

laid in 1972, and in 1973 the Killdeers failed to return to the roof. The season extended from early March (two eggs found in a nest on 3 March 1968) to late May (three chicks hatched 23 May 1971), the usual nesting period in southern Arizona according to Phillips et al. (Birds of Arizona, Univ. Ariz. Press, Tucson, 1964, p. 33). From 1967 through 1970, I observed the Killdeers two or three times a week during the nesting period. During April and May of 1971 I conducted 31 watches, ranging from 15 min to 14 hr. A trap door provided a good view point of the roof.

The nests were all unshaded and during May the roof-surface reached 53°C in the sun. Temperatures were recorded by placing a mercury thermometer on the roof beside the nests. At roof-surface temperatures above 48°C, the incubating bird would cease incubating and stand at the side of the nest shading the eggs. The eggs were left unattended for only a brief period between 05:30 and 06:05 and again around 17:00.

An incubation period of 26 days was noted for the nest observed in 1971. Bent (1929:207) quoted incubation periods ranging from 24 to 28 days and Nickell (Wilson Bull. 55:27, 1943) showed periods ranging from 24 to 26 days. In 1971 the first egg in the second clutch was laid 22 April and the fourth egg, 27 April, when incubation began. Both adults incubated. The male usually spent 3–4 hr incubating in the morning and 3–4 hr in the afternoon. When not incubating he was usually either in the grassy area or on the roof. Three eggs hatched 23 May. As soon as a chick hatched, the male carried the egg shells off the roof. The fourth egg did not hatch and I removed it from the nest 25 May. It had developed about 20 days according to Robert Ohmart, who examined it.

The first egg in the 1971 second clutch was laid the same day that the surviving chick from the first clutch began flight, (its 20th day after hatching). Reilly (The Audubon Illustrated Handbook of American Birds, 1968, p. 153) stated that the age of first flight is unknown. Nickell (1943) mentioned a second clutch laid 34 days after the hatching of the first clutch, at which time the chicks were able to fly short distances.

The adult birds were quiet when eggs were present in the nest. When I entered the roof area, the incubating bird would run noiselessly from the nest and hide near an air vent which projected approximately 1 m above the roof. If I approached the adult bird within 2 m, it would fly from the roof. When the eggs began to hatch, there was much activity and calling, both adults flying to and from the nest area. I had only to raise the trap door

slightly and the adults would call rapidly and feign a broken wing in the manner common to the species.

All-night lighting on the four corners of the roof attracted many insects, and the adult Killdeers fed on the roof as did a Mockingbird (*Mimus polyglottos*). The chicks were never seen to feed on the roof. I often saw the male at night sitting under the lights but could not tell whether he fed at night. The birds also fed on the grassy area, where water was available. No water was on the roof and, during one hatching, a pan of water that I placed near the nest was untouched by the adults and chicks.

Some chicks left the roof on the first day after hatching and the others on the second day. Three eggs in the 1971 first clutch hatched between 11:00 and 12:00 on 2 April. The remaining egg hatched at 15:30. The chicks stayed close to the nest that day. On 3 April at 11:00 the female called the chicks from the nest to the shade of the air vent. One chick was much more precocious than the others and at 16:45 went to the north edge of the roof and looked over. At 17:00 the female led the remaining chicks to the north edge but none went off. The male was calling excitedly from the grassy area. At 18:10 the precocious chick tumbled from the roof into the shrubbery and was led by the male to the grassy area. On 4 April at 08:40 the female led the three remaining chicks to the north edge of the roof. She began flying back and forth from the roof to the grassy area calling all the time. The male remained in the grass calling excitedly. At 09:05 one chick walked off the edge and tumbled down, flapping its partly-developed wings. The two remaining chicks went off the roof at 12:00 after much calling by the adult birds. All dropped from the north side of the building (height 6.8 m) where the shrubbery grew at the base (except in a 2 m space). During the observation period I watched six chicks leave the roof. Two that landed in the planted area became active immediately and were led by the male to the grass. Three that seemed to survive the fall were found dead in the shrubbery 2 days later. One chick was killed upon impact with the concrete paving.

Of the 44 eggs laid, two did not hatch (suggesting that roof-surface temperatures were not excessive). All the chicks left the roof except for one that I found dead of dehydration on the roof. Six were killed in the parking lot. I know of only two chicks that developed to flight stage. The fate of the other 30 was unknown.

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ROLE OF THE CHICK'S BEGGING BEHAVIOR IN THE REGULATION OF PARENTAL FEEDING BEHAVIOR OF *LARUS GLAUCESCENS*

BRYAN A. HENDERSON

Institute of Terrestrial Ecology
Blackhall, Banchory
Kincardineshire, AB3 3PS
Scotland

Norton-Griffiths (1969) suggested that parental feeding (defined as the behavior of the parents feeding

their young) in the European Oystercatcher (*Haematopus ostralegus*) occurred only if the parents were sufficiently motivated to feed for themselves. Once parental feeding had begun, its maintenance on a short term basis depended on how long the young took to seize the presented food; there was a "waiting-time threshold" within which the chicks must take the presented food before the parent would give another item. Von Haartman (1953) demonstrated with a Pied Flycatcher, *Ficedula hypoleuca*, that what regulated parental feeding frequency was not the number of young but rather the hungriest chick's behavior.

Do Glaucous-winged Gulls (*Larus glaucescens*) adjust their parental feeding behavior to brood size and if so what controls the adjustment? To answer these questions, I observed the parental feeding of gulls on two sea-bird colonies situated on either side of Vancouver Island, Canada. I made exploratory observations on Mandarte Island in 1970 and detailed observations and experiments on Cleland Island in 1971. The breeding biology of the Glaucous-winged Gull has been studied on both Mandarte (Vermeer 1963) and Cleland (Ward 1973).

METHODS

Gulls with artificially enlarged or reduced broods were observed continuously for 18 hours, one day each week for 5 weeks after hatching. Brood sizes of 1 and 2 were obtained by removing chicks from natural broods of three chicks; larger broods were made by addition of chicks of the same age from natural broods of three chicks to other natural broods of three. For each brood, two of each brood size, I recorded the arrival and departure of individually recognizable adults and the time of each parental feeding.

In both study areas I watched twelve individually marked broods of one to six chicks until each brood was approximately 35 days old; the broods were sufficiently close to the blind to be easily heard and observed. The number of times the chicks struck the parent's bill before a feeding was recorded for broods of one, three, and six chicks. The number of begging calls (Impekoven 1971) given in a unit of time by the entire brood or an individual in the brood was recorded before, after, and between feedings for broods of one to six chicks. The calls and pecks were registered on a counter and the time recorded with a stop-watch.

Six recently hatched chicks were taken from six randomly selected nests from Cleland Island, individually marked, and reared in a $9 \times 3 \times 4$ m wire cage built near the field station. The relationship between hunger and begging intensity was obtained by recording pecking rate, calling rate, and call loudness for different lengths of food deprivation during the chicks' first, third and fifth week. Hunger was defined as the weight of food required to satiate a gull chick which had been deprived of food for a known time. The pecking rate as a function of food deprivation was obtained by presenting the mandibles of a stuffed gull to caged chicks and then recording the number of pecks given by one chick striking the bill in one minute; the procedure was repeated for 8 different periods of food deprivation, three trials for each age group. The calling rate for all six chicks was determined by tallying all calls given within 39 successive five-minute intervals after a satiation feeding. With a Scott type 450 sound-level meter held one foot from a chick, the loudness of the begging call was measured at intervals after a satiation feeding; 4 different trials done on 4 different days were completed for each age group.

RESULTS

Parental feeding behavior. The arrival on territory of an adult usually was heralded by "long calls" (Tinbergen 1953) given by the incoming, attendant, and neighboring adults. If the female was attending the chicks, she was often fed by the male, both engaged in pre-copulatory behavior. The attendant parent sometimes gave a mew call followed by

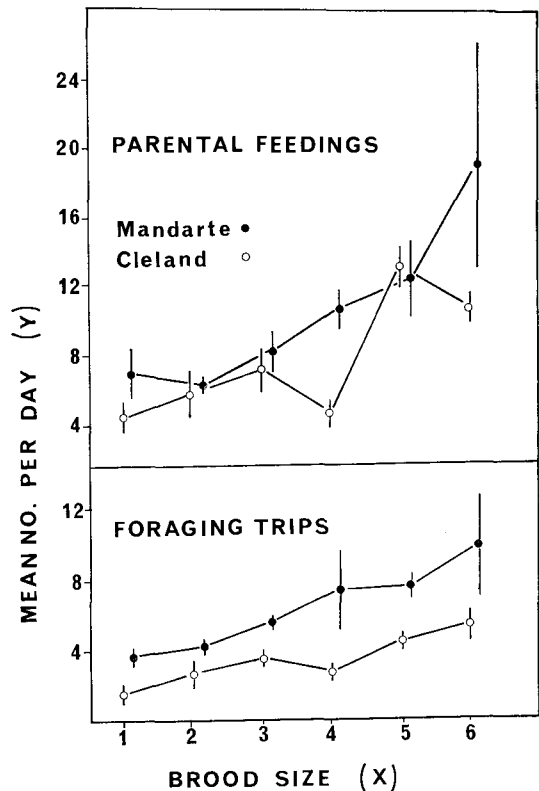


FIGURE 1. The mean rate of feeding and foraging ($\bar{x} \pm S.E.$) is shown for a range of brood sizes (1-6). The feeding rates of Mandarte ($y = 2.03x + 3.40$) and Cleland ($y = 1.16x + 4.84$) did not differ significantly (analysis of covariance, $P > 0.05$), but the foraging rates for Mandarte ($y = 1.17x + 2.27$) were greater than Cleland ($y = 0.86x + 0.61$) (analysis of covariance, $P < 0.05$). All regressions were significant at $P < 0.05$.

a feeding or attempted feeding of the chicks but always the incoming adult gave a feeding call preceding the feeding. The attendant parent left after this brief ritual of nest relief and the other parent called the chicks.

The soliciting behavior of the parent accompanied every feeding. The feeding call, a sustained low-pitched sound, is characteristic of individual adults whom the chicks might recognize by call (Evans 1970). The feeding call was given most frequently while the adult stretched its head toward the ground. Holding this crouched and stretched posture, the parent walked back and forth between two points within the territory, with the chicks in pursuit.

At all ages the chicks attempted to peck the parent's mandibles, particularly after it had returned from a foraging trip. In the first week, the chicks' activities were confined to the immediate vicinity of the nest cup with the result that the parents' soliciting behavior was restricted to a small area, but later their activity was mainly on ground away from the nest. As the chicks grew, the pecking and calling were accompanied by an up-and-down movement of the head, called "bobbing." At this stage the parent was stimulated to regurgitate food.

The adult twisted its neck from side to side as

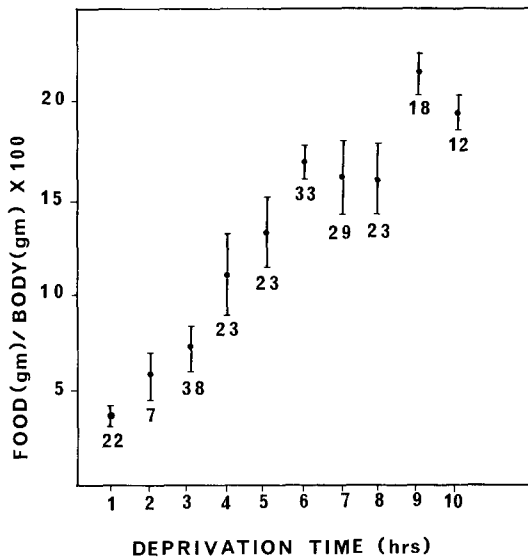


FIGURE 2. The amount of food (expressed as a % of body weight) eaten after a period of food deprivation. The mean, sample size and standard error are shown for each hour of deprivation. The regression ($y = 2.1x + 1.9$) is significant ($P < 0.05$).

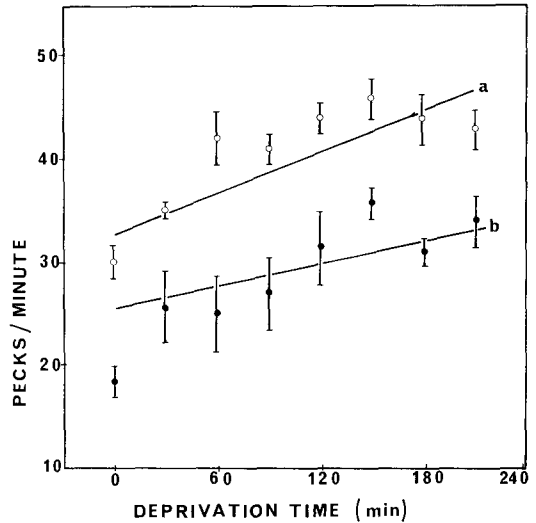


FIGURE 3. The mean pecking rate ($\bar{x} \pm S.E.$) of chick deprived of food is shown for each 30 minute interval of deprivation:

- a) $y = 4.0x + 32.6$, $N = 40$, $P < 0.05$, five wks. old
- b) $y = 2.1x + 25.5$, $N = 58$, $P < 0.05$, one and three wks. old.

the food moved up its esophagus; this grotesque posture was maintained as the chicks pecked at the parent's face and bill. Earlier in the chick's development, a pulpy mixture was held between the mandibles as the chick ate, but later, large pieces of partially digested food were dropped on the ground. As the parent did not feed individual chicks selectively, the larger, more aggressive chicks would usually take food first. After a feeding the chicks' pecking and calling subsided but their calling rate increased during the absence of the foraging parent.

Feeding behavior of parents and chicks. Feeding and foraging rates per brood were positively correlated with brood size but foraging and feeding rates per chick were negatively correlated with brood size (fig. 1). The cumulative calling rate of the brood also increased with brood size (table 1); the cumulative calling rate was obtained by recording broods which were calling during forty 5-minute sampling periods selected randomly during the fourth and fifth week of observations. Table 2 shows that the mean foraging absence did not differ between Mandarte and Cleland ($P > 0.05$; t-test). As might be expected if foraging activity increased with brood

size, the foraging absence was greater for small broods (1-3 chicks) than for large broods (4-6) (table 2; $P < 0.05$ for both Mandarte and Cleland; t-test). The foraging absence is a measure of the time between the departure of a parent and the return of that parent with food for the chicks.

Chick begging behavior. There was no correlation between brood size and the total number of pecks/brood preceding a feeding from a parent (table 3). From the more intensive observations on Cleland, it was evident that a feeding was preceded by an average of 18.4 pecks striking the parent's mandibles (table 4). As with pecking behavior, the call frequency per chick appeared to reach a critical level before the parent regurgitated food, and declined after a feeding (table 5).

Deprivation experiment. The relationship between deprivation time and food eaten is shown in figure 2. Although not shown on this figure, the asymptote

TABLE 1. The cumulative calling rate of different-sized broods (3-4 wks. old).

	Brood size					
	1	2	3	4	5	6
Total number of calls heard	7	20	24	15	35	80
No. of broods observed average	1	2	1	1	1	2
	7	10	24	15	35	40

$Y = 5.7X + 3.4$, $r = 0.87$, $P < 0.05$, $Y =$ cumulative calls, $X =$ brood size.

TABLE 2. Foraging absence of parents with different-sized broods observed during the first 5 weeks after hatching.

Colony	Normal brood-size (1-3)	Supernormal brood-size (4-6)	
Cleland	n^a	42	86
	\bar{x}^b	122	93
	SE	13.2	6.9
	95% CL	96-149	79-105
Mandarte	n	22	35
	\bar{x}^b	156	91
	SE	34.5	5.1
	95% CL	89-213	81-101

^a Average number of minutes for n trips.
^b Number of observations.

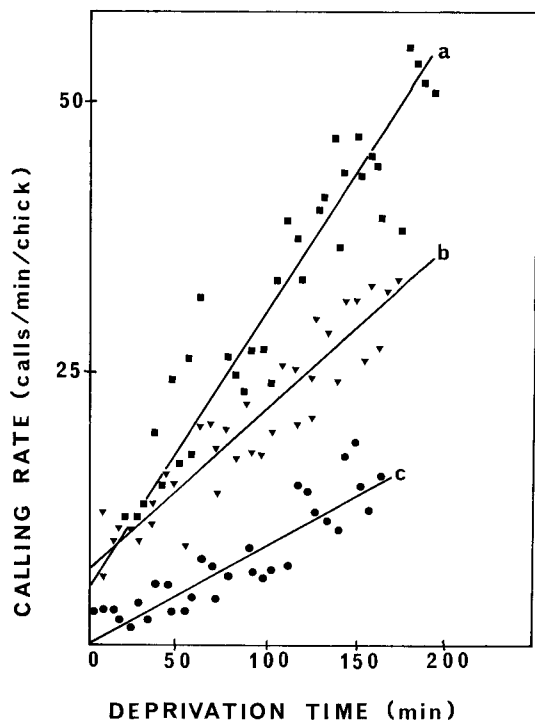


FIGURE 4. The calling rate of chicks deprived of food for various deprivation periods is shown for each 5 minute interval. Analysis of covariance showed that all regression lines were significantly different ($P < 0.05$). a) $y = 0.25x + 5.3$, $r = 0.95$, five wks. old. b) $y = 0.13x + 7.3$, $r = 0.93$, three wks. old. c) $y = 0.08x + 0.7$, $r = 0.73$, one wk. old.

of food eaten was reached after 10 hrs of deprivation. As the hunger level (i.e., deprivation time) increased, the pecking rate increased (fig. 3). At comparable deprivation times, the mean pecking rate increased from one week old to chicks older than three weeks. The calling rate also increased with deprivation time and increased from one- to three- to five-week old chicks (fig. 4). The loudness of the begging call increased, then reached an asymptote after one hour of deprivation; the begging call was louder for three- and five-week chickens than for one-week old chicks (fig. 5).

DISCUSSION

Observations of artificially enlarged and reduced broods indicated that parents adjusted their parental behavior to the brood size. The foraging rate was increased by decreasing the foraging absence in re-

TABLE 3. The number of pecks per brood preceding a feeding for different-sized broods observed during the first 3 weeks after hatching.

	Brood size		
	1	3	6
n^a	27	44	87
\bar{x}^b	20	15	16

^a Mean for n observations.

^b Number of observations.

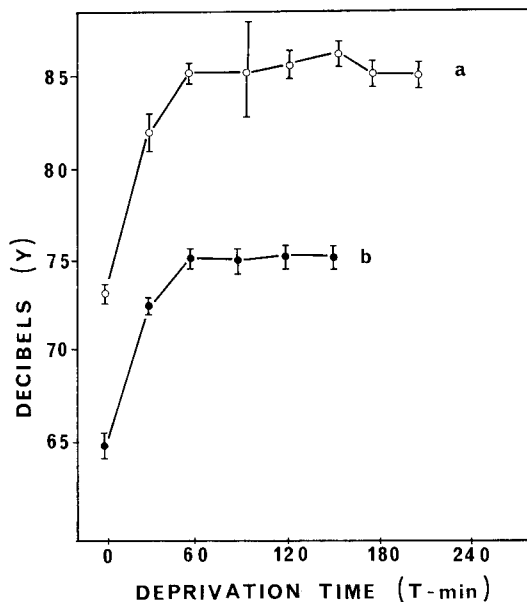


FIGURE 5. The loudness of begging calls ($\bar{x} \pm S.E.$) is shown for a range of deprivation times:

a) $y = 84.6 - 10.9e^{-0.042T}$, $N = 745$, $r^2 = 0.60$, three and five week old chicks

b) $y = 74.9 - 9.7e^{-0.048T}$, $N = 465$, $r^2 = 0.82$, one week old chicks.

sponse to a larger brood. Although the foraging absence for a comparable range of brood sizes did not differ between Mandarte and Cleland, the foraging rate per day was greater on Mandarte. Therefore, Mandarte parents must have increased their foraging rate by decreasing the time spent on the territory or in other non-parental activities. These changes may have been controlled by the chicks' behavior.

The foraging rate was probably regulated by the brood's cumulative calling rate, which increased with brood size and hunger. The parent fed the chicks only if they pecked at its bill approximately 18 times, regardless of brood size, therefore the feeding rate was probably regulated by the pecking behavior. If pecking behavior did regulate feeding, the feeding rate could be controlled by the hungriest chick. Without further experiments, it would be impossible to distinguish conclusively between the effects of calling and pecking on the parent's behavior.

TABLE 4. The number of pecks preceding a parental feeding for observations during the first 4 weeks after hatching.

	Pecks that stimulated a feeding	Pecks that did not stimulate a feeding
n^a	165	94
\bar{x}^b	18.4	6.2
SE	1.12	0.67
95% CL	16.1-20.6	4.9-7.6

^a Mean for n observations.

^b Number of observations.

TABLE 5. The calling rate before, after, and between parental feedings observed during the first 4 weeks after hatching.

	Resulted in feeding	No feeding ensued	After a feeding
<i>n</i>	70	64	35
\bar{x}^a	0.8574	0.4103	0.2534
SE	0.0370	0.0354	0.0329
95% CL	0.7336–0.9312	0.3395–0.4811	0.1867–0.3202

^a Means (calls/sec/chick) for *n* observations.

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EFFECTS OF HUMAN ACTIVITY ON EGG AND CHICK MORTALITY IN A GLAUCOUS-WINGED GULL COLONY

WILLIAM HUMPHREY GILLETT

JAMES L. HAYWARD, JR.

AND

JOHN F. STOUT

Biology Department
Andrews University
Berrien Springs, Michigan 49104

Colville Island, located at the south end of Lopez Island, 11.7 km west of Rosario Beach, Skagit County, Washington is a part of the San Juan National Wildlife Refuge, and contains one of the largest breeding colonies of the Glaucous-winged Gull (*Larus glaucescens*) in the San Juan Islands. Thoresen and Galusha (1971) estimated that 1,486 pairs of gulls utilized the island during the summer of 1970. In addition to gulls, Colville supports smaller breeding populations of the Pelagic Cormorant (*Phalacrocorax pelagicus*), Pigeon Guillemot (*Cephus columba*), Black Oystercatcher (*Haematopus bachmani*) and Song Sparrow (*Melospiza melodia*).

Experiments and observations on the behavior of the Glaucous-winged Gull have been conducted on Colville almost every summer between 1963 and 1973. The effect of our activity on egg and chick mortality has been of considerable interest to us and the refuge management. It is well known how chicks scatter in response to disturbance within the territory

(Paynter 1949, Emlen 1956, Harris 1964, Kadlec et al. 1969). As the result of such displacement, chicks often enter other territories and are attacked by the owners of these adjacent territories. Young chicks are unable to retaliate and may be killed before they can return to their own territories.

Our research activities on the island necessitated entry into the territories resulting in chick displacement. This paper describes studies undertaken during 1972 and 1973 to determine the extent of our effects on egg and chick mortality and our influence on the full population.

Colville Island is situated in the southern part of the breeding range of the Glaucous-winged Gull. Colville is 445 m long and 128 m wide at its widest point. The total area was estimated at 3.82 ha. The vegetation consists mainly of two dominant species of grasses *Horedum murinum* and *Bromus carinatus*.

Blinds were set up at four locations on the island. Observations and experiments were usually conducted from the protection of one of the blinds. The experiments on the aggressive communication of the Glaucous-winged Gull involved placing models in gull territories (Stout et al. 1969, Stout and Brass 1969, Gillett 1973, Hayward 1974). Models were moved from territory to territory between experiments which resulted in walking through a number of territories each time. This activity, in addition to disturbances caused when we moved from blind to blind, resulted in chicks scattering to neighboring territories, thus exposing themselves to attack by the neighboring adult birds. This disturbance occurred intermittently for periods of a few seconds to one or two minutes. A given territory might be entered as often as two or three times in a day. The blinds in experimental plots were used daily.

In 1972, two plots measuring approximately 4045