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FIELD EXPERIMENTS ON THE ADAPTIVE SIGNIFICANCE OF AVIAN EGGSHELL PIGMENTATION

by

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(With 1 Figure)

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The dull colouration and irregular markings (disruptive colouration) of prey species have long been interpreted by naturalists as protective devices evolved in response to selective pressures exerted by visually hunting predators (POULTON, 1890; COTT, 1940; PORTMANN, 1959). Many experimental studies have demonstrated the survival value of the cryptic colouration, marking and behaviour of many prey animals (*e.g.*, SUMNER, 1934; DICE, 1947; DE RUITER, 1952; KETTLEWELL, 1955).

Many investigators have been unsuccessful in their attempts to demonstrate the anti-predator survival value of the pigmentation and marking patterns of the eggs of ground nesting birds. KRUIJT (1958) reported that Herring Gulls robbed simulated nests (outside the gullery) containing clutches of speckled and unspeckled eggs at equivalent rates. Carrion Crows, *Corvus corone,* showed no differential predation among a variety of Lapwing *Vanellus vanellus* egg models which were varied systematically in spotting pattern (DAVIES, 1973). Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls, *Larus fuscus,* induced to forage for Ringed Plover, *Charadrius hiaticula,* egg mimics took significantly more spotted (more cryptic to the

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human eye) than unspotted mimics (DAVIES, 1973). TINBERGEN *et al.* (1962) reported that avian predators showed no differential predation between white domestic hens' eggs and domestic hens' eggs artificially camouflaged to resemble Black-headed Gull, *Larus ridibundus,* eggs nor between white painted *ridibundus* eggs and *ridibundus* eggs which were artificially camouflaged with khaki paint and dark speckling. TINBERGEN *et al.* (1962) did, however, demonstrate the survival value of natural eggshell patterning in comparison with white eggs in the face of avian predation. The present series of experiments were designed to investigate the functions of eggshell pigmentation.

1. EGGSHELL PIGMENTATION AND CROW PREDATORS

During May, June and July of 1972 and 1973 batches of equal numbers of white (W), khaki (K) painted (M. A. Bruder and Sons Paint #689D), khaki painted-randomly spotted (S) domestic hens' eggs and (during June and July, 1972) natural Laughing Gull, *Larus atricilla,* (N) eggs, were set out in meadows on Little Beach Island in the Brigantine National Wildlife Refuge, New Jersey (39°28'N, 74°21'W). At least 4 Fish Crows, *Corvus ossifragus,* and a pair of Common Crows, *C. brachyrhynchos,* visited regularly to forage for the eggs. Eggs were hidden under a few strands of grass and spaced about 10 m apart in meandering lines of repeating sequence (*i.e.,* W-K-S-N-W-K-S-N, etc.). Eggs were usually set out in the morning and checked 2 to 8 hours later. Remaining eggs were collected, and the types of eggs missing and pecked open were recorded.

RESULTS

During the W-K-S tests the crows preyed on 33% (34/102) of the W eggs, 37% (38/102) of the K eggs and 39% (40/102) of the S eggs ($\chi^2 = 0.73$, df = 1, $p > .05$). White (nonpainted) and nonwhite (painted) eggs were not differentially vulnerable ($\chi^2 = 0.66$, df = 1, $P > .05$) nor were spotted and unspotted eggs ($\chi^2 = 0.40$, df = 1, $P > .05$). During the W-K-S-N tests 26% (7/27) of the W eggs, 15% (4/27) of the K eggs, 11% (3/27) of the S eggs and 22% (6/27) of the N eggs were pecked open and eaten or removed by the crows ($\chi^2 = 2.00$, df = 3, $P > .05$). A significantly smaller proportion of eggs were preyed on during W-K-S-N tests than during the W-K-S tests conducted earlier in the season ($\chi^2 = 35.94$, df = 1, $P < .001$).

DISCUSSION

Neither artificial nor natural eggshell camouflage enhanced the survival of eggs subjected to intense crow predation. These results were not expected, since the eggs differed markedly in crypticity to the human eye. A small sample size of natural *atricilla* eggs was used (it was felt inappropriate to remove a large quantity of eggs from the gullery for these tests), and this may partially account for failure to obtain the expected outcome. The crows showed a seasonal decrease in their visits to the gull nesting area (MONTEVECCHI, 1975), and this may account for the lower predation percentage found during the tests involving natural eggs that were run later in the season.

It is possible that white eggs might receive some protective advantage in a salt marsh or other coastal nesting areas. Due to local sea bird feeding activities many areas in the marsh were littered with bleached white molusc shells. American Oystercatchers, *Haematopus palliatus*, and European Oystercatchers, *H. ostralegus*, lay their eggs in shallow nest scrapes just above the reach of the high tides, regions frequently littered with bright, white and shiny shells and shell fragments. Oystercatchers frequently line their nests with "conspicuous" shells and shell fragments (BENT, 1921; HAUSMANN & HAUSMANN, 1972). The effects (functions) of this behaviour (TINBERGEN, 1963, 1973; BEER, 1973b), if any (WILLIAMS, 1966), have not been investigated, but the present expression of the behaviour pattern indicates that predation pressures have not strongly selected against it. The visual search image strategies (CROZE, 1970; MUELLER, 1971; KREBS, 1973; PAULSON, 1973; SLOAN & SIMMONS, 1973) of avian egg and chick predators hunting in coastal seabird nesting regions may exclude bright or white items on the ground. The natural and artificial eggshell "camouflage" studied in the present experiment may have been more representative of the crows' usual egg prey. As a consequence any possible advantages that the "cryptic" eggs might have held over the white eggs could have been effectively eliminated by search image hunting behaviour priorities. DAVIES (1973) and KAUFMAN (1973) have similarly interpreted the enhanced survival of "conspicuous" prey in terms of search image hunting strategies of predators.

2. PREDATION AT SIMULATED NESTS CONTAINING W-K-S CLUTCHES: SIMULTANEOUS CHOICE TESTS

Due to the spacing (rather than clustering) of eggs in the previous experiment each crow encountered individual prey items successively in time. Successive choice tests may test for different behaviour than simultaneous tests (FRANCK, 1966; HAILMAN, 1967; EVANS, 1970; HINDE, 1970; BEER, 1973a).

The eggshell patterning of many birds vary greatly within the clutch (PRESTON, 1957; LACK, 1958; WILSON, PRESTON & PRESTON, 1958; HOWELL, ARAYA & MILLIE, 1947).

The present experiment was designed to investigate the responses of crows when simultaneously confronted with eggs with different shell patterns.

METHODS

During May and June, 1973, 12 simulated Laughing Gull *Larus atricilla* nests constructed of dried *Spartina alternaflora* grass were set out around an observation hide in a meadow on Little Beach Island. Each nest contained a W, K and an S egg. At least 4 Fish Crows and a pair of Common Crows preyed regularly on these nests. The foraging and egg eating behaviour of the crows were observed from the hide. The dependent measure of primary importance was the order in which the eggs of a clutch were pecked or preyed on. The following scoring system was used: score of 1 was assigned to the first egg of a clutch contacted with the beak, 2 - second, 3 - third, 4 - any egg which was not touched in a nest in which at least 1 other egg had been pecked or preyed on. Eggs in nests where the crows made no contract with the eggs were not included in the scoring.

RESULTS

The mean predation rank scores of the different egg types were very similar (W=2.64, K=2.28, S=2.37), and these scores were not significantly different from one another (Kruskal Wallace 1 Way Analysis of Variance (SEIGEL, 1956), H=0.342, df=2, P>.05). In 20 of the 24 observed predations the crows picked up the eggs in their beaks and flew away from the nest sites with them. In 2 instances a crow punctured an egg, inserted its bill in the hole then flew off with it, and 2 eggs were pecked open and eaten at the nest. The proportions of these different predation methods were significantly different ($\chi^2=27.00$, df=2, P<.001, see MONTEVECCHI, 1976).

DISCUSSION

The crows showed no differential selection of the different eggs in the simulated nests. Individual animals were observed to fly off with an egg, cache (bury) it under some grass, return to the same nest and repeat this sequence until the nest was empty. The birds tended to prey on all the eggs of one nest before moving on to another, subsequent nest predations tended to occur at the closest neighboring nest. Unmarked crows (possibly different individuals) have often been seen returning to Laughing Gull and Clapper Rail, *Rallus longirostris*, nests in the Brigantine salt marsh nesting area where egg predation had occurred previously. Return to locations of previous prey capture is a useful and typical avian hunting strategy (CROZE, 1970; KREBS, MACROBERTS & CULLEN, 1972; ALCOCK, 1973; BOURGET, 1973).

The most common crow predatory method involved picking up an egg and flying off with it away from the nest site. The social anti-predator defenses of most larid species which nest colonially (NOBLE & WURM, 1943; HARDY, 1957; CULLEN, 1960; KRUUK, 1964; BAERENDS *et al.*, 1970; RYDEN, 1970; BUCKLEY & BUCKLEY, 1972; LEMMETYINEN, 1971, 1972; MCNICHOL, 1973) must necessitate quick response and get away on the part of a predator, if it is to be successful. Egg size appears to be a critical factor in this regard (MONTEVECCHI, 1976).

3. BLACK EGG TESTS

Failure to obtain positive results in the first two experiments led to an attempt to produce a supernormal eggshell camouflage. Black (B) painted eggs were found to be extremely cryptic to the human eye, when placed in the grass these eggs were easily "lost in the shadows". The present experiment investigated the survival of black eggs (in comparison with white and khaki eggs) subjected to intense crow predation.

METHODS

During September, October and November, 1973, batches of equal numbers of W, S and B eggs were set out in a meadow in South Mountain Reservation, South Orange, New Jersey. Procedure was the same as in the first experiment. At least 3 Common Crows came regularly to forage for these eggs; there were no Fish Crows in this area. Some tests were observed from a distance with binoculars.

RESULTS AND DISCUSSION

Thirty-four percent (25/74) of the B eggs, 38% (28/74) of the S eggs and 32% (24/74) of the W eggs were removed or eaten by the crows. These proportions are not significantly different.

Black eggs did not survive better than khaki or white ones. MÜLLER-SCHWARZE & MÜLLER-SCHWARZE (1973) found that South Polar Skuas, *Cataracta maccormicki,* did not prey on black eggs on either dark or white ground substrates, and they contended that black eggs were probably excluded from Skuas' search image strategy. Such was not the case with the crows tested in this experiment. DAVIES (1973) showed that egg spotting patterns, which could not be shown to have selective advantage in avian predation tests, did have survival value in the face of visual detection by humans.

Many colonial nesting birds have evolved elaborate and effective social nest defense systems (see references cited above). Eggshell camouflage might confer only a slight survival advantage, such as may not have been detected in the present tests, in which crows were allowed extended hunting time, unhindered by distractions of screeching, attacking birds. However, even a slight advantage might confer a strong survival value within the confines of a social seabird colony.

4. SHORT DURATION FIELD TESTS

The demonstrations by TURNER (1961) and TINBERGEN *et al.* (1962) of the survival value of prey camouflage in the face of crow predation resulted from field tests terminated after about half the prey items had been taken.

No such restriction had been imposed during the first three experiments presented here. During these tests the crows often took most of the eggs and at times all of the eggs that were set out. The following experiment involved field tests that were stopped when no more than half of the eggs were preyed on. It was hoped that by limiting the crows to short access periods to eggs and that by using natural rather than artificial eggshell "camouflage" these procedures would help naturalize the field experiments making them more comparable to predation sequences in nature.

METHODS

During February, March and April, 1975, batches of equal numbers of natural (N) and white (W) painted Japanese Quail eggs, *Coturnix c. japonica*, were set out under a few strands of grass about 6 m apart in meandering lines of alternating sequence (W-N-W-N, etc.) in a meadow of South Mountain Reservation (Figure 1). Tests were conducted around 10 AM, and about 12 eggs were set out each time. At least 3 Common Crows came regularly to the meadow to forage for these eggs. The crows were observed with binoculars from a position about 125 m away. The order in which the different egg types were preyed on was recorded. The contrast between the egg and the crows' beak and head allowed for an easy determination of the different egg predations from a distance. When a crow pecked open and ate an egg on the ground, the location was noted and a determination of the type of that egg was made at the termination of the test. A vulnerability score of the two egg types based on the first 5 predations of each test was also utilized. The first egg preyed on was given a score of 5, second - 4, third - 3, fourth - 2, fifth - 1. Tests were terminated when half of the eggs set out had been preyed on or after 1 hour. At the end of testing the number of each egg type which had been preyed on was recorded, and unpecked eggs were collected.

The data were analyzed by Chi-square tests. A Selection Index (SI) devised by DICE (1947) for the comparison of differential predation between 2 experimental prey items, which are exposed to predators in equal quantities, was also employed in the data analysis. The rationale of the SI index holds that if a and b represent the frequencies of the two types of prey items which were taken by predators, then the $SI = (a - b)\ (a + b)$ The SI can vary from 0.00 when there is no differential selection between the different items, to 1.00, when one prey is always taken over the other. The test of significance for the SI is the Chi-square test of a 50:50 ratio, $\chi^2 — (a - b)^2\ (a + b)$, df = 1.

RESULTS

Table I shows that significantly more white eggs were preyed on than were naturally pigmented quail eggs. A white egg was preyed on first in 6 of the 9

TABLE I

Eggshell pattern and egg vulnerability to crow predation

Egg type	Preyed on	Recovered	Total
Natural	19	55	74
White	47	27	74

$\chi^2 = 19.72$, df = 1, $P < .001$

field tests during which predation occurred. The total vulnerability score of the white eggs (80) and of the naturally pigmented eggs (27) were significantly different ($\chi^2 = 26.00$, df = 1, P<.001). The SI of the naturally pigmented and white eggs was 0.42, and this is a highly significant outcome ($\chi^2 = 11.88$, df = 1, P<.001).

DISCUSSION

The natural eggshell patterning of Japanese quail eggs conferred selective advantage in the face of intense crow predation when compared with unpigmented white eggs.

The Selection Index (SI) of 0.42 obtained in the present experiment is higher than indices yielded from other experimental studies of prey camouflage and survival rates. As calculated by DICE (1947), the SI of SUMNER'S (1934, 1935a, b) experiments in which Mosquito Fish, *Gambusia patruelis*, that matched or contrasted with the backgrounds of their laboratory habitats were subjected to predation by a penguin, a heron and a sunfish, respectively, ranged from 0.23 to 0.36. ISLEY'S (1938) experiments in which insects that matched or contrasted with their backgrounds were exposed to a variety of avian predators yielded a combined SI of 0.38. DICE'S (1947) experiments of owl predation on conspicuous and cryptic deer mice, *Peromyscus maniculatus*, yielded an SI range of 0.24 to 0.29.

The failure of the previous three experiments presented here to demonstrate the survival value of cryptic eggshell patterns may have been due simply to the decreased effectiveness of artificial as compared with natural camouflage patterns. However, the black eggs used in the third experiment appeared *more* cryptic to the human eye than natural eggs and *all* the artificially camouflaged models were more cryptic (to the human eye) than the white control eggs. In view of the strong survival effect of eggshell camouflage obtained in the present experiment the failure of the other experiments to demonstrate the survival value of cryptic eggshell pigmentation appears to be the result of test procedures. Since prey losses in the experiments were checked only after the crows had extended periods of access to the eggs, the initial finds of the predators (those seemingly most typical of predation under natural circumstances) were lumped with later longer latency predations.

Japanese Quail have been domesticated for some time (and thus not subject to natural predation pressures), yet the eggshell patterning of *coturnix* are still capable of concealing the eggs from avian predators. This implies that none of the selections associated with domestication have eliminated this characteristic, as may have been the case with domestic fowl, *Gallus gallus*

Fig. 1. Contrast between the natural and the white-painted Japanese Quail (*Coturnix c. japonica*) eggs used in the field experiments.

domesticus. Moreover, the shell marking patterns of *coturnix* appear similar enough to those of other ground nesting larid and gallinaceous birds (REED, 1904) to implicate the survival value of the eggshell patterning of these species as well.

5. EGGSHELL PIGMENTATION AND THERMAL STRESS

The eggs of hole nesting birds are generally lacking in pigmentation and markings, whereas those of open and ground nesting species are most often heavily pigmented and marked. These divergences are usually attributed to pressures exerted by visually hunting predators (VON HAARTMAN, 1957; RAND, 1967). While natural eggshell pigmentation may yield a camouflage advantage, other functions important to successful embryonic development may be served as well. Solar radiation intensity (PETTINGILL, 1970) and photic wavelength stimulation which impinge on the yolks and embryos of exposed or uncovered eggs are modified to various extents by different shell pigmentation patterns. Eggshell pigmentation patterns may play a functional role in embryonic development. During the second experiment presented here it was found that following exposure to sunlight white eggs were noticeably cooler to the touch than pigmented eggs. The present experiment investigated the effects of natural eggshell pigmentation patterns on the yolk temperatures of eggs exposed to direct sunlight.

METHODS

During June and July, 1974, egg groups comprised of a Laughing Gull egg, a white painted Laughing Gull egg, a white domestic fowl egg, and a khaki painted domestic fowl egg were set out on a wooden platform in direct sunlight. A small hole 2-3 mm in diameter was chipped in each shell and a temperature probe connected to a Yellow Springs Thermometer (Model No. 43TD) was inserted into the center of the egg. Eggs were usually set out in the early afternoon and ground level air temperature and egg yolk temperature were checked about every 2 hours after sunset. Eight trials were run and 37 readings were collected from each egg type.

RESULTS

The average air and egg yolk temperatures are shown in Table 2. A pigment × species factorial analysis of variance yielded a significant effect of pigment ($F=10.48$, $df=1,144$, $P<.005$), a nonsignificant species effect ($F=0.24$, $df=1,144$, $P>.05$), and a nonsignificant pigment × species interaction ($F=0.17$, $df=1,144$, $P>.05$). The significant pigment effect and nonsignificant species effect are striking in view of the fact that gull eggshells are significantly thinner than those of hens, when measured at both the mid (gull shell = 0.33 ± 0.01 mm, hen shell = 0.46 ± 0.01 mm,

$F = 151.60$, $df = 1,14$, $P < .005$) and pointed (gull shell = 0.35 ± 0.2 mm, hen shell = 0.45 ± 0.1 mm, $F = 19.27$, $df = 1,14$, $P < .005$) regions of the egg. A Duncan's Multiple Range Test (Edwards, 1960) showed further that the yolk temperature of each pigmented egg type was significantly higher than its respective white counterpart ($P < .05$).

No significant differences (either within or across species) were found between the regression equations (air temperature vs. yolk temperature) of eggs with white and with pigmented eggshells. However, the raw data revealed that the largest yolk temperature differences between the pigmented and unpigmented eggs were obtained at high air temperatures (>36°C).

TABLE 2

Average (± S. E.) air and egg yolk temperatures (°C)

	Egg		
	Hen	Gull	Air
Pigmented	33.2 ± 0.6	33.2 ± 0.7	36.4 ± 1.0
Unpigmented	30.4 ± 0.6	30.6 ± 0.6	

DISCUSSION

During exposure to direct sunlight the yolk temperatures of pigmented eggs were much higher than those of white eggs and often reached temperatures which were above lethal embryonic limits (Drent, 1970; Howell, Araya & Millie, 1974). This effect appeared applicable over a wide range of eggshell thickness. Overheating can be a very serious threat to the embryonic survival of many ground and open nesting avian species (Cowles and Dawson, 1951; Ytreberg, 1956; Howell, 1959; Russel, 1969; Drent, 1970, 1973; Orr, 1970; Hunt, 1972; Howell, Araya & Millie, 1974). Due to the continuous incubation rhythms of Laughing Gulls and other open ground nesting birds their eggs would only seldomly be exposed to sunlight and even then for very brief periods (such as during a nest relief). However, the presence of humans or other predators in a nesting colony may keep birds off their eggs for extended periods. During such circumstances dark cryptic eggshell pigmentation could be disadvantageous to the developing embryos. Hamilton & Heppner (1967; Heppner, 1970) and Lustick (1969) showed that dark and melanistic plumage can function to reduce the metabolic energy expenditure of birds when ambient temperature is below basal body temperature levels, such as at dawn and dusk. Surely a similar advantage might accrue to uncovered dark eggs at these times. However, since the open ground nesting birds usually cover their eggs continuously, and since overheating poses a much greater threat to embryonic survival than does chilling (*e.g.*, Drent, 1970), the dark, cryptic eggshell patterning of open ground nesting birds' eggs must be seen as an "adaptive compromise" (Tinbergen, 1967, 1973; Tinbergen, Impekoven & Franck, 1967) evolved in response to selective pressures associated with both the advantages of comouflage and the disadvantages of less effective embryonic solar shielding.

Negative selection associated with the ineffective solar shielding of dark eggshells should have produced eggs which are lighter among ground nesting species which lay large clutches (>6 eggs) and do not begin incubating until clutch completion (such as many ducks and rails) than among ground nesting species which lay small clutches (< 5 eggs) and begin incubation during laying (such as gulls and shorebirds). A general overall survey (see Reed, 1904) of the eggshell pigmentation of these groups of birds supports this prediction. In general rails lay pigmented-spotted eggs which are much buffier and lighter than the eggs of gulls nesting in the same general geographic regions. The eggs of most ducks have white or off-white shells, and like rails they often build their nests under concealing vegetation, though unlike rails, many species cover their eggs with down and vegetation when they leave their nests (*e.g.*, Conway & Bell, 1968). Gray Gulls *Larus modestus* nesting in the deserts of South America have evolved incubation strategies to cope effectively with the harsh thermal stresses of this habitat. The eggshell pigmentation of *modestus* eggs, which are not threatened by avian predators, are much lighter than those of most other *Larus* gulls which nest in less severe environments (Howell, Araya & Millie, 1974). The eggshells of some open nesting species, such as terns, which lay their eggs in thermally severe areas such as sandy beaches (light substrate) also tend to be lighter than those of other ground nesting birds.

It should be interesting to carry out a comparative investigation of eggshell pigmentation patterns in view of the breeding habitats, reproductive strategies and geographic nesting locations of closely related congeneric species such as *Larus* gulls. For a gull like *argentatus* with an extensive geographic distribution it might also prove informative to make intraspecific comparisons of the eggshell pigmentation characteristics of birds breeding at different latitudes and in different habitats. In this same regard an intraspecific comparison between different populations of a gull such as *glauscens* which nest in areas more (on the ground) and less (on cliffs) accessible to predators (see Smith, 1966) might also prove of interest.

SUMMARY

A series of four field experiments which tested the camouflage properties of different eggshell pigmentation and marking patterns was conducted. Neither natural (Laughing

Gull, *Larus atricilla*, eggs) nor artificial (khaki, khaki-randomly spotted, and black painted eggs) camouflage patterns conferred any selective advantage, when crows (*Corvus brachyrhynchos* and *C. ossifragus*) were allowed extended periods (over 2 hours) to hunt for the eggs. However, a natural eggshell pattern (Japanese Quail, *Coturnix c. japonica*, eggs) conferred a very strong survival advantage during field tests which were terminated either after half the eggs were discovered or after 1 hour, whichever came first. The selection index (SI) obtained for the quail eggs was higher than those yielded from other experimental investigations of the survival value of camouflage.

The results of these experiments were discussed in view of the different test procedures employed, and the extent to which such procedures are reflective of naturally occuring patterns of crow predation, such as in a gull or a tern colony.

A fifth experiment which tested the capacity of pigmented and unpigmented eggshells to shield egg contents from solar radiation was also conducted. Pigmented eggshells provided far less effective solar shielding than did unpigmented ones, and this effect appears to hold over a wide range of eggshell thicknesses. In view of these findings, the dark eggshell pigmentation patterns of open ground nesting birds are seen as an "adaptive compromise." That is, under different circumstances dark eggshell pigmentation may be either advantageous or disadvantageous to species and individuals which possess them. Based upon functional considerations an hypothesis was generated which predicts that natural selection should favor darker eggshell pigmentation patterns among certain avian species with particular types of reproductive strategies nesting in particular types of breeding habitat. Some general evidence in support of this hypothesis was offered, and some suggestions for further comparative tests of this hypothesis are suggested.

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ZUSAMMENFASSUNG

Eine Serie von vier Feldversuchen wurde durchgeführt, um die Tarn-wirkung von verschiedener Eipigmentierung und Musterung zu testen. Weder natürliche (*Larus atricilla*) noch künstliche Tarnung (khaki, khaki mit unregelmässiger Fleckung, und schwarz) zeigten einem Selektionsvorteil, wenn Krähen (*Corvus brachyrynchos* und *C. ossifragus*) für über zwei Stunden die Gelegenheit gegeben wurde, nach den Eiern zu suchen. Jedoch ein natürliches Eimuster (Zwergwachtel, *Coturnix c. japonica*) zeigte einen starken Vorteil in Feldversuchen, die entweder wenn die Hälfte der Eier gefunden worden war, oder nach einer Stunde beendet wurden, jenachdem was zuerst kam. Der Selektionindex (SI) für Wachteleier war höher als jener der in den andern Experimenten ermittelt worden war.

Die Resultate dieser Experimente wurden diskutiert im Hinblick auf die verschiedenen angewandten Testmethoden und dem Grad zu welchem solche Methoden die natürliche Form des Krähenraubs in einer Möwen- oder Seeschwalbenkolonie wiederspiegeln.

Ein fünftes Experiment wurde durchgeführt, um pigmentierte und unpigmentierte Eierschalen auf die Fähigkeit hin zu testen, die Eier vor Sonnenbestrahlung zu schützen. Pigmentierte Eierschalen ergeben weniger wirksamen Sonnenschutz als unpigmentierte, und diese Wirkung trifft für einen weiten Bereich von Eierschalendicken zu. Im Hinblick auf diese Resultate werden die dunklen Eierschalenmuster von bodenbrütenden Arten als „Anpassungskompromisse" angesehen. Das heisst, dass unter verschiedenen Umständen pigmentierte Eierschalen entweder vor oder nachteilhaft sein können. Basiert auf funktionellen Betrachtungen wurde eine Hypothese aufgestellt, wonach Selektion dunklere Eipigmentierung in gewissen Vogelarten mit bestimmter Fortpflanzungsweise und bestimmten Lebensraum bevorzugt. Einige allgemeine Beweise in Unterstützung dieser Hypothese wurden gegeben, und Vorschläge wurden unterbreitet für weitere vergleichende Teste dieser Hypothese