIDAL, M. N. 1976. *Aportación al conocimiento de la Isla Rasa, Baja California*. B. Sc. thesis, Facultad de Ciencias, Univ. Nacl. Autónoma México.

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