

# ROLE OF SIBLING AGGRESSION IN FOOD DISTRIBUTION TO NESTLING CATTLE EGRETS (*BUBULCUS IBIS*)

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**ABSTRACT.**—Sibling aggression occurs in a wide variety of asynchronously hatching bird species. In some, fights among siblings lead inevitably to death, in which case the benefits of winning are clear. In species where sibling aggression is common but usually not fatal, the benefits gained by winning and the methods used to achieve them are less obvious. In a Texas colony of Cattle Egrets (*Bubulcus ibis*), sibling aggression was frequent but siblicide rare. Parents rarely interfered with fights. Last-hatched chicks lost more fights and received less food than their elder siblings. Fighting limited the losers' immediate access to food and contributed to the senior sib's ability to monopolize boluses. These results are consistent with the hypothesis that monopolizable food can act as both a proximate and ultimate cause of sibling aggression. The main effect of sibling aggression lay in depressing food supplies to last-hatched chicks. First- and second-hatched sibs accrued roughly equal feeding advantages. *Received 19 August 1985, accepted 11 April 1986.*

MANY raptors, cranes, herons, and various other birds lay their eggs at intervals of a day or more and commence incubation before laying is complete. This pattern produces an asynchronous hatch (Gibb 1950, Inoue 1985), wherein the youngest typically grow more slowly than their senior nest mates and consequently are more likely to die as nestlings (see reviews in Lack 1954, 1968; Howe 1978; O'Connor 1978; Hahn 1981; Mock 1984a, 1985). These deaths may be due to starvation or to physical abuse inflicted by siblings (reviews in O'Connor 1978, Stinson 1979, Mock 1984a).

As in other asynchronously hatching species, the youngest members of a Cattle Egret (*Bubulcus ibis*) brood typically grow more slowly than their nest mates and are more likely to die as nestlings (Blaker 1969, Siegfried 1972, Fujioka 1984, D. F. Werschkul unpubl. data). Although starvation appears to be the primary cause of death (Siegfried 1972), fights among siblings can result in mortality (Skead 1966; Blaker 1969; Siegfried 1972; Fujioka 1985a, b; Werschkul unpubl. data). The consequences of sibling fights may be direct (the victim dies from injuries) or indirect (the victim becomes too intimidated to feed). The indirect effects of sibling aggression on Cattle Egret nestling growth and mortality

patterns remain unclear. We attempted to estimate the advantages and disadvantages of aggression among Cattle Egret siblings.

By creating asynchronous hatching, parents may facilitate adaptive brood reduction and thereby maximize their own reproductive output in the face of unpredictable food supplies (Lack 1947, 1954). If death of the youngest nestling enhances the survival chances of remaining brood members during food shortages, then the creation of competitive asymmetries among siblings can help maximize parental reproductive success. When food is abundant, all chicks are likely to survive, but if food is limited, the last-hatched siblings can be dispatched efficiently by nest mates. Parents thus may benefit because their surviving offspring gain food that might have gone to the doomed sibs.

In many avian species, sibling aggression is not required for brood reduction, size and age differences being sufficient to enforce the starvation of the smallest sibs (Lack 1954, 1968; Howe 1978; Werschkul 1979; Ryden and Bengtsson 1980; Hahn 1981; Mock 1984a; Inoue 1985). Theoretically, chicks that rely on non-aggressive brood reduction could avoid the costs of time and energy associated with fighting (Hamilton 1964, Hahn 1981). Therefore, for fighting to be advantageous, victors must accrue compensatory benefits, such as enhanced access to limited food. Mock (1984b, 1985) proposed that when food is delivered in monop-

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olizably small units, selection can favor assault on junior sibs by senior nest mates.

Sibling aggression appears to be widespread among ardeids (see examples in Blaker 1969, Milstein et al. 1970, Werschkul 1979, Fujioka 1985b, Mock 1985), but little is known about its effects on the distribution of limited food. Detailed demonstrations of the advantages of nestling aggression have been presented only for Great Egrets (*Casmerodius albus*; Mock 1985) and for a Japanese population of Cattle Egrets (Fujioka 1984, 1985b). Great Egret senior nest mates obtain significantly larger shares of food than younger siblings by (1) gaining more frequent access to the food source (parent's bill), (2) obtaining larger bolus portions, and (3) monopolizing more boluses. Elder Great Egret chicks also intimidate junior sibs and cause them to miss many food offerings.

We studied intrabrood competition in Cattle Egrets. Our work parallels Fujioka's (1985b) descriptive study, which was complicated by variable brood sizes and small sample sizes. We used a single brood size, which allowed more robust statistical treatments. We provide new information on how aggression affects the relative feeding success among sibs by investigating the effects of aggression on the frequency of failed feeding attempts and the estimated amounts of food consumed by each chick.

We propose the hypothesis that fighting is most intense between the two youngest sibs. This idea is based on the two fundamental attributes of brood reduction in asynchronously hatching birds. First, mortality falls disproportionately on the last-hatched individual, and second, following initial brood reduction, mortality risks drop for the remaining individuals (both points well documented for Cattle Egrets by Blaker 1969, Siegfried 1972, Fujioka 1984, Werschkul unpubl. data; also shown in related species by Werschkul 1979, Mock and Parker 1986). Furthermore, occasional "dominance reversals," in which one of the senior sibs comes to occupy the lowest social position in the linear intrabrood hierarchy, have been observed in other ardeids (Mock unpubl. data). Because the penultimate chick may be most vulnerable to such potentially fatal reversals, it might be expected to invest extra effort in reinforcing its supremacy. Therefore, we predicted that a disproportionate amount of fighting would involve the two youngest sibs. We also predicted

that if survival depends on avoiding the most subordinate position, then fights between the penultimate and last-hatched chicks should be more intense (longer, involving more blows) than those of the other two dyads.

#### METHODS

We studied natural 3-chick broods of Cattle Egrets on a Lavaca Bay dredge island (Calhoun Co., Texas; 28°39'N, 96°34'W) from May to July 1982. Newly hatched nestlings were marked on their heads with feather dye coded to hatch order: yellow (picric acid) on the first-hatched sib (hereafter, the *a*-chick), blackish brown (nyanzol-D) on the middle sib (the *b*-chick), and no marks on the last-hatched sib (*c*-chick). The dye marks did not appear to affect dominance rank among nestling Cattle Egrets (Mock and Ploger in press). The *a*- and *b*-chicks are referred to collectively as "senior siblings."

Detailed observations were made from two blinds within 10 m of observation nests. Activities of 7 broods were recorded on alternate days from the completion of hatching until all chicks had reached the age of at least 25 days. Only half the observation nests were watched each day (Ploger 1985), but the "off-watch" half were checked visually from the blind every hour on the hour for signs of imminent fatalities (such as intense harassment of the *c*-chick). Detailed behavioral observations were terminated when one or more brood members died or disappeared, but we continued to monitor the fates of surviving brood members.

Records were kept of all feeds and sibling fights. A "fight" by definition began with the first pecking blow and ended when (1) one sib conceded by crouching or fleeing; (2) combatants ceased exchanging blows for 10 s or more; or (3) the struggle was interrupted by parental activities (e.g. feeding). A chick was considered to have conceded if it (1) left the nest; (2) hung its head over the nest rim; (3) moved to the nest rim; (4) fled but remained in the nest; (5) crouched on the nest floor; (6) averted its head; or (7) failed to retaliate after being struck. Fights without a concession were scored as ties. Fighting rates were expressed as the number of fights per day. Blows were either simple pecks or forcible striking of a bill-grasped head against the nest structure. Fight duration was assessed by the number of blows per fight.

"Feeds" began with the regurgitation of the first bolus and ended when the parent failed to deliver boluses for at least 10 min. We counted the number of boluses delivered during each feed and estimated bolus sizes by comparing each bolus with known dimensions of the adult's skull (Mock 1985). In addition, a scale drawing of various-size boluses beside an adult's head was used to standardize bolus size estimates. These were later converted to cubic cen-

timeters based on the volume of water displaced by clay bolus models.

We estimated actual food amounts as well as bolus counts because these two variables can differ. Boluses varied in size and seldom were shared equally among sibs. Chick feeding success was assessed by total amounts ingested.

The proportions of each bolus ingested by each sibling were estimated to the nearest 10%. A chick that gained an entire bolus was considered to have "monopolized" the bolus. We coded as "zero shares" (nothing ingested) cases where a chick (1) tried and failed to feed on a given bolus, (2) was absent from the nest, (3) appeared disinterested in the food, or (4) had recently been beaten by a sib until totally passive during a bolus presentation ("intimidated"; *sensu* Mock 1985). If a chick with food packed in its neck sat passively during a bolus presentation, the chick was coded as temporarily satiated.

When attempting to intercept boluses straight from the parent ("direct" feeding; Mock 1984b, 1985), chicks grasped the parent's mandibles with a scissoring grip, but often failed to elicit a bolus. The total number of scissorings performed by each chick during a feed provides a measure of a chick's level of solicitation during feeds and also relates to the chick's access to food. A scissoring chick by definition held the "pole" position if it grasped the topmost position on the parent's mandibles at the moment of bolus delivery. We recorded the number of scissors and poles held per feed, and the "pole-shares" (estimated bolus percentages obtained by the pole-holding chick).

To assess causes of natural mortality, we censused 40 3-chick egret nests (including the 7 observation broods) during brief (5-10 s) visits every second night. Injured and freshly dead chicks were examined quickly for the extent and type of external damages. To minimize the risk that highly mobile chicks would flee the nest and become lost (e.g. see Blaker 1969, Siegfried 1972, Fujioka 1984), all censuses after chicks reached 1 week of age were conducted well after dark (2200-0100). Chicks that were approached by flashlight nearly always remained in their nests and could be identified without handling. When handling was necessary (e.g. to renew dye marks after 2 weeks), the target brood and other broods in the vicinity were covered temporarily with nest cloths (Thomas 1977).

The causes of chick mortality were categorized as "brood reduction" or "other." As used here, brood reduction refers only to cases where the first mortality in a nest affected only one individual. In a few cases where causes of brood reduction could be determined in detail, brood reduction was further divided into categories of nonaggressive starvation or siblicide. Predation and all other deaths were categorized as "other." In the observation nests, we could exclude from the brood-reduction category cases of partial brood loss that probably were due to predation

by Black-crowned Night-Herons (*Nycticorax nycticorax*). Many successful night-heron attacks in this colony were witnessed from blinds. We assumed that a disappearance between sunset and dawn of a single, healthy (nonemaciated) individual from an observation nest was due to such predation.

We determined chick survival to age 25 days, 5-10 days before fledging (Blaker 1969). Independence from at least partial parental support probably does not occur for some weeks after fledging. Brood reduction appears to be concentrated in the first month (Blaker 1969, Siegfried 1972).

Because the fates of some nestlings could not be determined, we analyzed brood fates twice, once for all fates (including all broods) and once for known fates (i.e. only those broods for which fates of all chicks were deduced). Similarly, chick fates were analyzed separately for known-fate and all-fate categories (this category might include chicks with unknown fates). In the known-fate category, the sizes of the brood- and chick-fate samples appear to disagree because inclusion of chicks in these samples is based on different criteria; although 58 chick fates were known and thus included in the chick-fate sample, only 15 broods were included in the brood-fate sample, for which all sibs' fates had to be known.

Statistical analyses were performed using SAS (1982 version) on an IBM 3081 computer. Details of the analyses performed, criteria for inclusion of data, and explanations for minor variations in sample sizes can be found in Ploger (1985).

## RESULTS

*Hatching intervals.*—Cattle Egret siblings typically hatched on different days, with similar hatch intervals between *a-b*-chicks and *b-c*-chicks (Table 1;  $t = 0.79$ ,  $df = 66$ , not significant; census  $n = 34$  nests).

*Nestling aggression.*—Nestling Cattle Egrets fought frequently and quickly established stable linear dominance hierarchies according to hatch order. *C*-chicks lost 15 times more fights than *b*-chicks and 25 times more fights than *a*-chicks (181 *c*-chick losses, 28 *b* losses, 7 *a* losses; goodness-of-fit test,  $G = 248.2$ ,  $df = 2$ ,  $P < 0.001$ ).

Despite considerable variability among nests, the mean fights per day differed among individual pairs of combatants (fight dyads; Table 2;  $F_{2,117} = 7.76$  based on log-transformed data,  $P < 0.001$ ), with *b-c* dyads fighting most often (Tukey-Kramer pairwise comparisons,  $P < 0.05$ ,  $df = 117$ ). *B-c* fights involved the fewest blows, but differences among dyads were not signifi-

TABLE 1. Frequency distribution of hatching intervals in 3-chick Cattle Egret broods. Data were drawn from census and observation (focal) broods in which the hatch intervals between all 3 chicks were known.

Inter-val (days)	Frequency					
	a-b-chicks			b-c-chicks		
	Total <sup>a</sup>	Cen-sus <sup>b</sup>	Focal	Total	Cen-sus	Focal
0	7	1	0	3	1	0
1	54	14	2	26	7	2
2	59	15	3	75	20	2
3	9	3	0	23	6	2
4	2	0	0	3	0	0
5	0	0	0	1	0	0
6	2	1	1	1	0	0
7	0	0	0	0	0	0
8	0	0	0	1	0	0
$\bar{x}$	1.6	1.7	2.3	2.1	1.9	2.0
SD	0.9	1.0	1.9	1.0	0.7	0.9
n	133	34	6	133	34	6

<sup>a</sup> Data include all census and focal broods, plus 99 broods censused for clutch sizes but not followed for fates sample.

<sup>b</sup> Includes observation (focal) broods.

cant (Table 2;  $F_{2,205} = 2.86$ ,  $0.05 < P < 0.06$ ; analysis based on log-transformed data).

Fighting rates were not obviously related to food supply. The daily fights per brood were not related linearly to the daily volume (in cubic centimeters) of food brought to the brood ( $R^2 = 0.0008$ ,  $n = 38$  nest-days). Fighting rates and amounts of food delivered to nests per day did not increase linearly with *c*-chick age ( $R^2 = 0.021$ ,  $n = 46$  nest-days and  $R^2 = 0.08$ ,  $n = 39$  nest-days for regressions of *c*-chick age on fights/day and food/day, respectively).

*Feeding activities.*—During the first few days after hatching, parents delivered food to their young by regurgitating boluses onto the nest floor, from which chicks pecked small pieces ("indirect feedings"; *sensu* Mock 1985). By the age of 2–4 days, the nestlings began to intercept boluses before their deposition on the nest floor. This was done by grasping the parent's mandibles in a scissor grip and catching the food as it fell from the adult's bill ("direct feeds"; *sensu* Mock 1985; Fujioka 1985b, Inoue 1985). The transition from indirect to direct feeds (the period when the proportion of direct boluses rises from 20% to 80%; see Mock 1985: fig. 3) occurred between the *c*-chick's second

TABLE 2. Dominance hierarchies, fighting rates, and blows per fight for 7 Cattle Egret broods.

	a vs. b	b vs. c	a vs. c
Elder wins <sup>a</sup>	79%	100%	99%
Fights per day <sup>b,c</sup>			
Mean	0.5	1.4	0.4
Upper 95% C.I.	0.7	2.2	0.7
Lower 95% C.I.	0.2	0.8	0.2
Blows per fight <sup>c</sup>			
Mean	2.2	1.6	2.3
Upper 95% C.I.	2.9	1.8	2.9
Lower 95% C.I.	1.8	1.5	1.8
No. of fights	38	137	46

<sup>a</sup> Ties ( $n = 5$ ) were excluded in calculations of percentage of victories, but contributed to the other two categories.

<sup>b</sup> Fights per day were based on 138 observations (46 nest-days per dyad).

<sup>c</sup> Upper and lower 95% confidence intervals (95% C.I.) and means of fights per day and blows per fight were back transformed after log transformation.

and eighth day. Thus, while *c*-chicks still had to get their food indirectly, much of the food was being intercepted directly by elder sibs.

Scissoring rates differed significantly among the chick ranks (Table 3;  $F_{2,78} = 5.62$ ,  $P < 0.01$ ). *A*-chicks scissored more often than did *c*-chicks (Tukey-Kramer pairwise comparisons,  $P < 0.05$ ,  $df = 78$ ; other two comparisons not significant).

The chick holding the pole position on the parent's bill obtained the most food, on average. The mean pole-share was 90%. Although seniors scissored more, they did not hold the pole position more often than *c*-chicks (Table 3;  $F_{2,123} = 0.45$ , not significant). However, *a*-chicks scissored more effectively. Consequently, when holding the pole position, they obtained significantly larger portions of boluses than did *c*-chicks (Table 3;  $F_{2,220} = 3.81$ ,  $P < 0.05$ ; pairwise comparisons,  $P < 0.05$ ,  $df = 10$ ). Other pairs did not differ significantly.

Parents fed broods an average of 5.2 boluses ( $\pm 2.4$  SD,  $n = 85$  feeds) in each of the 3.0 feeds ( $\pm 1.3$  SD,  $n = 47$  nest-days) delivered per day. Bolus volume averaged 6.7 cm<sup>3</sup> ( $\pm 2.8$  SD,  $n = 320$  boluses).

Boluses were not shared equally among sibs. Throughout the first month, the amounts of food consumed by chicks per feed and per day differed significantly among sibling ranks (Table 4;  $F_{2,237} = 14.97$ ,  $P < 0.001$  and  $F_{2,99} = 10.28$ ,

TABLE 3. Incidences of scissoring. Data are based on boluses delivered to 6 Cattle Egret nests. Values are means  $\pm$  1 SD.

Sib-ling rank	Scissors per feed <sup>a</sup>	Poles held per feed <sup>b</sup>	Pole-shares per feed <sup>c</sup>
<i>a</i>	4.4 $\pm$ 3.7	1.8 $\pm$ 0.8	96.8 $\pm$ 14.0%
<i>b</i>	3.8 $\pm$ 2.6	1.8 $\pm$ 1.0	92.5 $\pm$ 20.2%
<i>c</i>	2.2 $\pm$ 1.6	1.6 $\pm$ 1.1	80.9 $\pm$ 34.0%

<sup>a</sup> Scissors are based on 96 observations (32 feeds/sib rank).

<sup>b</sup> Poles held are based on 141 observations (53 *a*-chick poles, 58 *b* poles, 30 *c* poles).

<sup>c</sup> Pole-shares are based on 238 observations (92 boluses delivered when *a*-chicks held the pole, 100 boluses for *b*-chicks, 46 boluses for *c*-chicks).

$P < 0.001$ , respectively). *A*- and *b*-chicks obtained an average of more than twice as much food, both per feed and per day, than did *c*-chicks (pairwise comparisons,  $P < 0.05$ ,  $df = 12$ ).

Chicks were often unsuccessful during attempts to feed, frequently because a sibling controlled access to the food by monopolizing entire boluses. Bolus monopolization differed significantly among sib ranks (Table 4;  $F_{2,282} = 23.28$ ,  $P < 0.001$ ). Senior siblings were more likely than *c*-chicks to obtain entire boluses (pairwise comparisons,  $P < 0.05$ ,  $df = 12$ ), but monopolization rates did not differ between *a*- and *b*-chicks. Sibling rank significantly affected the frequency of receiving no food (zero shares) from boluses (Table 4;  $F_{2,282} = 17.99$ ,  $P < 0.001$ ). In pairwise comparisons, *c*-chicks got zero shares during significantly more bolus deliveries than did *a*- and *b*-chicks ( $P < 0.05$ ,  $df = 12$ ). Again, differences between *a*- and *b*-chicks were nonsignificant.

Occasionally, repeated beatings intimidated a sib completely (see Mock 1985). Such intimidations differed significantly among sibling ranks (Table 4;  $F_{2,282} = 3.69$ ,  $P < 0.05$ ). *C*-chicks were intimidated significantly more often than *b*-chicks (pairwise comparisons,  $P < 0.05$ ,  $df = 12$ ), but intimidation rates between the other two sibling-rank pairs were similar.

Temporary satiation also differed significantly among chick ranks (Table 4;  $F_{2,282} = 6.82$ ,  $P < 0.01$ ). *A*-chicks were satiated significantly more often than were *c*-chicks (Table 4;  $P < 0.05$ ,  $df = 282$ ; other pairwise comparisons not significant).

**Mortality.**—The fates of all chicks were known in 15 broods. These broods produced an average of 1.4 survivors: 33% of the broods were totally successful, 20% were partially successful (1 or 2 chicks survived), and 47% failed completely. Twenty-seven percent of the known-fate broods had at least one brood reduction (20% of 40 broods in the all-fate sample). Of 58 chicks with known fates, 45% survived, 14% died during brood reductions, and 41% died of other causes.

Five *c*-chicks, 3 *a*-chicks, and no *b*-chicks were brood-reduction victims. The first brood reduction took place an average of 9.8 days after the *c*-chick hatched ( $n = 8$  brood-reduction victims). Of these brood reductions, causes of death were determined in detail for two broods that were observed directly. In one of these broods, the *c*-chick starved; in the other, the *c*-chick was a siblicide victim. Deaths from causes other than brood reduction did not differ in frequency by chick rank (Table 5;  $G = 0.58$  for known fates,  $G = 0.31$  for all fates; both tests not significant with  $df = 2$ ). Similarly, the overall probability of the *c*-chick surviving the study period was not significantly lower than that of seniors (Table 5;  $G = 1.82$  for known fates,  $G = 0.70$  for all fates; both tests not significant with  $df = 2$ ).

## DISCUSSION

Aggression among Cattle Egret nest mates plays an important, but circuitous, role in the brood-reduction process. Last-hatched chicks fight more, lose more, control the parent's bill less effectively, and eat less than senior siblings. They grow more slowly and are victims of brood reduction more often than elder nest mates (Fujioka 1984, Werschkul unpubl. data). Although complete intimidations were rarely observed in our study, they involved *c*-chicks disproportionately. More commonly, fights during feeds caused victims to hesitate momentarily at the critical moment of bolus delivery ("partial intimidations"; *sensu* Mock 1985). Thus, defeats of *c*-chicks apparently contributed to their being deprived of food. Senior sibs may have scissored more often in part because of such *c*-chick hesitation. Although all chicks held the pole position with similar frequency, seniors were more effective at it, monopolizing boluses more frequently and thus

TABLE 4. Comparisons of nestlings' abilities to control food. Means for food-control events per feed are based on 101 feeds per sibling rank, food amounts per feed are based on 86 feeds per sibling rank, and food amounts per day are based on 40 nest-days per sibling rank. Values are means  $\pm$  1 SD.

	Sibling rank		
	<i>a</i>	<i>b</i>	<i>c</i>
Events per feed			
Monopolizations	1.5 $\pm$ 1.2	1.5 $\pm$ 1.2	0.6 $\pm$ 0.8
Satiations	0.5 $\pm$ 0.8	0.3 $\pm$ 0.8	0.1 $\pm$ 0.4
Zero shares	1.9 $\pm$ 1.5	1.4 $\pm$ 0.9	3.2 $\pm$ 2.1
Intimidations <sup>a</sup>	0.1 $\pm$ 0.6	0.0 $\pm$ 0.0	0.2 $\pm$ 0.7
Food amounts (cm <sup>3</sup> )			
Per feed	9.7 $\pm$ 8.8	8.9 $\pm$ 7.5	4.3 $\pm$ 5.1
Per day	21.0 $\pm$ 16.7	19.1 $\pm$ 14.6	9.2 $\pm$ 8.0

<sup>a</sup> "Complete" intimidations, *sensu* Mock 1985.

gaining more food. That *c*-chicks held pole positions as often as did seniors probably is because *c*-chicks seemed to hold the pole position during delivery of the final boluses of each feed, when seniors often were satiated. Similarly, in a Japanese colony of Cattle Egrets, first boluses usually were secured by senior nest mates, but all chicks were equally likely to obtain final boluses (Fujioka 1985b). The ability of seniors to gain priority access to food means last-hatched chicks may go without food if the number of boluses delivered is insufficient (see Inoue 1985 for Little Egrets, *Egretta garzetta*, and Mock 1985 for Great Egrets). We found that sibling competition led an average senior to gain twice as much food as the *c*-chick.

Sibling competition created and maintained feeding disadvantages for *c*-chicks and feeding advantages for senior sibs; feeding advantages accrued to *a*- and *b*-chicks equally, rather than to *a*-chicks disproportionately. Fujioka (1985b) showed a similar pattern across a variety of Cattle Egret brood sizes, as did Mock (1985) for Great Egrets. Senior sibs thus may achieve equivalent, high growth rates, sufficient for postfledging survival, by causing retarded growth of their last-hatched nest mate. Such last-hatch disadvantages may be common among asynchronously hatching species, where last-hatched chicks often exhibit markedly slower growth than their senior nest mates (Langham 1972, LeCroy and LeCroy 1974, Parsons 1975, Fujioka 1984, Inoue 1985, Mock 1985).

Growth retardation could increase the postfledging mortality of *c*-chicks. Starvation of *c*-chicks may contribute disproportionately to deaths in the first few months postfledging,

when mortality is greater than at any other time in adult life (Siegfried 1970). Because hunting skills in Cattle Egrets probably improve with age (as in other ardeids; Recher and Recher 1969, Quinney and Smith 1980), fledglings probably face periods of food shortage caused by their less efficient foraging. Chicks with low reserves may be unable to survive such shortages.

Both parents and senior sibs may benefit from concentrating the competitive handicaps on a single nestling (O'Connor 1978). Cattle Egret parents almost never interfered with fights and made no obvious attempts to feed *c*-chicks preferentially. Rather than discouraging harassment of last-hatched offspring overtly, parents may influence *c*-chick prospects only through the initial hatch asynchrony; the resulting competitive disparities presumably enhance parental fitness by facilitating brood reduction when food is limiting (O'Connor 1978).

Assuming *b*-chicks face greater risks than *a*-chicks of becoming victims of dominance reversal, we predicted fighting would occur most intensely between *b*- and *c*-chicks. In this study, fighting rates differed significantly among sib dyads, with *b-c* dyads fighting most often. Data from Great Egret sibs suggest a similar pattern (Mock 1985). In our 7 nests, however, we observed no *b-c* dominance reversals, as have been seen in other Ardeidae (Mock unpubl. data).

The number of blows per fight did not differ significantly among sib dyads, although *b-c* dyads tended to deliver the fewest blows, a trend opposite to that predicted. This could result if the *c*-chick's situation is not yet desperate. If last-hatched chicks have a good chance of

TABLE 5. Fate summaries for 3-chick broods of Cattle Egrets censused in a Texas colony. Results are presented separately for chicks of all fates (including chicks with unknown fates) and for chicks with known fates only. Values are means  $\pm$  1 SD.

	All fates			Known fates		
	<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>
Total no. of chicks	40	40	40	20	17	21
Percentage of unknown fates	50%	58%	48%	—	—	—
Percentage of chicks surviving	25%	22%	18%	50%	53%	33%
Percentage of chicks dying from:						
Brood reductions	8%	0%	13%	15%	0%	24%
Other causes	18%	20%	23%	35%	47%	43%

obtaining uncontested food (e.g. when seniors are satiated), the best tactic may be to concede fights quickly, thereby reducing the risk of injury (Mock and Parker 1986).

The variability in fighting rates and blows per fight observed among nests (see Ploger 1985) could be due to differences in hatching intervals. Theoretically, small hatch intervals would promote fighting among food-stressed siblings because competitors are more evenly matched (Maynard Smith and Parker 1976). Experimental manipulations of hatch intervals based on larger sample sizes have demonstrated that reduction of hatching intervals enhances fighting among nestling Cattle Egrets (Fujioka 1985a, Mock and Ploger in press).

Food limitation is usually considered the ultimate cause of both avian brood reduction (Lack 1968) and sibling aggression (O'Connor 1978, Stinson 1979, Mock 1984a). Many workers have also assumed that food shortages and consequent chick hunger also act as proximate cues eliciting sibling aggression (Skutch 1967, Procter 1975, Brown et al. 1977, Gargett 1977, Stinson 1980, Braun 1981, Braun and Hunt 1983). A few studies have suggested that fighting increases with reduced food (Procter 1975; Stinson 1980; Poole 1982; Braun and Hunt 1983; H. Drummond, E. Gonzalez, and J. Osorno unpubl. data). Although Cattle Egret fighting rates in this study did not correlate inversely with food, differences in food supplies between nests may have been too small to create detectable changes in fighting rates.

Prey size also may act as a proximate cue for nestling aggression (Mock 1984b, 1985). The prey-size hypothesis predicts sibling aggression where nestlings are fed on a diet of small food that they can monopolize. Cattle Egret aggression is consistent with this hypothesis:

the study broods were fed mainly on Orthoptera (with a few small vertebrates) packed in discrete boluses readily monopolized by scissor feeding.

Although overall mortality was high, brood reduction was rare in this study. The behavioral disadvantages of *c*-chicks did not lead clearly to *c*-chick biased mortality in this sample. Strongly *c*-chick biased mortality may be common in Africa, however: Blaker (1969) reported that for 12 brood reductions in 3-chick nests, 11 were *c*-chicks and only 1 was a senior sibling; similarly, Siegfried (1972) found that 85% of 32 partial brood failures involved *c*-chick deaths. Although brood reduction is common in many Cattle Egret populations (e.g. Skead 1966, Blaker 1969, Siegfried 1972, Werschkul unpubl. data), it is not common in all areas or seasons (Jenni 1969, Fujioka 1984, this study). Competitive asymmetries may facilitate brood reduction only when food is sharply limiting or predation is not sufficiently common to reduce the need for sibling competition and consequent mortality. The unbiased chick survival observed in our study may have resulted because either food was sufficiently abundant for *c*-chicks to survive despite frequent beatings (Mock 1985), or the causes of mortality independent of brood size (especially predation) occurred frequently before starvation thresholds were reached. Our data support the latter alternative more than the former.

The single siblicide case took a form not described previously for this species. After being deprived of food and beaten repeatedly by its siblings during its last three days in the nest, the victim entered a neighboring nest, where it may have been attempting to steal food (as was observed in numerous unmarked chicks). The chick was also evicted from that nest, how-

ever, and vanished shortly thereafter. Once evicted, the survival chances of a wandering chick are probably quite low (Mock 1984a). Unmarked chicks that we observed scavenging underneath nests and kleptoparasitizing observation broods typically appeared to be starving and dying of exposure. They were frequently attacked by adults and stalked by Black-crowned Night-Herons. However, scavenging and kleptoparasitism sometimes may enable wandering Cattle Egret chicks to survive, as do wanderers of other bird species (Mock 1984b, Pierotti unpubl. data). Because wandering Cattle Egret chicks frequently bore the bloody marks of sibling persecution, we speculate that these chicks were evicted subordinates. Survival of such wanderers could reduce the fitness costs to parents and sibs of evicting a subordinate chick.

We believe aggression among Cattle Egret nestlings helps seniors skew parental investment (here, food) toward senior sibs at the expense of the last-hatched sib. Because food may be insufficient for all sibs to thrive, the improved access to food gained by seniors through fighting may have lethal consequences for the last-hatched sib. We found that the penultimate chick was involved in a disproportionate share of the attacks on the youngest, which may be a tactic for the penultimate chick to ensure its own survival.

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