

E&EB 240: Animal Behavior
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By submitting this essay, I attest that it is my own work, completed in accordance with University regulations. —Casey L. McLaughlin

The Influence of Egg Crypsis on the Broken-Wing Display of the Killdeer

by Casey McLaughlin

I. Abstract

Avian nest defense manifests itself in a variety of complex and interesting antipredator behaviors. In this experiment, the behavior of the killdeer, a common ground-nesting plover that engages in distraction display, will be studied. The nesting killdeer exhibits a behavior called the “broken-wing display” in response to predators, leaving the nest to simulate being injured, to lure predators away from its cryptically-colored eggs. This experiment would test whether making the eggs conspicuous has any effect on the broken-wing display of the bird. To this end, killdeer will be hatched and raised in captivity. Once they begin to show courtship behaviors during their second summer of life, pairs of birds will be randomly assigned to one of three groups, and each will be moved to the corresponding enclosure in which to mate and nest. In the treatment enclosures, the ground will be covered in blue rocks to prevent egg crypsis. One control group will consist of enclosures that are the same as the treatment enclosure, but covered in cryptically colored rocks, and birds in the other control group will be moved to pens identical in ground covering to the original enclosure. Once the birds have nested, a human predator will enter and approach the nest from time to time, making behavioral measurements to determine how the presence or absence of egg crypsis affects the broken-wing display of the killdeer. It is hypothesized that those birds with non-cryptic eggs will either display more intensely than those

with cryptic eggs, engage in an atypical behavior in response to the predator, or refuse to nest on the provided substrate.

II. Introduction

There are few things with greater influence on an organism's survival than the threat of being eaten by a larger, stronger individual. For this reason, predation plays an enormous role in the evolution of traits and behaviors in prey. Animals have adopted a wide range of solutions to the problem of being eaten – from the predator-specific alarm calls of vervet monkeys (Seyfarth, Cheney, & Marler, 1980) to the induction of premature hatching in tree frogs in response to the presence of egg predators (Chivers et al., 2001).

Particularly vulnerable to attack by predators are an individual's young, and numerous antipredator behaviors exist in many species to specifically protect the developing offspring. In most species of birds, one or both parents remain with their eggs after they are laid and even look after their offspring for some time, both of which are extremely vulnerable to predation. For this reason, many birds engage in a type of antipredator behavior called nest defense, which Montgomerie and Weatherhead (1988) succinctly define as "...behavior that decreases the probability that a predator will harm the contents of the nest (eggs or chicks) while simultaneously increasing the probability of injury or death to the parent."

One interesting form of nest defense is the distraction display. During such performances, as a predator approaches the nest, one or both parent birds actually engage in

behaviors, such as uttering loud calls, fluttering their wings, or running, that increase their conspicuousness to the predator. At first glance, such behaviors may seem counter-intuitive and puzzling, but they are actually designed to call attention to the displayer to divert the predator's focus from the much more vulnerable chicks or eggs. It has been suggested that these behaviors best serve their intended purpose when the nest is particularly vulnerable yet not easily seen, and the predator is a diurnal hunter that can be avoided by flight, such as a mammal (Armstrong, 1954). In such situations, becoming more obvious to a predator to lure it from the nest may be less risky. However, such behaviors still carry a degree of risk, for several different reasons, as Sordahl outlines in his review of the literature (Sordahl, 1990).

Regardless of their risks, distraction displays have persisted as a means of nest defense by many species of birds, including common nighthawks (Gramza, 1967), black-capped chickadees (Clemmons & Lambrechts, 1992), and piping plovers (Cairns, 1982). Of relevance to this study, the killdeer, *Charadrius vociferus*, a common ground-nesting plover, also engages in distraction display while nesting. Once the nest has been built and the eggs have been laid, both killdeer in a pair participate in sitting on the eggs and engaging in distraction displays. Though these birds employ many different distraction displays, this paper will focus on one often called the "broken-wing display," a variety of "injury-feigning" distraction display common to many species of plover. The video at the link, <http://www.youtube.com/watch?v=Oq76Y3Ram5o>, shows the killdeer engaging in the extremely complex broken-wing display. As can be seen in the video, the bird leaves the nest and feigns injury to lure the predator away from its eggs.

Many species of birds that engage in distraction displays, including the killdeer, are ground nesters. These birds create their nests, lay their eggs, and care for their young on the ground. When the killdeer engages in its broken-wing display, it actually leaves the nest,

exposing its vulnerable eggs. These eggs are cryptically colored, and therefore difficult to see. The display is primarily employed in response to mammalian predators (Brunton, 1990). Since mammals approach from the ground, rely heavily on scent when hunting, and can easily be evaded by flight, perhaps leaving the nest unattended in order to engage in the broken-wing display is feasible in the case of these predators. But what if the eggs were not cryptically colored? Would the killdeer have the same behavioral response to an approaching predator?

If an area with appropriate ground coloration and nesting materials is chosen, killdeer eggs are very difficult to see. Figure 1, which depicts a killdeer pair that nested on a small, mulch-covered island in a parking lot, makes this very apparent, as the materials on which the eggs were laid make it very difficult to differentiate them from the background (personal observations). With such indiscernible eggs, it would seem that the broken-wing display would be even more effective, since, not only would the display itself lead the predator from the nest, but the crypsis of the eggs should prevent the predator from even noticing the vulnerable developing offspring. It has been shown that killdeer preferentially seek out white sticks and avoid black sticks when making their nests, and it has been suggested that the basis for this preference is either thermoregulation or concealment of eggs, or perhaps both (Kull, 1977). In another ground nester, the yellow hammer, evidence suggests that having cryptically colored eggs may result in decreased predation, as compared to having conspicuous eggs (Weidinger, 2001). In a study on the ground-nesting stone curlew, it was found that eggs that did not match the background were taken more often by avian predators than those that did match the background (Solis & Delope, 1995). It seems, then, that egg crypsis itself can help prevent nest predation.



Figure 1. Photograph of a Nesting Killdeer. This picture was taken in West Islip, NY during the summer of 2012 by Casey McLaughlin. Upon closer inspection of the image, one can just make out the eggs beneath the parent killdeer, which is standing, presumably in reaction to the proximity of the photographer to the nest. The material on which the eggs were laid clearly closely matches the patterning on the eggs, which, though difficult to make out here, were grayish-white with darker speckles.

Perhaps egg crypsis is a necessity for the killdeer. As one might expect, the risk of predation is rather high for ground nests. In one study, with no parent bird sitting on the nest, the majority of dummy ground nests (approximately 63%) were robbed of their eggs by the end of the experiment, seemingly by mammalian predators (Storch, 1991). Another study showed that artificial nests placed on the ground were plagued by more predation than artificial nests placed above the ground (Loiselle & Hoppes, 1983). These two studies represent just some of the evidence that ground nesters are at a very high risk for predation, making nest defense and other protective measures an absolute necessity.

The actual sites at which killdeer nest vary greatly. Typically, they prefer habitats with sparse, short, and heterogeneous vegetation, far from other shorebirds (Colwell & Oring, 1990). Killdeer have been documented to nest in uplands (Colwell & Oring, 1990), as well as shallow depressional wetlands (Conway, Smith, & Ray, 2005). They have been seen nesting in parking lots (personal observations), and they seem to be increasingly taking advantage of rooftops as well (Fisk, 1978). But with escalating urbanization, it is unclear whether killdeer and related ground-nesting plovers will always be able to find substrates that match the color of their eggs, which may be necessary for offspring survival. With such elegant behavioral responses to predators, however, it is possible that they might be able to adapt to increased egg conspicuousness, though it is unclear whether or not this is possible, and what this adaptive response might be. The broken-wing display of the killdeer provides a robust behavior that can be measured in response to changes in egg crypticity.

I am curious what effect conspicuous eggs might have on killdeer behavior in response to approaching mammalian predators, specifically humans. To this end, experimental killdeer will be raised and bred in captivity. After courtship behaviors have been observed during the second summer of life of the birds, each pair of experimental animals will be randomly assigned to one of several different groups. In one group, each killdeer pair will be placed in a pen with nesting materials and substrates that would prevent egg crypsis. Assuming the birds can be made to nest in such a habitat, it is predicted that, upon approach of a human predator to the nest, the birds will respond when there is more distance between the nest and the intruder (they will be quicker to respond) than in control groups, and with greater intensity than control individuals. This prediction would be consistent with predictions based on optimality theory, which states that less vigorous nest defense should be employed when the nest is cryptic, as there are fewer benefits in

defending a cryptic nest than a conspicuous one (Montgomerie & Weatherhead, 1988). It is also consistent with observations in the American robin, as it was found that mobbing in response to an approaching human was more intense if wild robin nests were poorly concealed than if they were well concealed (McLean, Smith, & Stewart, 1986). It is reasoned that the killdeer in the non-cryptic environment will react more quickly and intensely in order to overcompensate for the lack of crypsis of their eggs, devoting greater effort to making themselves noticeable and drawing attention away from the eggs. It is also possible that those birds with conspicuous eggs may employ an alternative strategy in response to an approaching predator, exhibiting a completely new behavior or employing a different, previously-documented distraction display with greater frequency and/or intensity. Finally, the birds may simply choose not to nest on material that does not provide crypticity. The null hypothesis would be that the broken-wing display intensity and threshold will not differ between the non-cryptic group and the cryptic controls; there will be no difference in the occurrence of any unusual behavior across the three groups; and approximately the same number of birds will successfully nest in all three groups. The null hypothesis is consistent with the fact that mammalian predation success may not be affected by egg crypsis or lack thereof, since mammals tend to rely more on scent than sight when hunting. On this basis, removal of egg crypsis would not merit a behavioral change.

III. Materials & Methods

Study Setting and Duration

This study will be carried out in an experimental setting, rather than the wild, to allow for the manipulation of variables in the birds' habitat. If this study were performed in the wild, it is

likely that the killdeer would seek out nesting sites that would provide egg crypsis. In order to prevent this, a habitat must be constructed in which this is not possible.

The study will be carried out over the course of approximately one and a half years. During the summer, killdeer eggs will be collected from the wild, as described by Malone and Proctor (1966). This process essentially consists of locating killdeer pairs early in the summer, removing the eggs while the parent is away, and putting the eggs in an incubator as soon as possible (Malone & Proctor, 1966). The birds will be hatched and reared in captivity for approximately one year, at which point they will be ready to breed. Parent killdeer begin to engage in the broken-wing display after the breeding territory for that summer's nest is determined, and this behavior continues to be observed until about a week or two after the young have hatched (Deane, 1944). Therefore, the experiment will take place during the second summer of the birds' life, at which time they first begin breeding, and it will culminate two weeks after the offspring have hatched.

Raising Killdeer in Captivity

Malone and Proctor (Malone & Proctor, 1966) outlined procedures for preparing the birds' pen, feeding the birds, and providing the essentials to the growing killdeer. This experiment will adhere to their procedures for raising killdeer in captivity, with a few exceptions. Handling of the killdeer will be kept to an absolute minimum, since it has been suggested that this may disrupt the breeding behavior of the birds (Malone & Proctor, 1966). Though the birds raised by Malone and Proctor (1966) did not breed and therefore did not exhibit the broken-wing display, there is a report of hand-reared killdeer not only breeding in captivity, but also exhibiting the broken-wing distraction display while in captivity (Davis, 1943).

For the purpose of this study, the wings of the killdeer will not be clipped, as this may interfere with breeding behavior and the broken-wing display. As such, it will be necessary to create a large and tall enclosure, and, as recommended by Malone and Proctor, the enclosure will be covered with 1-inch mesh poultry wire (Malone & Proctor, 1966). In this experiment, approximately 35-40 eggs will be obtained if possible, in hopes that at least 30 will survive for experimentation. Malone and Proctor (1966) suggest an enclosure of dimensions 8 x 10 feet for 10-20 birds. Since this experiment will ideally make use of thirty birds, the birds will be raised in an outdoor enclosure with dimensions 24 x 30 feet.

It should be possible to obtain all of the eggs in Connecticut. In particular, open public areas such as parks, fields, and parking lots should be searched, as these should be easily accessible, and, based on literature studies and personal observations, nesting birds might be easily located in these types of areas. The enclosure will be at least ten feet tall, so that an average human being can easily walk inside without hitting his or her head, and a killdeer could easily fly over the intruding human.

In an effort to encourage the killdeer to learn to recognize predators, a tape recording of the alarm call of an adult killdeer will be played whenever a human visibly comes into the vicinity of the birds, a strategy that has been employed in the captive rearing of both killdeer and piping plovers that were later released into the wild (Cairns, 1982). Further, as was also outlined in this study, the birds will be fed from behind a blind, or in some other way that prevents the birds from easily noticing the human caretaker, in an effort to prevent the birds from habituating to the human "predator" (Cairns, 1982), a concern in studies of broken-wing displays in wild killdeer as well. The birds will be banded so that they are easily identifiable as male or female, and each will receive a unique number so that individual killdeer can be easily recognized.

Courtship typically begins as early as mid-April in the birds' second summer of life. Once two birds are observed to have an interest in one another, as gauged by persistent receptivity of the female to male courtship displays, the pair will be randomly assigned to one of three groups, the treatment, control #1, or control #2. A similar method was reportedly used in order to encourage breeding in captive killdeer (Davis, 1943). The pair will then be moved to the selected enclosure. The preferred number of killdeer pairs per group is approximately five, but it is difficult to predict how many killdeer will survive to this stage and what the male:female ratio will be.

Each pair will be placed in a separate enclosure dedicated only to those two birds. Regardless of which group the bird is assigned to, all enclosures will be the same size, 10 feet wide and 50 feet long, to allow ample room to simulate predator approach. Enclosures will all be built side by side if possible, to save time and money. The side or sides of the enclosure adjacent to the enclosure of another killdeer pair will be covered with opaque blue tarp approximately six feet high, over poultry wire that will extend up ten feet and cover the top of each enclosure. This should block nearby killdeer and approaching humans from view, while still allowing light and air to filter into the enclosures.

Conditions of the Treatment Group: Prevention of Egg Crypsis

The enclosures for this group will have the same conditions as the first enclosure, with the exception of size, as mentioned previously, and several variables manipulated for the purpose of the experiment. In the experimental pens, instead of using the grassy ground outlined in previous experiments (Malone & Proctor, 1966), the ground will consist of a large sandbox of sorts. This will be filled with blue rocks of the same shade, not light or dark enough to resemble

the colors of the killdeers' eggs. Since many mammals cannot see red or green, blue should be visible to most mammalian predators and will certainly be recognizable to humans. Some sparse vegetation will be added to provide nesting materials for the birds, but it will be painted to match the color of the rocks. To prevent the birds from digging into the rocks and revealing the perhaps cryptically-colored soil beneath, treatment enclosures will ideally be set up on top of a wood, tar, or concrete base (whichever is most readily accessible, though the same material should be used for each treatment enclosure) that can be painted to match the color of the rocks.

This may seem like a strange environment, but, as mentioned previously, killdeer have been observed to nest in an extremely diverse array of habitats. The key feature of this experimental habitat is that, given the blue color and matching shade of all available nesting substrates and materials, there is no possibility that the whitish-gray and black eggs will be perceived as cryptic on this background.

Conditions of Control Group #1

Each pair in control group #1 will be placed in a separate pen that is exactly identical to those of the treatment group, with one exception. Rather than using blue rocks, the rocks in control group #1 pens will be of varying shades of gray, black, and white. Further, the vegetation placed in these habitats and the ground beneath the rocks will be of this color as well. The rocks obtained for use here will be the same type of rock as the blue rocks to control further for the effects of the nesting substrate alone on behavior. This habitat should, in effect, allow for the crypsis of eggs, while controlling for the effects of a rocky habitat on behavior and nesting.

Conditions of Control Group #2

If sufficient funds are available, and enough birds survive, it would be ideal to include a second control group. For this group, the new habitats would be exactly the same as the first in their contents, but each pen would be the same size as those of the treatment group. This should control for the effects of moving the birds to a new habitat on behavior. Further, it may serve as a good standard for how the birds court, nest, breed, and behave in captivity.

Simulation of Predation

The procedure for simulating the approach of a mammalian predator (a human) to the killdeer nest will be the same across all conditions (the treatment and both controls). The same person will be designated to enter all of the enclosures for each predation simulation, wearing the same color each time, in order to control for the effects of different intruders on behavior. Further, it has been suggested that, when studying the broken-wing display of nesting killdeer using approaching humans, the individual simulating the predator approach the nest no more than once every two days in order to prevent the bird from habituating to the human (Brunton, 1990). Therefore, in this study, approaches will be made every three days. In previous experiments involving wild killdeer, the human predator approached the nest at a slow walk from approximately 200 m away, and, once the nest had been reached, the person stood there for approximately three minutes (Brunton, 1990). In this case, the human predator will begin his or her approach from fifty feet away from the enclosure, so that he or she is within view of the birds. This person will then enter the enclosure, continuing to approach the nest at the same rate, and, upon approaching the nest, the person simulating the predator will stand there for approximately three minutes, as suggested. This individual will be equipped with a tape recorder for recording observations directly, as well as a camera to film the behavioral response of the

bird for review at a later time. If possible, it may be a good idea to have another person observing and recording notes on the behavior as well, but this should only be done if it is possible for he or she to do so without being visible to the killdeer.

Predation simulation will begin once the nest has been made and the mother killdeer begins laying her eggs. It will continue until the chicks are two weeks old. Predation simulation will only occur once every three days. The timing of approach will be randomly selected each time it occurs, so that the birds do not learn to expect human approach at any specific time of the day, but predation simulation will only occur during full daylight.

Behavioral Measures and Data Analysis

All measures will be exactly the same for each predation simulation. The approximate distance between the human and the nest before the broken-wing display is elicited will be recorded, as well as the approximate distance between the human and the nest before any behavior change is observed. Both will be recorded approximately, as being within some range of values (for example, between 5-10 ft from the nest). A behavior change will be defined as follows: if the bird is sitting on his or her nest before the human begins his or her approach, then standing up from the nest, moving from the nest, calling out (unless the bird had been calling out before), or engaging in any sort of distraction display will be considered a change in behavior, as any of these behaviors suggest awareness of the intruder. Minor movements such as head turning would not fall under this category. The approximate distance between the human and the nest before the bird actually leaves the nest will be recorded in the same way. This distance will only be recorded if the bird actually leaves the nest, rather than simply standing above the nest.

Such recordings will be filmed by a video camera and spoken into a tape recorder by the experimenter.

In the same way as the other measures discussed, the approximate distance between the bird and the nest once any distraction display begins, if that behavior is not the broken-wing display, will be recorded. This requires that the individual entering the territory be familiar with the common displays of nesting killdeer, so that he or she can easily recognize them. If any sort of unusual behavior occurs, this will be captured on camera, and the experimenters will take note of it. The intensity of the broken-wing display will be recorded as well, using the system outlined by Brunton (Brunton, 1990), which labels the behavior as either low, medium, or high intensity based on certain characteristics. While this may be coded by the experimenter vocally at the time of approach, it may be easier for the intensity of the behavior to be determined after the experiment, during review of the video recordings taken during approach. Ideally, the person analyzing the video will not be the person who actually entered the habitat, and that person will not be made aware of which condition the killdeer was in, in order to avoid biasing the results.

IV. Expected Results

Support for the "Overcompensation Hypothesis"

The first hypothesis purported in this paper was that the killdeer antipredator response would be more intense in cases in which the eggs are not cryptic than in cases in which the eggs are cryptic, and these birds would be quicker to react to predators. In essence, the expectation is that the birds will need to overcompensate for the fact that their eggs are more conspicuous by going to greater lengths to draw attention to themselves and away from their eggs. In support of this "overcompensation hypothesis," it would be expected that, on average, across time and

individual birds in each group, the distance between the approaching human predator and the nest when the broken-wing display first occurs would be larger for the birds in the non-cryptic group than for those in either control group. Figure 2 illustrates one example of the results expected in this case. The data for the average distance between the human and the nest before any distraction display is first observed, as well as the data for the average distance between the human and the nest before any behavioral change or before leaving the nest is first observed, should show very similar trends to that illustrated in Fig. 2 if this hypothesis is supported.

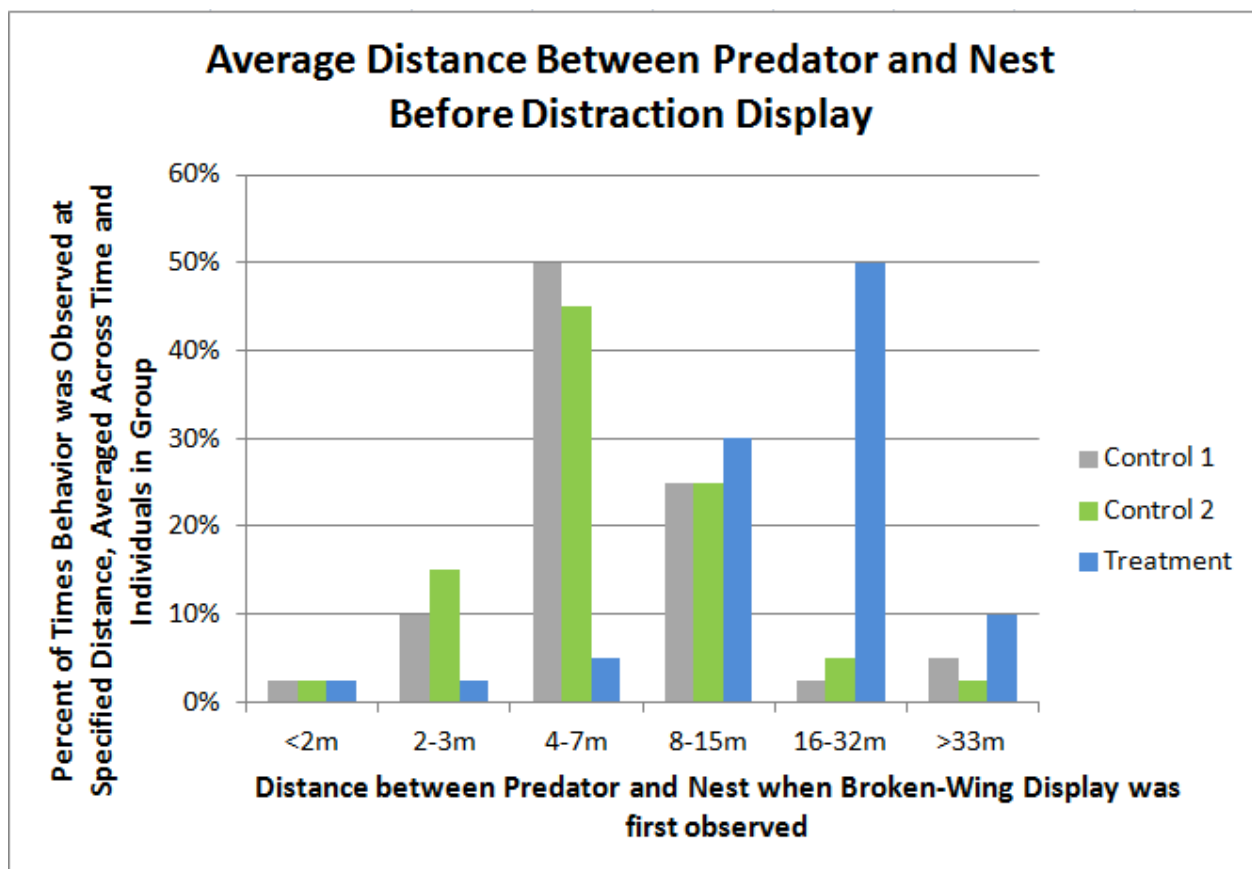


Figure 2. Possible Results in Support of the Overcompensation Hypothesis, in Terms of Predator-Nest Distance. If the hypothesis that distraction would be more intense in the case of non-cryptic eggs is true, it would be expected that the distance between the approaching human predator and the nest before the first observation of the broken-wing display in the killdeer would be larger in the treatment group than in the control group. Distance ranges were selected based on reported findings of Brunton (1990). Since these ranges are based on observations of wild killdeer, the actual ranges observed in this experiment will likely differ. Percentages represent the number of times a display was observed at a specific distance out of the total number of broken-wing displays observed for a particular pair during this entire experiment. A group average would be determined using the values for each pair in the group.

In support of the overcompensation hypothesis, it might also be expected that the killdeer on non-cryptic substrates would engage in broken-wing displays that are, on average, more intense than the displays of those on cryptic substrates. In this case, it is presumed that such differences in behavior would occur due to the fact that, on the non-cryptic background, the bird must go to greater efforts in order to draw the attention of the predator from the more-conspicuous eggs and to itself. An example of what these results might look like graphically is depicted in Fig. 3.

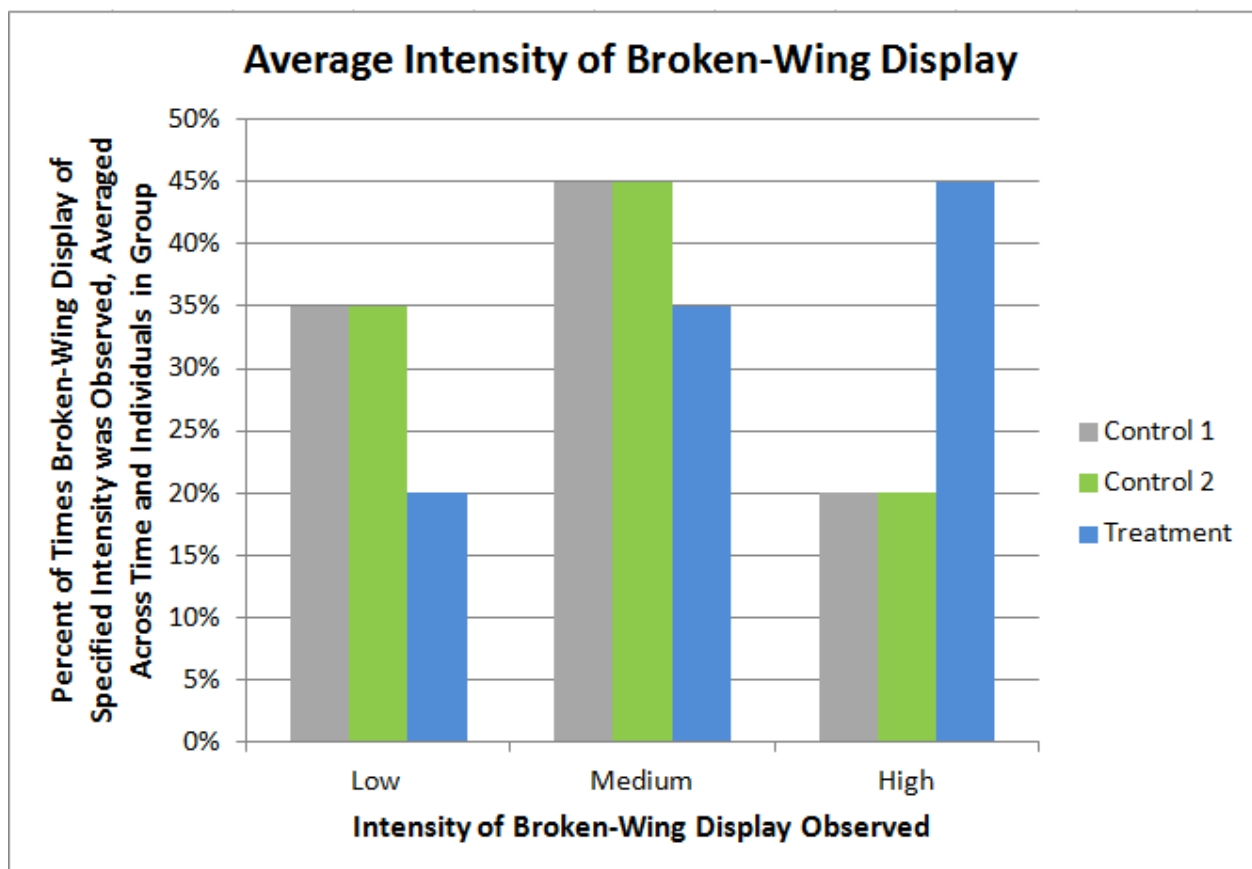


Figure 3. Possible Results in Support of the Overcompensation Hypothesis, in Terms of Behavioral Intensity. In this case, it might be observed that, on average (across time and individuals within each group), the percentage of broken-wing displays that were of higher intensity would be greater for the treatment group than for the control groups. By contrast, in the control groups, it would be expected that the highest percentage of observed broken-wing displays would fall into the medium to low intensity category. A detailed explanation of how behaviors would be categorized by this method is provided by Bruntion (1990). Percentages represent the number of times a display of a specific intensity was observed out of the total number of displays observed for a particular pair during this entire experiment. A group average would be determined using the values for each pair in the group.

The results in Figs. 2 and 3 would lend fairly strong support for the overcompensation hypothesis. While it is possible that the observed effects may be due to the nesting material (rocks), the movement of the birds from one enclosure to another, or even the raising and breeding of the killdeer in captivity, the results from the two control groups should control for these effects. It is also important to note that support for this hypothesis could be provided by data that do not resemble Figs. 2 and 3 in the raw numbers, but rather only in the trends. It is specifically the tendency of the birds in the treatment group to react more quickly to predators and engage in more intense displays than those in control groups that would support this hypothesis. If the vast majority of birds in the control group exhibit low intensity displays on average, then if the majority of the birds in the treatment group exhibited medium intensity displays on average, the hypothesis would still be supported.

Support for the “Alternative Strategy Hypothesis”

As mentioned previously, it is possible that birds that nest on non-cryptic substrate will not react with broken-wing displays of greater intensity, but rather may develop a new behavior, or an “alternative strategy” in response to approaching predators. For example, it is possible that, when the eggs are not cryptic, the birds may actually behave more aggressively towards the intruder. For example, when an ungulate approaches the killdeer nest, the bird will lunge towards the intruding animal (Brunton, 1986). It is clear that the killdeer has adapted different displays in response to different predators, and it seems to be able to differentiate between types of predators and adjust its display accordingly. Perhaps the killdeer will adapt different displays in response to different environments as well. It is possible that, in the case of the human approach on the non-cryptic background, the killdeer will adopt a new, more aggressive

behavior, choosing to fend off the enemy rather than distract it. It is possible that a different alternative strategy would be adopted, but, in this case, any unusual behavioral response towards a human predator would be supportive of this hypothesis.

Data in support of this hypothesis would likely come from the video footage of the killdeer taken by the approaching “predator.” The film would be watched, any unusual behavior would be noted, and its occurrence in each group would be counted. An expert in the typical behaviors of the killdeer would be needed to analyze the footage, so that no typical responses would be mistaken for unusual behaviors. Results resembling those in Fig. 4 would support this hypothesis.

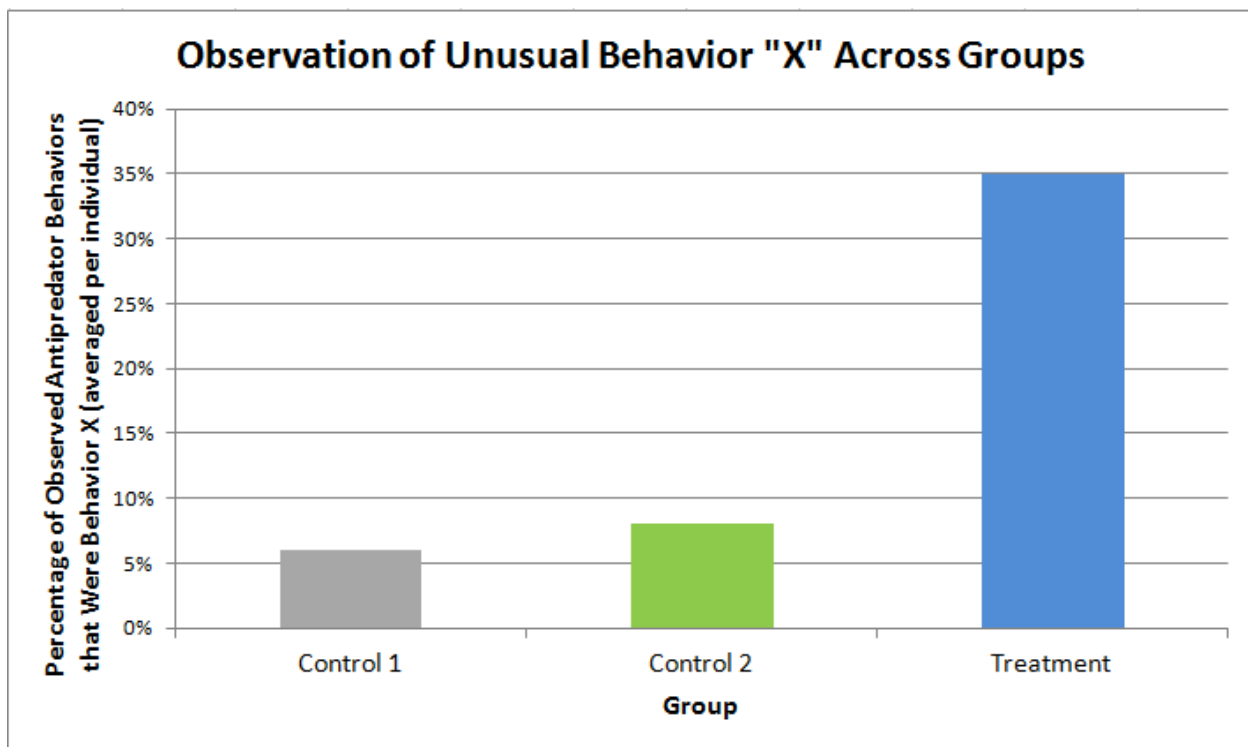


Figure 4. Possible Results in Support of the Alternative Strategy Hypothesis, in terms of Unusual Behaviors Observed. These data indicate that, on average, a greater percentage of the antipredator behaviors exhibited by birds in the treatment group were considered atypical or unusual than those observed in the control groups. This could support the idea that the birds in the treatment group have adapted a new behavior in response to the non-cryptic background on which they laid their eggs. The unusual behavior is described as “Behavior X,” as it is uncertain at this point what that behavior would be. Percentages represent the number of times behavior X was observed out of the total number of antipredator behaviors observed for a particular pair during this entire experiment. A group average would be determined using the values for each pair in the group.

Support for the “Refusal to Nest Hypothesis”

The third and final hypothesis to be tested would be whether the birds would in fact nest on the non-cryptic material, or if they would simply refuse to nest on such material. Given the great lengths to which killdeer go in order to seek out cryptic nesting material, it is possible that they will simply not nest if such material is not available to them. In this case, support for this hypothesis would be gained simply from the observation of how many birds actually nest in each enclosure. If significantly fewer birds nest in the treatment enclosures than do in the control enclosures, this could support the idea that the birds will refuse to nest on a non-cryptic substrate. Figure 5 illustrates what results in support of this hypothesis might look like.

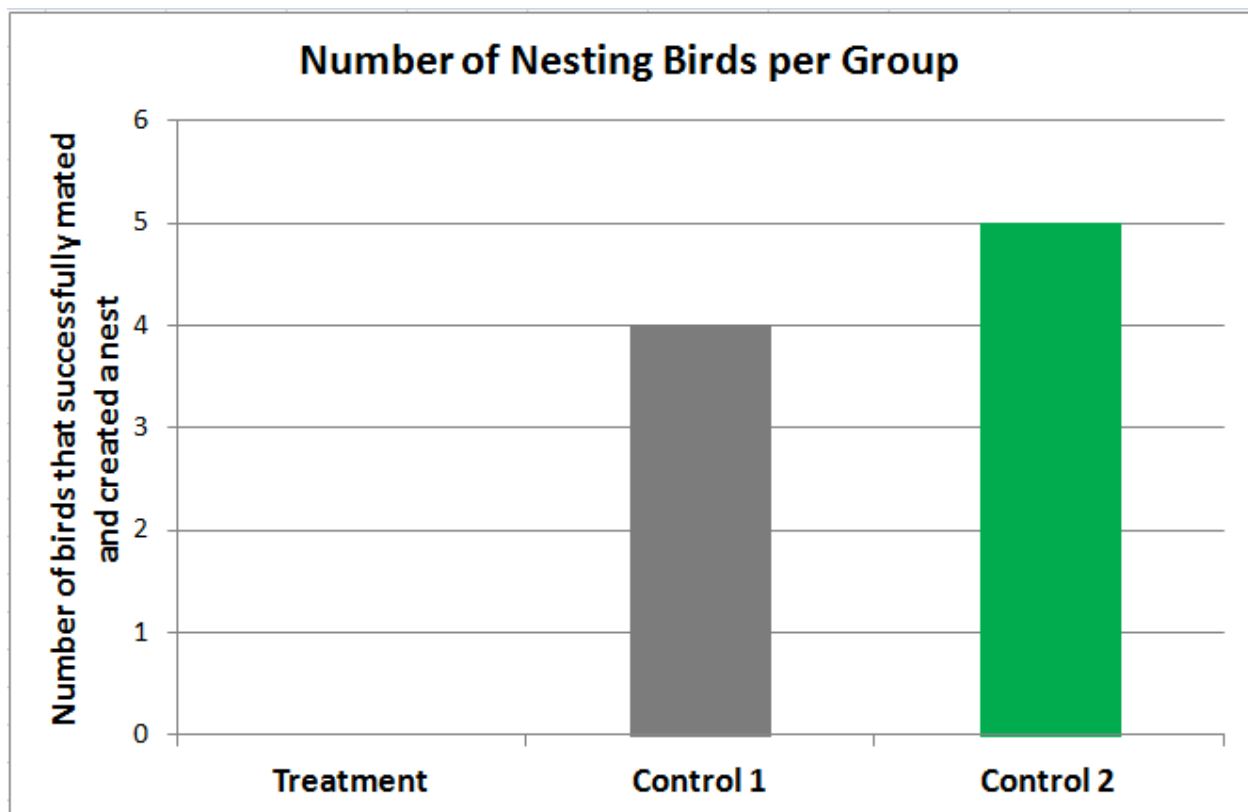


Figure 5. Possible Results in Support of the Refusal to Nest Hypothesis. In order to obtain these results, the number of birds that actually attempted to mate and create a nest would have to be counted in each group. If there were significantly fewer birds in the treatment group that nested than those in the control groups, it may be that these birds simply will not nest if cryptic nesting materials are not available.

Support for the Null Hypothesis

The null hypothesis states that, regardless of whether or not the eggs of the killdeer are cryptic, there will be no observed difference in behavior or nesting habits. In support of the null hypothesis, no significant difference would be observed in the intensity of displays between the treatment and the control groups, and there would be no significant difference in average predator-nest distance for the treatment and control groups. Further, for the null hypothesis to be supported, either no unusual behavior would be observed, or, if it is observed, there must be no significant difference in its frequency of occurrence across the three groups. There would also be no significant difference in the number of birds that nest in the treatment and control enclosures, if the null hypothesis is supported.

V. Discussion

Feasibility

This experiment should be very feasible. Killdeer are fairly common birds, and they are not threatened. Further, all of the necessary materials, including wood, chicken wire, tarp, etc., are readily obtainable. The enclosures could easily be set up outside in a backyard or open field, as the birds are accustomed to the climate of the Northeast. For the blue and gray rocks, aquarium gravel, readily obtainable at any pet store, can probably be used. Further, all of the feed for the birds is easily obtainable at a pet store.

The budget for this experiment should not be too expensive. The greatest cost will likely be the wood needed to build the enclosures and the wages of workers hired for the experiment. The estimated cost of the study is approximately \$35,990. Figure 6 provides the cost breakdown. All things considered, this is fairly reasonable.

Item	Estimated Cost
Gas for vehicles	\$ 10.00
Incubator	\$ 150.00
Lamp x17	\$ 340.00
Poultry wire	\$ 1400.00
Wood	\$ 8,500.00
Tarp	\$ 450.00
Chicken eggs	\$ 40.00
Mealworms	\$ 40.00
Cat food	\$ 500.00
Bird food	\$ 30.00
Stones	\$ 70.00
Tape recorder	\$ 20.00
Camera	\$ 100.00
Workers to feed birds	\$ 17,500.00
Workers to clean enclosures	\$ 2,340.00
Researchers to watch videos	\$ 4,500.00
Total	\$ 35,990.00

Figure 5. Cost Break-Down for the Experiment. All costs are estimates, and this study could end up costing more or less than the total listed here. Estimates for the cost of workers were based on the assumption that this study will last exactly 1.5 years, that the birds will need to be fed three times a day throughout the course of the study, that feeding will only take approximately one hour, and that the hourly wage for workers will be \$10 per hour. Further, it is assumed here that the enclosures will only have to be cleaned out once every week, that this process will only take approximately three hours to complete, and workers will be paid \$10 per hour. This estimate also assumes that the enclosure for raising the birds would be approximately 24 x 30 ft in size, and each nesting enclosure would be 10 x 50 ft in size. It was assumed that video analysis would take approximately one hour per clip, and workers would be paid \$10 per hour.

Relevance

It is interesting to consider, in the context of this study, whether the killdeer are indeed aware of the crypsis of their eggs and the effect this may have on predators. While killdeer do seem to actively seek out nesting material that will provide greater crypsis (Kull, 1977), it is possible that, as suggested by Kull, the observed nesting material preference does relate more to concerns of thermoregulation than crypsis, or perhaps this preference is simply instinctual, or occurs for another reason entirely. Further, just because most mammals rely on scent more than sight when hunting does not mean that they would not be more likely to notice conspicuous eggs than cryptic ones. In the case of a human “predator” this is especially apparent, since anyone can imagine seeing a red beach ball on the sand more easily than one that is sand-colored. As

humans commonly approach killdeer nests, and the nests of other plovers, the human, upon first encounter with the bird, would surely be perceived as a threat. This study could provide insight into the ability to adapt of the killdeer and related plovers, many of which rely on similar distraction behaviors in combination with egg crypsis to prevent nest predation. If the bird is truly aware of its environment and of the conspicuousness of its eggs, one would expect it to alter its behavior in response to the more detectable nature of its eggs.

Since many plovers engage in broken-wing displays and other distraction behaviors, nest on the ground, and have cryptic eggs, the results of this study could be extended to other species of plover. Of particular interest would be the endangered piping plover. If this study results in new insights into the adaptive ability of plovers, it could provide new ideas for the conservation of piping plovers. For example, the presence of houses, piers, parking lots, boardwalks, and other human constructions along the beaches where plovers nest results in the alteration and covering of nesting grounds (Melvin, Griffin, & Macivor, 1991). Though the killdeer might be apt to capitalize on real estate available in parking lots and on rooftops, piping plovers seem to suffer more as a result of human encroachment. If the present study were to reveal that killdeer do not nest on non-cryptic substrate, perhaps these results could be extended to piping plovers. It is possible that they are not simply averse to man-made structures and humans, but rather, these structures do not provide a cryptic substrate for egg-laying. If this is the case, perhaps conservation efforts could involve coloring rooftops, parking lots, or other large, open structures near the beach to match the color of the plover's eggs. Plovers nest in a much narrower range of habitats than killdeer, keeping mainly to shorelines, so efforts need to be made to make the most of these habitats.

On the other hand, if there is a great deal of support for the overcompensation or alternative strategy hypotheses, there will be evidence that killdeer can in fact nest on non-cryptic substrate and can adapt their behavior in response to this change in their environment. Extending these results to the piping plover could provide more ideas for conservation as well. Perhaps captive piping plovers could be raised and bred on non-cryptic substrate, allowing them to adapt to the setting and perhaps conditioning them to nesting in more unusual spaces. These birds might then be more apt to nest in non-cryptic environments in the wild, which might be more available than the depleted cryptic habitats of the birds. This would of course require further experimentation.

Regardless of the actual results, carrying out this experiment could lead to a better understanding of the courtship, nesting, and antipredator behaviors of captive killdeer and related plovers. There is currently very little information in the literature documenting such behaviors in killdeer reared in captivity, and there is certainly no specific protocol for breeding the birds in captivity, to the best knowledge of the author. Therefore, by simply successfully breeding these birds in captivity, this experiment could lay the foundation for a number of subsequent experiments studying the breeding behavior of killdeer and related plovers in a captive setting. It could even help to make breeding piping plovers in captivity more feasible, which might allow for the reintroduction of captive-born birds into the wild to increase their numbers.

This highly feasible and fairly basic experiment could provide a wealth of information and insight into plover behavior, captive breeding of plovers, the evolution of distraction display, the adaptability of these birds, and conservation efforts, making it an extremely worthwhile study to undertake.

VI. References

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