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EGG SIZE AND THE EGG PREDATORY BEHAVIOUR OF CROWS

by

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(With 2 Figures)
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INTRODUCTION

A number of studies have demonstrated the protective advantages of the cryptic colouration and marking patterns of prey items subjected to crow predation (TURNER, 1961; TINBERGEN *et al.*, 1962; CROZE, 1970). TINBERGEN, IMPEKOVEN & FRANCK (1967), CROZE (1970), and GÖRANSSON *et al.* (1975) have further shown that the spatial distribution of cryptic influences corvid predation success.

Observations made during previous experiments on eggshell camouflage and egg predation by crows (MONTEVECCHI, 1976) suggested that egg size may influence the manner in which crows prey on eggs. The present experiments systematically investigated the predatory patterns of corvids and the effects of prey (egg) size on their behaviour and predation success.

1. *CORVUS BRACHYRHYNCHOS* PREDATION ON LARGE, MEDIUM AND SMALL EGGS

Previous observations suggested that crows would fly off with eggs whenever they could easily pick them up in their mandibles. The crows usually flew with the eggs from the site of predation to a location fifteen to one thousand meters distant where the eggs were usually hidden under grass or sometimes eaten. This method of predation has frequently been

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observed in the Laughing Gull *Larus atricilla* colony in the salt marsh of the Brigantine National Wildlife Refuge (New Jersey). Corvids have often been reported to fly off with prey and cache them at a distance (TINBERGEN, 1953; TINBERGEN *et al.*, 1962; KRUUK, 1964; TINBERGEN, IMPEKOVEN & FRANCK, 1967; CROZE, 1970; GÖRANSSON *et al.*, 1975).

The present experiment investigated the vulnerability of different sized eggs subjected to intense *brachyrhynchos* predation, and the influences of these different sized eggs on the predation behavior of the crows.

METHOD AND PROCEDURE

During February, March, April and May, 1974, batches of eggs containing equal numbers of large white domestic fowl eggs (L), small white domestic fowl eggs (M), and white painted Japanese Quail *Coturnix coturnix japonica* (S) were set out in a meadow in South Mountain Reservation, South Orange, New Jersey. The approximate dimensions of the eggs were: mean length ± S.E. × mean breath ± S.E. of the L eggs = 60.8 ± 0.5 × 43.2 ± 0.3 mm, M eggs = 53.2 ± 0.5 × 39.0 + 0.5 mm, S eggs = 31.0 ± 0.7 × 24.0 ± 0.2 mm, (based on measurements of 8 eggs from each size group, see Fig. 1). The eggs were set out conspicuously on the tops of grass tufts and were spaced about 10 meters apart in meandering lines of repeating sequence (L-M-S-L-M-S, *etc.*). The behaviour of crows in the meadow was either observed with binoculars from a position about 400 meters distant or egg fates were checked 4 to 8 hours after setting. At least 2 Common Crows came regularly to prey on eggs. Records were kept of whether eggs were a) preyed or not, b) eaten at the egg site, c) eaten within 6 meters of the egg site, or d) removed (not found within a 6 meter diameter circular area around the egg site).

The white eggs contrasted sharply with the black beaks and heads of the crows (Fig. 2), and it was usually easy to judge with certainty the egg type which the crows manipulated or carried. The ways in which the crows preyed on (flew off with, cached, *etc.*) and the number of times they dropped the different sized egg were recorded. Distances which the crows flew with the eggs from the egg site were estimated.

RESULTS

Table 1 summarizes the results. Ninety-four percent (222/236) of the eggs were preyed on. Sixteen percent (36/222) of the eggs which were preyed on were eaten at the egg site, while seventy-four percent (164/222) were removed more than 6 meters from the egg site. All of the observed predations (39 eggs) in which the eggs were removed more than 6 meters involved the crows flying off with the eggs. Ten instances were observed during which a crow walked off with an egg, but none walked more than 6 meters before pecking open or caching an egg.

There was no differential predation among the different sized eggs: 96% (75/78) of the L eggs were preyed on, 94% (74/79) of the M eggs, and 92% (73/79) of the S eggs. Proportionately more of the M and L eggs were pecked open at the egg site than S eggs ($X^2 = 14.55$, df = 1, $P < .001$). Eighty-eight percent (64/73) of the S eggs which were preyed on were

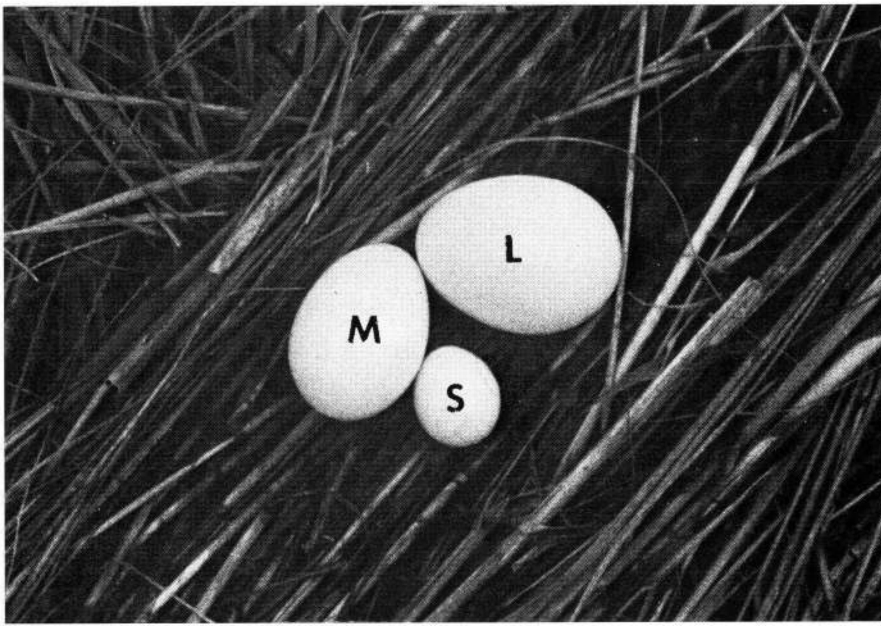
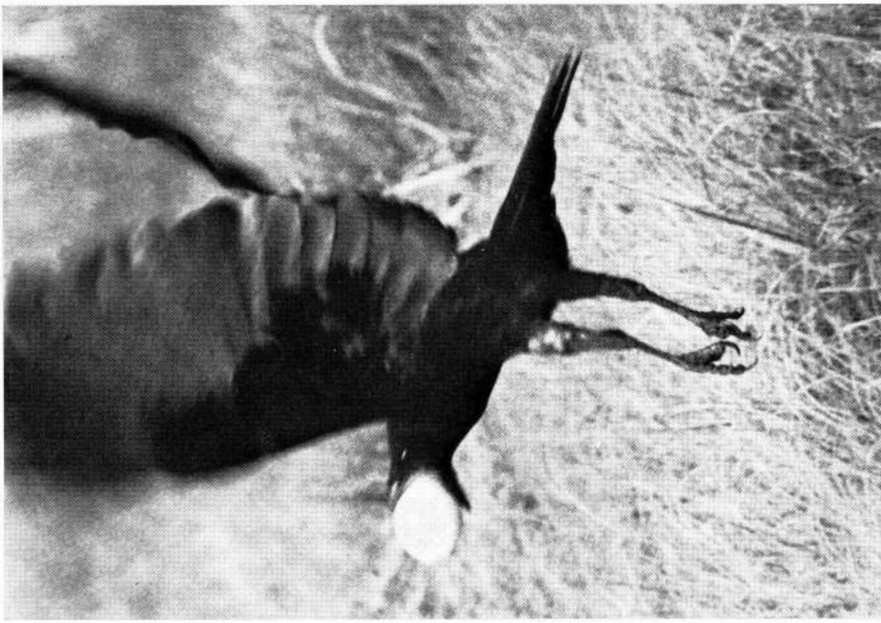


Fig. 1. Small (S), medium (M) and large (L) eggs used in predation tests.

Fig. 2. Crows in flight with eggs: A) small (S) egg, B) medium (M) egg, and C) large (L) egg.



2C

2B

removed more than 6 meters from the egg site, while 70% (52/74) of the M eggs and 64% (48/75) of the L eggs were so removed ($X^2 = 11.48$, df = 2, $P<.01$).

It became evident during the course of testing that the crows became much less hesitant and more efficient in the test situation. During the initial trials crows took at least 2 hours or longer to remove the 18 to 24 eggs from the meadow, while toward the end of testing all eggs were often removed within 20 minutes of setting. During the first three trials 31% (5/16) of the L eggs which were preyed on were removed more than 6 meters, while 74% (26/35) and 71% (17/24) of the L eggs which were preyed on during the fourth through the seventh and during the eighth through the eleventh trials, respectively, were so removed. During the first three field trials 33% (5/15) of the preyed on M eggs were removed more than 6 meters, while 71% (25/35) and 92% (22/24) of the M eggs which were preyed on during the fourth through the seventh and during the eighth through eleventh trials, respectively, were so removed. A significantly greater proportion of M eggs which were preyed on ($X^2 = 12.28$, df = 1, $P<.001$) and of L eggs which were preyed on ($X^2 = 9.38$, df = 1, $P<.01$) were removed in the fourth through eleventh trials than during the first three trials. No significant differences were found in the estimated distances that crows were observed to fly with the different sized eggs.

TABLE 1

Egg fates of the different sized eggs set out for common crows at South Mountain Reservation

Egg Type	Preyed Eggs At Site	Preyed Eggs 6 Meters	Preyed Eggs Removed	Total	Recovered Eggs	Totals
L	19	8	48	75	3	78
M	15	7	52	74	5	79
S	2	7	64	73	6	79
Totals	36	22	164	222	14	236

DISCUSSION

The most common predation method of *brachyrhynchos* involved flying with the egg away from the egg site, caching the egg, then repeating this behavioural sequence until all or most of the eggs were taken (see Discussion of Experiment 3). Although there was no differential predation among the different sized eggs, egg size greatly effected the ways the crows preyed on the eggs. This lack of differential predation probably represents a ceiling effect, since checks were usually made after most or all of the eggs had been preyed on. Crows were more apt to eat the larger eggs at the egg site, while they were more likely to fly off with the smaller eggs. Under natural predatory conditions the social defenses of a gull or tern colony (NOBLE & WURM, 1943; CULLEN, 1960; KRUUK, 1964; BAERENDS, DRENT, GLAS & GROENEWOLD, 1970; RYDEN, 1970; BUCKLEY & BUCKLEY, 1972; LEMMETYINEN, 1971, 1972; MCNICHOL, 1973) would most likely deter crows from eating eggs in the vicinity of nests. In these circumstances the crows would probably exert a pressure against smaller eggs.

The crows carried the small and medium eggs more efficiently (*i.e.*, dropped fewer) than large eggs. After experience (trials) with medium and large eggs the crows flew off with more of them. The birds were not individually marked (identifiable), but this trend of flying off with a greater proportion of the medium and larger eggs over trials seemed to be due at least in part (if not wholly) to a division of labor, *i.e.*, larger crows taking larger eggs, smaller animals taking smaller eggs. Corvid hunting patterns appeared cooperative in many respects (see Discussion Experiment 3).

2. SIMULTANEOUS CHOICE TESTS: PREDATION AT SIMULATED NESTS WITH L-M-S CLUTCHES

The nests of Laughing Gulls in the Brigantine salt marsh are preyed on by both Common Crows and Fish Crows *Corvus ossifragus*. The egg sizes of Laughing Gulls are quite variable both within and among clutches. Third eggs are on the average reliably smaller in length, breadth and volume than earlier laid eggs (PRESTON & PRESTON, 1953; MONTEVECCHI, 1975), and this is a general trend among gulls and terns that lay three egg clutches (*Rissa tridactyla* - COULSON, 1963; *Larus ridibundus* - YTREBERG, 1956; *L. delawarensis* - VERMEER, 1969; *L. canus* - BARTH, 1968; *L. californicus* - BEHLE & GOATES, 1957; VERMEER, 1969; *L. argentatus* - PALUDAN, 1951; HARRIS, 1964; PARSONS, 1970; *L. fuscus* - PALUDAN, 1951; *L. marinus* - HARRIS, 1964; *Sterna hirundo* - NISBET, 1975).

Due to the spacing (rather than clustering) of eggs in the previous experiment individual crows encountered the prey successively in time. There is ample evidence that successive and simultaneous choice procedures test for different behaviour (FRANCK, 1966; HAILMAN, 1967; EVANS, 1970; HINDE, 1970; BEER, 1973). In the present experiment simulated nests containing three different sized eggs were used in an attempt to investigate the behaviour of crows when simultaneously confronted with eggs of different size.

METHODS AND PROCEDURE

During May, 1974, 6 tests, employing 12 simulated nests each containing an L, M and S egg (see Fig. 1) set out around an observation hide, were conducted in a meadow on Little Beach Island (Brigantine Refuge). At least 4 Fish Crows and a pair of Common Crows regularly preyed on these eggs. The dependent measure of primary interest was the order in which the crows preyed on the different sized eggs within a nest. The ways in which the crows preyed on the eggs was also recorded.

RESULTS

Thirty-eight egg predations were observed at full L-M-S nests. The S egg was preyed on first in all 38 cases. The crows always flew off with the S egg and cached (or ate) them at a distance. S eggs were almost always the first eggs mandibulated in the L-M-S clutches. No S eggs were eaten at the nest. The few times crows initially mandibulated an M or L egg in the nest, they did not succeed in picking these up. They would then pick up an S egg and fly off with it first. During predatory sequences in which an individual crow could be continuously observed, they usually flew off with an S egg, cached it under some grass, then returned to the same nest and mandibulated the M or L egg a few times or simply looked into the nest. They would then go to a nearby nest, and if the nest was full, take the S egg, and so on.

In general, *only* S eggs were preyed on during a trial, and more S eggs were always preyed on. During the trials (72 eggs of each size set out) 38 S, 3 M and 5 L eggs were preyed on; 4 of the 5 L eggs and 1 of the M eggs were eaten at the nest site.

A combined analysis of the predation methods used by crows to prey on different sized eggs in this experiment and the next is presented in Experiment 3.

DISCUSSION

The smallest eggs in the simulated nests were the most vulnerable to corvid predation. Observations indicated that this was due to the crows' ability to easily pick up and carry the small eggs (see also Slack, 1975). The crows probably maximized predation efficiency in terms of energetic costs and benefits. Although the within nest variability of the egg sizes of the simulated L-M-S nests is very much greater than that of 3 egg *atricilla* clutches ("runt" eggs and Clapper Rail *Rallus longirostris* about the size of quail eggs have been found in *atricilla* clutches), the present findings support the contention that corvid predators are more likely to prey on the smaller eggs of a nest and thus, exert a differential selection against small eggs.

Crows were extremely cautious in alighting near the observation hide. They would often watch the area from a distance for hours and fly reconnaissance flights over the nests and hide, before a crow would land in the area. When on the ground they often seemed highly agitated and aroused.

Often the crows would startle at their own behaviour (*e.g.*, a step on a dry Spartina stalk, a peck at an egg) and fly off rapidly without an egg. Frequently a crow would alight silently at a nest and quickly (10-15 seconds) pick up the small egg and fly off. The crows seemed aware of my presence in the hide, and this may account for the arousal they showed during the hide tests of this experiment and the next. In this regard these tests in contrast to the meadow tests of Experiment 1 are probably more comparable with other aspects of natural predation in the gull colony.

3. SIMULATED NESTS CONTAINING L, M OR S EGGS

Egg size may affect the vulnerability of eggs among as well within nests, and this influence could act either intraspecifically (as among the different sized eggs of different age classes of females, *e.g.*, NICE, 1937; ROMANOFF & ROMANOFF, 1949; RICHDALE, 1955, 1957; ANDERSEN, 1957; SERVENTY, 1966; RYDER, 1975) or interspecifically (as among Herring Gull *Larus argentatus*, Laughing Gull and Clapper Rail nests in the Brigantine marsh). The mean dimensions (1 × b) of Herring Gull eggs approximately 71 × 50 mm (PALUDAN, 1951), of *atricilla* eggs 53.6 × 38.3 mm (n = 951), of Clapper Rail eggs approximately 43.2 × 30.5 mm (DAVIE, 1889; REED, 1904).

The following experiment investigated the predatory behaviour and success of the crows at nests with L, M *or* S eggs.

METHODS AND PROCEDURE

During June, 1974, simulated nests were set out according to the procedure of Experiment 2. During testing four nests contained 3 S eggs each, 4 other nests — M eggs, and 4 other nests — L eggs. These clutches were rotated among the 12 nest positions from one trial to the next in order to control for position biases (preferences) which the crows exhibited at nests during the proceeding experiment. Crows usually made initial predations at nests nearest bushes and trees (see LEMMETYINEN, 1971).

The data collected included: number of different eggs and nest types preyed on, number of visits and predation attempts (mandibulations) at different nests, and predator success ratios (number of successful predations/number of predation attempts) among different nests. The predatory methods employed with the different sized eggs and the success rates of various sized corvid groups were also recorded. An analysis of the combined predation method data of this and the previous experiments was conducted.

RESULTS

Table 2 shows that most predation occurred at S nests, while L nests were preyed on least. The proportions of the S, M and L nests which were preyed on are significantly different ($X^2 = 7.65$, df = 2, $P < .05$), while the proportions of these nests in which all eggs were preyed on are not ($X^2 = 5.82$, df = 2, ns). Although the crows visited the different nest types equally often, and the predation attempts among the different nests were not significantly different (X^2 = 1.70, df = 2, ns), predator success ratio was greatest at the S nests (X^2 = 15.2, df = 2, P <.001) (see Table 2).

In the simulated nest tests of Experiments 2 and 3, 44% (184/422) of the eggs were preyed on. This breaks down: 62% (89/144) of the S eggs, 24% (34/144) of the M eggs, and 19% (28/144) of the L eggs (X^2 = 65.92, df = 2, P<.001). The crows flew off with 83% (124/148) of the eggs they preyed upon: 84 of 85 (98%) S eggs, 23 of 33 (69%) M eggs and 16 of 26 (61%) L eggs, while 1% (1/85) of the S eggs, 27% (9/33) of the M eggs and 23% (6/26) of the L eggs were eaten at the nest site (X^2 = 21.03, df = 2, P<.001). The combined data on egg size (Experiments 1, 2 and 3) show that the crows flew off with (or removed to more than 6 meters) 94% (148/158) of the S eggs, 70% (75/107) of the M eggs, and 63% (64/101) of the L eggs. Overall 15% (53/366) of the eggs which were preyed on were pecked open at the nest: 2% (3/158) of the S eggs, 22% (24/107) of the M eggs and 26% (26/101) of the L eggs (X^2 = 27.80, df = 2, P<.001).

TABLE 2

Crow predation at S, M and L egg nests

	Egg nest types			
	S	M	L	Totals
Nests set out	24	24	24	72
Nests preyed on	18	11	9	38
Nests — all eggs preyed	15	9	7	31
Crow visits	55	57	57	169
Predation attempts	51	48	39	138
Successful predations	47	31	23	101
Success ratio (successes/attempts)	0.92	0.65	0.59	0.73

Eleven instances (1S, 5M, 5L) were observed during which the crows punctured an egg at the nest, then inserted a mandible in the hole, picked it up, and flew off with it. A significantly greater proportion of M and L eggs were removed in this way than were S eggs (X^2 = 10.52, df = 1, P<.01).

Ninety nest area *landings* by single crows resulted in the successful predadion of 64 eggs, 92 crows landing in pairs (46) obtained 20 eggs, while 59 crows landing in groups of 3 or more obtained 41 eggs. The success ratios are significantly different (X^2 = 54.10, df = 2, P < .001. The proportionate success of individuals in pairs are significantly less than that of singles (X^2 = 42.64, df = 1, P < .001) and groups *per capita* (X^2 = 32.09, df = 1, $P < .01$), while the proportionate successes of singles and groups are not significantly different from one another.

The mean number of nests (of a possible 12 during each of 6 tests) which were preyed on during each L-M-S nest test of Experiment 2 was 6.33 nests, while in the present experiment it was 4.67 nests. The total proportion of nests preyed on in these experiments are significantly different ($X^2 = 5.65$, df = 1, $P < .02$).

DISCUSSION

Egg size differences among nests influenced the vulnerability of these nests to corvid predation. Nests with small eggs were much more vulnerable than those with larger eggs, and the crows were more efficient preying on smaller eggs. It would appear to be easier for a crow to steal a Common Tern *Sterna hirundo* or a Clapper Rail egg than an *atricilla* egg, or easier to steal an *atricilla* egg than a Herring Gull egg or a smaller than a larger *atricilla* egg. Crows appear to prey more heavily on Clapper Rail than *atricilla* eggs in the Brigantine marsh. Crows have frequently been seen rapidly snatching a rail egg of the nest, scarcely alighting on the ground (pers. obs.; H. F. ANDREWS, pers. comm.). Such short latency stealing has also been observed at *atricilla* nests, although crows have also been seen picking up and dropping these larger eggs or eating them at the nest.

The combined analysis of predation methods revealed that the smaller an egg the greater its chances of being carried away from the nest site, and the larger the egg the greater its likelihood of being pecked open and eaten at the nest. Overall the most common method of egg predation involved a crow flying off with an egg and caching it at a distance. In the gull colony the harassment of defending gulls must make it advantageous for avian predators to fly away from the nest site with any prey they obtain. During Experiments 1, 2 and 3 recognizable individuals carried off and cached more eggs than they could have possibly eaten within the same time span. Eight eggs were carried off in rapid succession by a single crow. The opportunistic ability of predators to cache prey in times of plenty (or after the predator is satiated) presents a great potential threat to prey species (TINBERGEN, *et al.*, 1962; KRUUK, 1964, 1972; TINBERGEN, 1965; TINBERGEN, IMPEKOVEN & FRANCK, 1967; CROZE, 1970; SMITH, WILSON & Frost, 1974). California Gull, Herring Gull and Greater Black-backed Gull egg predator specialists also fly with eggs away from the nest (SUGDEN, 1947; TWOMEY, 1948; VERMEER, 1967; BOURGET, 1973), but are more apt to eat them on the spot than are crows.

Crows were often seen puncturing eggs then picking them up by inserting a mandible in the hole and flying off with them. It has previously been reported that Common Crows (GROSS, 1946), Carrion Crows (TINBERGEN, 1953) and Jackdaws *Coleus monedula* (LORENZ, 1931) may remove eggs in this way (see also BOWMAN & CARTER, 1971).

Single crows were not more successful than groups of three or more animals, although pairs were less successful than either singles or groups. The members of pairs hunted silently and often startled one another to flight. Crows in larger groupings were quite loud and raucous in their egg foraging activity, and there were few panic flights away from the nests by birds in these groups. KRUUK (1964) found that larger groups were less efficient than singles or pairs of Carrion Crows preying on baited eggs, the apparent result of greater interindividual interference in larger groupings. Crows usually hunt in pairs and larger groups in the gullery, and this hunting strategy probably confers benefits to individual group members by distributing and distracting the attention of the gulls (see also AXEL, 1956). Chimango Caracaras *Milvago chimango* (BURGER, 1974) and Ruddy Turnstones *Arenaria interpres* (CROSSIN & HUBER, 1970) also employ group hunting strategies.

There is a division of labor and cooperation among individual members of corvid hunting groups. During many of the predations in the study areas one (or more) crow(s) would perch high in a nearby tree, while the other group member(s) foraged at the nests. A "caw" from the perched bird would quickly put the birds on the ground to flight (see BENT, 1946; PRESTON, 1957). On many occasions a pair of crows were seen eating side by side from the same egg, and on one occasion after one member of a pair dropped an egg which it was carrying, the other bird alighted and buried it. It would be interesting to mark individual animals and to document the extent of corvid cooperation, particularly if and how items cached by one individual are utilized by other individuals.

The selection of the small eggs at the L-M-S nests (Experiment 2) resulted in a greater scattering of egg loss than was found when there were egg size differences among but not within nests (Experiment 3). This finding is striking in view of the fact that many more eggs were preyed on in Experiment 3. The ease of carrying small eggs modified the crows' tendency to prey at sites where prey had been obtained previously (*e.g.*, CROZE, 1970).

Common Crows are larger than Fish Crows, and they can open their longer, larger mandibles (BENT, 1946; JOHNSTON, 1961) wider than can *ossifragus*. Despite this interspecific predator size difference both *Corvus* species exerted greater predation pressures on smaller eggs, and this influence can probably be generalized to other corvid predators as well. Taken together the results of Experiments 1, 2 and 3 support the hypothesis that crows exert greater selection against smaller third and "runt" eggs within *Larus* clutches and against smaller eggs among clutches (both intra- and interspecifically).

Herring Gulls are more effective incubating (fewer interruptions) larger than smaller eggs (DRENT, 1973: 293). Smaller Herring Gull eggs are also less successful than larger ones, and since there are no differences in embryonic death and infertility among the various sized eggs, greater predation pressure upon smaller eggs appears responsible for this outcome (PARSONS, 1971b; DRENT, 1973). Increased predator pressure (corvid, larid or other) coupled with the likelihood of less effective incubation and parental behavior among younger, less experienced birds (COULSON, 1966; LEHRMAN & WORTIS, 1960, 1967; LEHRMAN, 1961; WORTIS, 1969; but cf., HANSEN, 1971, 1972; MILLS, 1973) which tend to lay smaller eggs probably contributes to the poorer reproductive success of first year breeding birds. Differential predation pressure against differently sized eggs (both within and among nests) could account for the differential hatching success reported by PARSONS (1971b) for large and small *argentatus* eggs.

There is evidence to indicate that among gulls the third chicks of three chick broods grow more slowly, suffer greater predation and in general survive less well than either of the first two chicks (HARRIS, 1964; PARSONS, 1969, 1971a, pers. comm.; for related findings with terns see LEMMETYINEN, 1972; NISBET & DRURY, 1972; SOIKKELI, 1973). Moreover, if a gull's nest was preyed on, predation of the third (or smallest egg) would result in a minimal reproductive loss. The parental investment in terms of quantity of egg material and incubation time is less for third than for either of the two earlier laid eggs (see TRIVERS, 1972, for a discussion of parental investment; cf. ORIAN & JANZEN, 1974). MABLE (1943) has reported a genetic basis for within clutch variation in egg shape. Taking these factors into account it is conceiveable that the selection of smaller third eggs may have been favored during the evolution of a balanced predator-prey system between corvid (avian) egg predators and ground nesting gull species.

SUMMARY

Patterns of corvid predation on different sized white eggs were studied in a series of field experiments. Different sized eggs were set out singly and in simulated nests containing clutches of same sized and different sized eggs. The eggs were set out in meadows where they were subjected to intense predation by crows.

The most common predation method of the crows was to fly off with eggs and to cache (bury) or eat them at a distance from the site of predation. The larger eggs were more frequently pecked open at the egg site and were less effectively

picked up and carried off by the crows. Apparently as a result of the ease of grasping smaller eggs, these eggs were much more vulnerable to predation than were larger eggs. These results combined with field observations and previous findings indicate that Corvus predators may exert differential pressures on different sized eggs both within and among clutches, intra- or interspecifically. These patterns of crow predation analyzed in terms of the gulls' parental investment among the different eggs within a three egg clutch suggest that smaller third eggs may have been (and continue to be) selected in the evolution of a balanced predator-prey system between crow predators and ground nesting gulls.

Cooperative aspects of corvid group hunting patterns are also discussed.

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ZUSAMMENFASSUNG

Freilandversuche über das Raubverhalten von Krähen wurden durchgeführt mit weissen Eiern von verschiedener Grösse. Die Eier wurden ohne Nester einzeln und in simulierten Nestern in Gelegen von gleich grossen und verschieden grossen Eiern auf einer Wiese ausgelegt, wo sie dem Raub der Krähen ausgesetzt waren.

Die bevorzugte Raubmethode der Krähen war, mit den Eiern wegzufliegen und sie zu verstecken (vergraben), oder aber, sie in einiger Entfernung vom Raubort zu vertilgen. Grössere Eier wurden öftes an Ort und Stelle angepickt, da sie weniger leicht weggetragen werden konnten. Kleinere Eier waren dem Raub vermehrt ausgesetzt, vermutlich deshalb, weil sie leichter aufgepickt und weggetragen werden konnten.

Diese Resultate zusammen mit Feldbeobachtungen und früheren Ergebnissen lassen darauf schliessen, dass Krähen einen unterschiedlichen Selektionsdruck auf verschieden grosse Eier, sowohl innerhalb eines Geleges sowie ganzer Gelege, mit andern Worten, sowohl innerhalb einer Art als zwischen verschiedenen Arten, ausüben. Diese Art des Rauberverhaltens von Krähen lässt, im Hinblick auf den elterlichen Aufward für die verschiedenen Eier innerhalb eines Geleges, vermuten, dass kleinere dritte Eier stammesgeschichtlich gewählt wurden (und weiterhin gewählt werden) in der Evolution eines ausgewogenen Räuber-Beute Systems zwischen Krähen und bodenbrütenden Möwen.

ADDENDUM

Some relevant information bearing on the possible relationship between egg size and predation pressure has recently come to my attention. Dr. R. B. G. BROWN has pointed out to me that consistent with the notion of a greater pressure being exerted against smaller eggs there is among larids a general inverse relationship between body size (egg size) and the intensity of anti-predator behaviour. This trend may represent an adaptive continuum reflecting heightened pressures exerted against smaller eggs by avian predators. RYDER (1975) has recently reported that pairs of immature-plumaged Ring-billed Gulls *Larus delawarensis* had a lower hatching success than pairs in which only one member had immature-plumage, and the latter pairs had a lower hatching success than pairs of mature-plumaged gulls. Predation by Common Crows appeared the most important factor producing hatching failure, and it was shown that younger gull pairs laid smaller eggs (RYDER, 1975). Reproductive inexperience and an enhanced predation pressure on smaller eggs may have interacted to produce the differential reproductive success of the different aged pairs. Professor G. P. BAERENDS has informed me of unpublished data which indicate that Herring Gulls show stronger incubation patterns when sitting on larger eggs.

The intraspecific and intraclutch implications of the hypothesis may be tested in nature (in larid colonies) by measuring and marking eggs and determining their fates. Such data are hard to come by, however, and intraclutch data are confounded by the fact that first (largest) eggs are often the most vulnerable eggs, since egg predation is most intense during the laying period, when incubation behaviour is not yet fully developed.