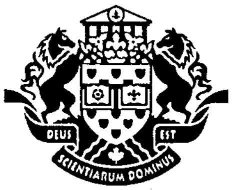

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Does aposematic coloration of prey facilitate acquisition of feeding avoidance by the American Crow (*Corvus brachyrhynchos*) ?

Marie-France Roussel

A thesis submitted to the Faculty of Graduate and Postdoctoral Studies in partial fulfillment of the requirements for the degree of Master of Science

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Abstract

Warning (aposematic) coloration generally involves highly conspicuous colors, which are usually displayed by different prey species in characteristic patterns. The key function of warning coloration is to advertise prey unpalatability to potential predators as well as to facilitate avoidance learning. Many studies have examined the effect of conspicuousness of prey compared to cryptic prey on avoidance learning by predators. However, no previous studies examined the effect of warning coloration of prey compared to conspicuous and cryptic coloration of prey on avoidance learning in wild-ranging birds.

Therefore, this problem was the central theme of my experimental study in which I used the American crow as a predator and chicken eggs of the three coloration patterns with palatable or unpalatable contents as prey. I hypothesized that avoidance of unpalatable eggs would be acquired through learning rather than being genetically determined. Further, I predicted that crows would learn faster to avoid eggs with warning coloration than those with either conspicuous or cryptic coloration. Finally, I predicted that avoidance of originally unpalatable eggs should persist longer during the subsequent control trials (contents of all eggs made palatable) for eggs with warning coloration compared to eggs with conspicuous or cryptic coloration patterns. To test these predictions, I trained crows in several series of trials to avoid potential food by offering them an opportunity to learn to associate unpalatability of prey (eggs) with selected coloration patterns (conspicuous, cryptic, and warning coloration).

My results indicated that the American crow did not exhibit an innate avoidance of eggs with warning coloration. I also found that crows did not learn faster to avoid unpalatable prey with warning coloration compared to prey with conspicuous or cryptic coloration. Finally, I found that crows did avoid eggs with warning coloration longer as compared to eggs with conspicuous or cryptic coloration, (the trend was weakly significant in series 1 and nearby significant in series 2). These results are consistent with the fact that crows seem to possess highly flexible behavior allowing them to adjust to changes in food availability. My results were not representative of those of other studies, but we must be cautious when applying results from laboratory studies to those conducted under natural conditions. Therefore, no generalization can be made on the role of warning coloration because, depending on the type of predators involved, specific coloration may have different effects.

Résumé

Les colorations aposématiques sont dans la plupart des cas des couleurs vives et contrastantes. Les proies considérées aposématiques affichent habituellement plus d'une couleur contrastante, et ces couleurs sont associées pour former des patrons de colorations spécifiques. Le rôle principal des colorations aposématiques est d'avertir les prédateurs de la nature toxique ou du moins fortement indigeste des proies en plus de favoriser l'apprentissage des prédateurs à éviter ces proies. Plusieurs études se sont donc concentrées sur l'effet que provoque une couleur contrastante sur l'apprentissage des prédateurs à éviter ces proies comparativement à l'effet provoqué par une couleur cryptique (de camouflage). Par contre, aucune étude n'a tentée de comparer l'effet que provoquent une couleur aposématique (au moins deux couleurs réunies formant un patron de coloration spécifique), une couleur contrastante et une couleur cryptique sur l'apprentissage des prédateurs à éviter ces proies. De plus, les prédateurs généralement utilisés lors des expérimentations étaient des oiseaux gardés en captivité.

Mon étude s'est plutôt concentrée sur l'apprentissage des corneilles d'Amérique à éviter dans leur environnement naturel, des proies (œufs de poule), caractérisées par ces trois types de coloration et traitées de façon à ce qu'elles soient indigestes ou non. Trois prédictions principales ont été émises. La première était que les corneilles ne posséderaient pas de prédisposition génétique à éviter les proies de couleurs aposématiques. Les corneilles se baseraient donc sur l'apprentissage pour éviter ces proies. La deuxième prédiction était que les corneilles apprendraient plus rapidement à éviter les proies de couleur aposématique comparativement aux proies de couleur contrastante ou cryptique. Finalement, la troisième prédiction était que les corneilles devraient en principe éviter les proies de couleur aposématique de façon plus prolongée que les deux autres types de coloration. Afin de tester ces prédictions, j'ai entraîné les corneilles à éviter des proies, rendues indigestes, en leur offrant l'opportunité d'apprendre à associer ces proies à différentes colorations (couleur aposématique, couleur contrastante et couleur cryptique).

Les résultats ont démontré que les corneilles d'Amérique ne possèdent pas de prédisposition génétique à éviter les proies de couleurs aposématiques. Les résultats ont aussi démontré que les corneilles n'apprenaient pas plus rapidement à éviter les proies de couleurs aposématiques comparativement aux deux autres types de coloration. Finalement, les résultats ont démontré, de façon plutôt ambiguë, que les corneilles évitaient de façon plus prolongé les proies de coloration aposématique comparativement aux deux autres types de coloration (une faible tendance statistiquement significative pour la série 1 et une tendance près du seuil de signification pour la série 2). Les résultats sont congruants au fait que les corneilles d'Amérique possèdent une certaine flexibilité leur permettant de s'adapter à différents changements selon la disponibilité des ressources. Puisque mes résultats ne sont pas similaires aux résultats obtenus par d'autres études, il faut être prudent lorsque nous comparons des résultats obtenus en laboratoire avec ceux obtenus dans des conditions naturelles. Par le fait même, nous ne pouvons généraliser l'effet des couleurs aposématiques, car selon les prédateurs, les couleurs peuvent avoir des effets différents.

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Warning coloration

Remember someone saying: "there will always be someone bigger than you"? Well this basically summarizes how nature works. Thus, in fact there will always be a predator and a prey. This interspecific interaction is subject to evolutionary changes. Therefore, on one hand, prey have evolved different types of adaptations to reduce there risk of depredation upon. These adaptations include various behavioral, morphological and physiological traits. Examples of behavioral adaptations are alarm calls, direct attacks, distraction, harassment (mostly in groups) and run and hide (Alcock, 1997). Morphological adaptations include mechanical defenses with spines, thorn or hairs, camouflage or cryptic coloration, or, on the other hand, aposematic coloration (also known as warning coloration).

Warning colors usually include black, yellow, red, orange and white (Guilford and Dawkins, 1991; Lindström, 1999). Characteristically, different prey species tend to

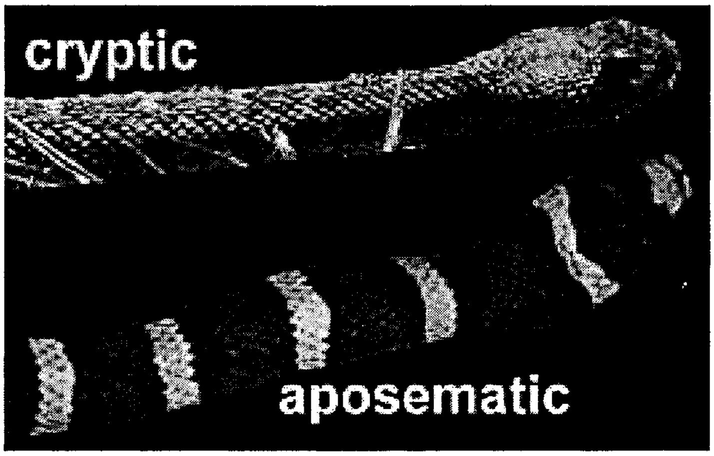


Figure 1: Examples of cryptic and aposematic coloration.

utilize more than one “warning” colors and also display them in distinctive patterns (e.g. spots, stripes or rings; Lindström, 1999). These patterns frequently make the animal look larger or smaller than it really is or may even dramatically change the overall appearance (disruptive coloration) of the prey individual (Guilford and Dawkins, 1991). However, the effectiveness of particular colors and color patterns depends on the receiver involved, because some predators detect certain features that others do not (Guilford and Dawkins, 1991).

Moreover, aposematic coloration is usually associated with additional anti-depredation adaptations such as chemical defences. This allows the visual signal to become more distinctive and memorable when learning is involved (Guilford and Dawkins, 1991). Factors such as the presence of a reward or punishment, the familiarity of the signal, or the intensity of it affect the effectiveness of the association between events (such as edibility and appearance) and how long the association will be retained (Guilford and Dawkins, 1991).

Thus, the main function of warning coloration is to advertise unprofitability, or more specifically unpalatability of the prey to potential predators (Schuler and Hesse, 1985; Marples et al. 1998). Moreover, it has been argued that one of the most important roles of warning coloration is to help predators learn faster to avoid unpalatable or unprofitable prey even though they also can learn to avoid even cryptic prey (Schuler and Hesse, 1985; Servedio, 2000). What makes a signal (in this case warning coloration) easier to learn and remember is the degree of its conspicuousness (color of a prey contrasting with color of the background), coloration, symmetry and size of patterns, size of the prey, coloration of the patterns, novelty and the interaction between stimuli (e.g. taste, color and odor; Guilford and Dawkins, 1991).

Conspicuousness

Evolutionary biologists have faced a challenging issue which is how conspicuousness could evolve and how it could have spread throughout a population (Roper and Wistow, 1986). This is because a conspicuous prey attracts more attention from predators and therefore is likely to suffer increased mortality (Roper and Wistow, 1986). The benefits of conspicuousness must exceed all its costs to be maintained (Gamberale-Stille and Tullberg, 1999; Roper and Wistow, 1986). This assumption was the starting point of many investigations concentrating on the adaptive value of conspicuousness (Roper and Wistow, 1986). However, it is known that some species perform deimatic displays (i.e. these animals are toxic, but also cryptic, and when startled by a predator, they display conspicuous colors; Roper and Redston, 1987).

Nevertheless, many prey do not perform deimatic displays and instead are conspicuous at all times. Therefore, a possible adaptive value is that conspicuousness might facilitate the learning process leading to avoidance (Roper and Wistow, 1986).

Thus in 1980, using young naive chicks as predators and dyed unpalatable crumbs as prey, Gittleman and Harvey established that predators could more easily learn to avoid conspicuous prey compared to cryptic prey (Gittleman and Harvey, 1980; Gittleman et al., 1980). During these experiments, chicks at first selected more conspicuous crumbs.

However, chicks required less time to learn to avoid conspicuous prey than cryptic prey (Gittleman and Harvey, 1980; Gittleman et al., 1980).

Roper and Wistow (1986) and Roper and Redston (1987) suggested that the results obtained by Gittleman et al. (1980) could have been biased by differences in the ingestion rate rather than reflecting the effect of conspicuousness itself (i.e. the depredation rate was not controlled). Therefore, Roper et al. (1986-1987) tried to determine if the speed and strength of learning were due to conspicuousness rather than due to the overall rate of ingestion by controlling the rate of depredation on conspicuous and cryptic prey. They offered the same number of baits to each predator. Their results showed that ingestion rate did not affect the learning process (Roper and Wistow, 1986; Roper and Redston, 1987). Furthermore, their results demonstrated that the speed and strength of avoidance learning were affected by the degree of conspicuousness of the prey, thereby confirming the results of Gittleman et al. (1980). Finally, Roper and Redston (1987), found that the avoidance lasted longer with conspicuous prey than with cryptic prey.

Moreover, Roper and Wistow (1986) reported that predators learn faster to avoid unpalatable prey if they do not encounter mimics (Roper and Wistow, 1986). The effect of encountering mimics on the speed of avoidance learning was addressed by Roper (1994). The goal of his work was to establish the effect of encountering a mimic on 1) the speed of avoidance learning and 2) the speed of extinction of the avoidance response (i.e. how fast the avoidance is lost; Roper, 1994). The results of this study confirmed the findings of Roper and Redston (1987), that 1) a stronger avoidance appeared after only one trial when conspicuous prey were associated with a negative stimulus and 2) that the avoidance was gained faster with multiple trials. Finally, his results also showed that conspicuousness facilitated learning and retarded the extinction of the avoidance. Therefore, the information acquired will be less easily lost if the prey is conspicuous rather than cryptic (Roper, 1994).

Sometimes, for example when competitors are present, predators may initiate attack without having sufficient time to assess their prey (Gamberale-Stille, 2000; Guilford, 1985). Roper and Wistow (1986) affirmed that, in addition to the effect of conspicuousness on the strength and speed of learning, warning coloration could delay attack by predators, thereby allowing the prey to escape.

Guilford (1985) also hypothesized that a conspicuous prey could be detected at a greater distance, increasing the time between its detection and its capture. Conspicuousness should therefore reduce recognition errors, thereby preventing premature attacks on familiar unpalatable prey by experienced predators (Guilford, 1985). The results of Guilford (1985) showed that the predators (domestic chicks) ate mildly aversive prey (crumbs) when time was constrained. However, when the time available was sufficiently long, the predators were able to distinguish between both prey types. Therefore, the more time predators had to observe the prey, the fewer errors they made, and the more protection the prey gained against an experienced predator (Guilford, 1985).

In addition, Gamberale-Stille (2000, 2001) proposed a compromise between speed of avoidance learning and competition. This author suggested that since chicks (predator) had to make a faster decision in the presence of a conspecific competitor, the innate avoidance was reduced towards live aposematic seed bugs (*Tropidothorax* *leucopterus*). Moreover, a group of prey, probably increases the signal, making prey more conspicuous and therefore, easier to detect at a greater distance (Gamberale-Stille, 2000). For this reason, predators should have more time to observe the prey which should facilitate avoidance learning or should produce a stronger neophobic (i.e. fear of novel things) avoidance (Gamberale-Stille, 2000).

To summarize results of these experiments, it appears that a contrasting prey is 1) more attractive for predators at first; 2) facilitates avoidance learning; 3) results in a greater persistence of the avoidance response (predators remember longer), and 4) retards the extinction of the learned avoidance where palatable mimics are encountered. Furthermore, conspicuousness could also reduce errors by increasing the viewing time, allowing a delay of attack. This would be true especially when prey are grouped, increasing the signal effectiveness. Therefore, conspicuousness of prey is particularly important when competitors are present. This allows predators to react more effectively even with an already learned (i.e. acquired by experience) or innate (i.e. fixed predisposition) aversion.

A prey can be encountered in several kinds of environments such that a cryptic prey may not be cryptic on a different background (Lindström et al., 2001). Therefore, conspicuousness according to some authors (e.g. Sillèn-Tullberg, 1985) is not a reliable cue on which predators should base themselves. However, unpalatable prey are likely to be conspicuous (Lindström et al., 2001).

Moreover, contrast is probably not the only factor determining conspicuousness of a prey (Roper, 1994). The color per se, the pattern (color, symmetry and size) and gregariousness could also affect avoidance learning by the predator.

Coloration

Sillèn-Tullberg (1985) investigated the importance of color per se, independent of background. She used zebra finches as predators and two color forms of seed bug larvae as prey (5th instar of *Lygeus equestris*: one was red and the other was grey (mutant)). Both color forms were unpalatable. The results showed that the grey larva was attacked more often than the red larva independently of the color of the background, demonstrating a strong effect of color per se (Sillèn-Tullberg, 1985). Thus, contrast with background is not a useful cue according to Sillèn-Tullberg (1985). These results imply that a prey can appear to be cryptic from a greater distance and conspicuous from a shorter distance (distance hypothesis). Also, contrast and coloration as well as other characteristics should be considered complementary features whose relative importance probably varies with different predators (Sillèn-Tullberg, 1985).

Patterns

Symmetry and Size of patterns

To be effective, a warning signal should be easy to detect, learn and remember. The efficacy of a signal could also be influenced by other things such as symmetry of the pattern and the size of the pattern (Forsman and Merilaita, 1999). Forsman and Merilaita (1999) offered chicks artificial butterflies associated with either palatable or unpalatable crumbs. The black butterflies were presented with palatable crumbs, whereas the patterned butterflies with unpalatable crumbs. The symmetric signal was two red dots of the same size and the asymmetric signal consisted of two red dots of different size

(Forsman and Merilaita, 1999). The results showed that a warning signal is more efficient with large size and symmetric patterns. The asymmetric patterns were more difficult to detect, learn and remember compared to symmetric patterns (Forsman and Merilaita, 1999).

Gamberale and Tullberg (1996) also demonstrated that the aversion predators exhibited towards aposematic prey increased with the size of that prey. By increasing the size of the prey, the prey conspicuousness also increases, making the signal more effective.

Color patterns

Smith (1975) investigated the innate aversion of avian predators to coral snake (genus *Micrurus*). The predators were hand-reared motmots (*Eumomota superciliosa*). The coral snake presents ring patterns with three colors; red, yellow, and black. Snake models made of wood were painted yellow with red rings, yellow with red stripes and green with blue rings (Smith, 1975). Two models were made for each pattern; one entirely covered with the pattern and the other with only one third (the end) painted (Smith, 1975). In addition, several other models were also used: plain red, yellow, blue, green and unpainted. Birds did not hesitate to peck the plain models, and the yellow and red stripes model (Smith, 1975). However, they avoided the yellow and red rings model. Because the birds did not avoid the green and blue rings model, the pattern itself did not cause the aversion in this case (Smith, 1975). Finally, the predators did not avoid the "end-third" models (Smith, 1975). Smith (1975) suggested that hand-reared turquoise-browed motmots have an innate aversion to a generalized coral snake pattern (Smith, 1975). Actually there is no poisonous snakes with the selected patterns in the area where the birds were captured (Smith, 1975). Therefore, the birds did not have any prior experience. This implies that an innate aversion exists towards yellow and red rings pattern and that this reaction is adaptive (Smith, 1975). Moreover, Brodie III and Jansen (1995) also found that, in Costa Rica, free-ranging birds exhibited a generalized avoidance of ringed patterns since the predators were avoiding both three-color and two-color ringed models.

Caldwell and Rubinoff (1983), for their part, conducted a study on the avoidance of venomous sea snake (*Pelamis platurus*) by naive herons (*Butorides striatus*) and egrets (*Casmerodius albus* and *Egretta thula*). The yellow-bellied sea snake is a very dangerous potential prey for birds. In fact, the sea snake is considered more lethal than coral snakes, cobras and rattlesnakes. This snake species is yellow with a black back and a yellow and black patterned tail (Caldwell and Rubinoff, 1983). Prey presented to herons and egrets were : a dead sea snake, a dead sea snake without the tail, a live sea snake, a live tree snake (*Imantodes cenchoa*), a dead speckled snake eel (*Myrophis punctatus*), a dead spotted snake eel (*Myrichthys tigrinus*) and a dead synbranchid eel (*Synbrachus marmoratus*; Caldwell and Rubinoff, 1983). Patterns for both the spotted snake eel and the tree snake were yellow associated with a dark brown to black coloration. The speckled snake eel and the synbranchid eel were grey (Caldwell and Rubinoff, 1983). The spotted snake eel and the sea snake for their part were similar in appearance.

The birds strongly reacted to the three sea snake specimens. However, the birds ignored tree snakes and synbranchid eels, and ate speckled snake eels even if they had never encountered eels before (Caldwell and Rubinoff, 1983). On the other hand, results with the spotted snake eel were not consistent and Caldwell and Rubinoff (1983) proposed that the avoidance was due to genetic predisposition. To support their proposition they argued that movement and novelty could not have influenced the avoidance response since some of the prey were dead, and that novel prey were also depredated upon (Caldwell and Rubinoff, 1983). Thus, the reaction was due to a specific coloration pattern of the sea snake although the tail did not seem to affect the acquisition of the aversion.

Schuler and Hesse (1985) also investigated the innate response towards certain color patterns of aposematic prey. Naive domestic chicks with no prior feeding experience were offered mealworms painted yellow with black rings and mealworms painted green (larvae of *Tenebrio molitor L.*). Depredation occured on both prey types. However, chicks ate fewer yellow/black prey than green prey (Schuler and Hesse, 1985). Therefore, Schuler and Hesse (1985) concluded that the avoidance of aposematic prey (yellow and black in this case) was innate since the predators had never experienced this prey (Schuler and Hesse, 1985). After a period of time, chicks realized that the yellow/black prey were also palatable, which reduced the avoidance response. Schuler and Hesse (1985) proposed that permanent avoidance requires complementary negative reinforcement such as bad taste.

Roper and Cook (1989), who based their study on earlier work of Schuler and Hesse (1985), investigated three aspects of the innate aversion towards yellow/black prey. These aspects were : 1) what is really responsible for the aversion, 2) what role does early experience play, and 3) the role of innate aversion in determining the strength of "subsequent avoidance learning" (Roper and Cook, 1989). Chicks were presented with green mealworms, mealworms painted with a single color such as black, yellow or red, or painted with stripes (black/yellow, black/red and yellow/red) and finally, with half of the mealworm painted with one color and the other with another color (black/yellow, black/red and yellow/red) (Roper and Cook, 1989). Chicks avoided mostly black mealworms. A weaker aversion was displayed towards black/yellow striped prey and the weakest aversion was shown towards red prey. Chicks did not avoid any other patterns (Roper and Cook, 1989).

The investigators concluded that prey with striped patterns or unstriped bicolored patterns were not necessarily more aversive than unicolored prey. Roper and Cook (1989) suggested that the aversion was related more to specific colors and patterns, and probably not to conspicuousness or novelty of the prey (Roper and Cook, 1989). Subsequently, Roper and Cook (1989) placed chicks in black and yellow cages to habituate them to these colors. This manipulation was performed to demonstrate the effect of early experience on the innate avoidance response. They found that innate avoidance was affected by early experience, leading in this case a strengthening of their preference towards black/yellow prey. Finally, Roper and Cook (1989) placed chicks in the presence of unpalatable, colored, mealworms and subsequently presented to the same chicks palatable mealworms of the same colors. They showed that the innate avoidance evident during the first exposure of certain prey colors did not affect the strength of learning during subsequent multiple exposures (Roper and Cook, 1989).

Mastrota and Mench (1995) investigated what factors could influence color avoidance in bobwhites (*Colinus virginianus*). The factors evaluated were sex, previous experience, and age. First, they established that the most avoided color was red, then yellow, green and, finally, the least avoided color was blue (Mastrota and Mench, 1995). The results showed that the three examined factors did not affect the color avoidance (Mastrota and Mench, 1995). Moreover, previous exposure to a red prey did not affect the strong avoidance of this color. Therefore, Mastrota and Mench (1995) concluded that bobwhites exhibit an innate avoidance towards red coloration. Furthermore, this avoidance persisted into adulthood, suggesting that this predisposition to avoid red is adaptive since several unpalatable insects are red (Mastrota and Mench, 1995). According to the investigators, this avoidance is completely different to the avoidance of unfamiliar colors (such as blue) caused by neophobia, which do not persist (Mastrota and Mench, 1995). They also proposed that neophobia could interact with genetics to produce stronger aversions.

However, some authors believe that the avoidance of conspicuous palatable prey is due to novelty rather than attributed to genetics. Jones (1986) found that domestic chicks avoided blue dyed mash since it was a novel coloration. However, the avoidance of blue mash was reduced when foods colored differently (red, green, and yellow) were offered to chicks before the experiment. This confirmed the effect of early experience, as seen previously in the study of Roper and Cook (1989). However, Jones (1986) used mash food instead of a solid food such as crumbs or mealworms. In addition, Jones commented that the chicks could have failed to recognize the blue mash as food because of its altered appearance. In fact, it has been shown that chicks will preferentially use colors to learn to avoid solid food (Marples et al., 1994).

According to Marples et al. (1998), since some predators exhibit neophobia towards certain prey types, this could have allowed conspicuous morphs (i.e individuals with different appearance are called morphs) to survive long enough thereby leading to the evolution of aposematism. Marples et al. (1998) investigated the reaction of wild birds towards novel bait coloration. They used wild blackbirds (*Turdus merula*) and robins (*Erithacus rubecula*) in their natural environment with familiar and novel colored baits (pastry). First, compared to previous laboratory studies, Marples et al. (1998) found a greater individual variation in the response by predators (Marples et al., 1998). Secondly, the red and yellow bait were avoided for a shorter period of time than the green bait (green representing a commonly encountered color in nature). This result is in contradiction with previous investigations. Therefore, we cannot always assume that results of laboratory studies can be applied in natural conditions (Marples et al., 1998).

We can see that depending on the predator involved the avoidance is directed towards different colors. Still the innate aversion presumably is adaptive because it allows avoidance of very dangerous prey. The novelty of prey also plays a role and may influence the learning process or even innate aversions.

Avoidance of the prey: an innate or learned response?

First, it is important to note that no behavior is solely innate or solely learned (Alcock, 1997). Both genes and learning play an important role in the development of an individual. However, many investigations have attempted to determine whether the avoidance response towards an aposematic prey is innate or learned. It has been shown that warning coloration helps predators to recognize, learn faster, and to remember longer to avoid unprofitable prey (Gittleman and Harvey, 1980;

Roper and Wistow, 1986; Roper and Redston, 1987). However, there is also evidence for innate avoidance caused by some of the prey features (Caldwell and Rubinoff, 1983; Smith, 1975; Schuler and Hesse, 1985). Thus, if a prey is highly poisonous it is important that the predator can avoid it upon recognition.

On one hand, innate avoidance could facilitate learning or could be influenced by early experience (Lindström et al., 1999; Roper and Cook, 1989). Early experience could also affect the avoidance learning although some authors argued against this proposition (Lindström et al., 2001; Mastrota and Mench, 1995). Some authors proposed that this avoidance could simply be due to novelty and not due to genetics (Lindström et al., 1999). Novelty effect could interact with genetic or already learnt aversion creating stronger aversions. However, according to other authors novelty has no effect on the avoidance learning (Lindström, 1999; Lindström et al., 2001). Still, the issue of whether avoidance of certain prey is innate, learned or due to novelty is controversial and once again probably depends on the predators involved in a given situation.

Moreover, studies examined so far have concentrated on coloration but did not evaluate the importance of taste or odor or even the effect of the combination of these elements.

Multimodal display

It is also believed that conspicuous coloration helps a predator learn to avoid a prey by facilitating the association between the color and the toxicity of the prey (Marples and Roper, 1996). Therefore, toxicity could be associated with some taste or an odor. The function and the effectiveness of certain colors, odors or chemicals making the prey distasteful will vary depending on the predator species involved (Marples et al., 1994).

Several odors could, in low concentrations, attract predators but could be considered as a warning signal if present in high concentrations (Kaye et al., 1989). Pyrazines possess a specific odor and are found in toxic plants and insects including butterflies, moths, beetles and many others (Kaye et al., 1989). An investigation was performed on the ability of rats to discriminate between plain water and an aversive quinine solution when both are in presence or absence of a pyrazine odor (Kaye et al., 1989). It was shown that pyrazine odor alone is not aversive but the discrimination between plain water or water altered with quinine is facilitated by the presence of pyrazine odor (Kaye et al., 1989).

Similarly, Rowe and Guilford (1996) and Lindström et al. (2001) investigated the avoidance response by combining pyrazines odor with conspicuous colors. The results of both investigations showed that an innate aversion towards certain colors, remained hidden, may be triggered by the presence of a second warning signal like pyrazine odor (Rowe and Guilford, 1996; Lindström et al., 2001). Marples and Roper (1996) reported that the innate aversion to pyrazine odor or almond odor (odors that are naturally associated with toxicity in plants and insects) increased neophobia only with novel colored prey.

Roper and Marple (1997) concentrated on the properties of two odors, almond and vanilla. The goal of their study was to determine if the two odors were used as "discriminative cues" in the same way as colors. They found that almond odor, acting as a discriminative cue, facilitated the learning process compared to vanilla that did not affect the process (Roper and Marple, 1997). The investigators believed that predators can learn to associate the odor with different kinds of punishment the same way they do with colors (Roper and Marple, 1997).

Marples et al. (1994) conducted a study on the importance of coloration, taste, odor and the combination of these factors (Marples et al., 1994). In this study, quails were used as the predator (*Coturnix coturnix japonicus*). The seven-spot ladybird beetle (*Coccinella septempunctata*) possesses the three cues. The beetle is toxic to blue tit (*Parus caeruleus*) nestlings because of the presence of two alkaloids (coccinelline and precoccinelline) and the reflex bleeding is characterized by a smell of pyrazines (Marples et al., 1994). Pyrrolizidine alkaloids are substances from the secondary plant metabolism acting as a chemical defense (Klitzke and Trigo, 2000). By eating a plant, the insect sequesters pyrrolizidine alkaloids. Precoccinelline, and others related alkaloids, could be synthesized by the insect itself (Klitzke and Trigo, 2000).

Marples et al. (1994) showed that, when presented alone, color pattern was the most effective cue while odor was the least effective one (Marples et al., 1994). When color and taste were paired, or the three cues were combined, the quails avoided the beetle almost as much as when the whole beetle was offered (Marples et al., 1994). However, even when the avoidance was strongly biased towards the whole beetle, it did not last (Marples et al., 1994). The eventual extinction of the avoidance could be the result of an occasional sampling performed by the predators. This means that the predator could detect a change in the quality of the prey (e.g. prey being palatable again) and would, therefore, be able to feed on it if needed (Marples et al., 1994). Thus, color was considered the most important factor and taste a secondary and complementary cue. The odor was not associated with toxicity but could act as an attractant (Marples et al., 1994). The toxicity of the prey is then necessary to maintain the avoidance.

In summary, conspicuousness, coloration, color patterns, symmetry and size are all important elements of the prey from the predator's perspective and facilitate the avoidance learning by the predator. Other cues, such as odor and taste, may also be important secondary cues facilitating the learning process.

The above review demonstrates that several investigations have been done on how warning coloration and other aspects of the prey (such as conspicuousness, coloration per se, patterns, taste, smell etc.) influence the avoidance by the predator. However, the major predator used in these experiments were naive chicks or wild birds captured and then tested in laboratories. Only a small number of studies used wild ranging birds in their natural environment (Lindström, 1999). The nature of existing experimental evidence is hardly conclusive. Because of limitations of the laboratory type of approach, in my own study on the role of aposematic coloration of prey, I used wild crows as predators and examined their responses to palatable and unpalatable prey (eggs). Although there are also problems associated with the use of wild predators, the results from such studies are likely to be more relevant. Crows are used since the background information on their ecology and behavior is available. Moreover, crow are abundant in the Ottawa area and are not an endangered or otherwise protected. Finally, crows are effective avian egg predators and are also known as a major artificial ground nest predator and therefore, offers an excellent opportunity for the study proposed (Hogrefe et al., 1998).

The American crow

Generalist

Range and habitat

The American crow (Corvidea: *Corvus brachyrhynchos*) is broadly distributed. This family is generally considered very successful since it is found in many parts of the world (Savage, 1996).

Crows are habitat generalists. However, crows prefer open fields to forage on and woodlots for nesting and roosting (resting and sleeping in a particular area with available perches) (Jonhson, 1994). In the North part of their breeding range, they are found from Newfoundland (as far east as Havre St-Pierre) to British Columbia and their breeding range extends south to Florida, Texas and the Gulf of Mexico (Bent, 1946; Godfrey, 1966; Jonhson, 1994). Most of the northern crows migrate south and spend winter in the regions close to the Canada-US border (Jonhson, 1994). Moreover, crows began to move towards urban and suburban areas in the middle of the 50's possibly to escape from shooting by farmers (McGowan, 2001).

Food

Crows are omnivorous and also described as scavengers, and will eat nearly anything. They are capable of adapting themselves to changing environments, seasons and even to available food supply (Bent, 1946; Jonhson, 1994). Crows can depredate on and eat over 600 different kinds of nutritional resources (Jonhson, 1994). Their diet includes insects (e.g. caterpillars, grasshopers, beetles, beetle larvae, spiders and millipedes), dead fishes, road kills, frogs, salamanders, snakes, seeds from crops, corn, fruits, nuts, garbage and nestlings and eggs of other species (Jonhson, 1994; Kilham, 1990; Savage, 1996). They eat eight to ten times a day (Bent, 1946).

Foraging behavior and food storing

According to Savage (1996) the foraging behavior of the American crow is strongly influenced by their prior experience. The learning process begins at the nest (Savage, 1996). However, adults normally continue learning from other members of their group (Savage, 1996).

Moreover, it is believed that crows make decisions about their food (Savage, 1996). For example, it was shown that crows chose snails and whelks by evaluating their size similarly to jays that chose palatable pine seeds based on color, the weight of the seed and even based on the sound they made when the jays pecked them (Savage, 1996).

Crows may sometimes pair or group to optimize their depredation efficacy (Savage, 1996; Montevecchi, 1976). However, Montevecchi (1976) noticed that an individual was not really less successful than a group of crows, but crows still usually hunted in pairs or in groups during his study. Most of the time, juveniles will group to gain advantage against adults (Savage, 1996). Kilham (1990) also proposed that a group of crows might form an «intelligence network» to take advantage of most resources (i.e crows would communicate important information to the others). There is also a specialized behavior that can be observed in a cooperative foraging group called «sentinel behavior» (Kilham, 1990; Montevecchi, 1976). This is performed by one or two members of a group, who observe and guard the area, while the other group members forage (Kilham, 1990). Kilham (1984) also observed that American crows never robbed each other and even helped one another to chase away an intruder.

The use of certain tools by *Corvus moneduloides* and *Corvus brachyrhynchos* was observed (Hunt, 2000). The Caledonian crow (*Corvus moneduloides* a member of the same Family as the American crow) uses leaf-stem as a tool to extract a larvae from dead wood (Hunt, 2000). Caffrey (2000) observed an American crow modify an object (branch) to use it as a tool.

Furthermore, crows are known to store and cache their food (Kilham, 1984; Montevecchi, 1976; Saunders and Ydenberg, 1995). The majority of birds who perform this behavior are usually territorial (Kilham, 1984). Crows store their prey in the ground or in trees usually 15 to 1000 meters away from the site of capture and may also use it to feed the female during the incubating period (Kilham, 1984; Montevecchi, 1976). Caching generally occurs when food is abundant (Montevecchi, 1976; Verbeek, 1997). In addition, an investigation was made to learn how crows relocate their caches (Verbeek, 1997). This study used Northwestern crows (*Corvus caurinus*). The results showed that they relocated their caches within 24 hours and that the relocation is more successful if they remember the location (spatial memory) compared to a random search when the investigator displaced the cache (Verbeek, 1997).

Egg depredation

The reputation of the American crow as a pest is partly attributed to their depredation on nestlings and eggs of many other species. The high level of crow depredation is an important source of nesting mortality in birds (Avery and Decker, 1994;

Chace et al., 1997; Meilvang et al., 1997; Sugden, 1987; Sullivan and Dinsmore, 1990; Sullivan and Dinsmore, 1992).

It was shown that crows are important predators on waterfowl nests, sometimes dramatically reducing nesting success (Sullivan and Dinsmore, 1990). Therefore, Sullivan and Dinsmore (1990) conducted a study using artificial nests (knowing that depredation rates are similar to natural nests) to examine which factors affect egg depredation (Sullivan and Dinsmore, 1990). These authors found that, first, the depredation rate decreased in the absence of crows. Similarly, Broyer et al. (1995) found that the control of *Corvus corone* decreased the depredation pressure on Anatidae nests (Sullivan and Dinsmore, 1990). However, Parker (1984) did not believe that the removal of corvids affected the depredation rate for willow ptarmigan and black grouse. Sullivan and Dinsmore (1990), also discovered that the further away the crows nest is, the greater the chance that the waterfowl eggs survived, suggesting to locate managed habitats at a distance of 700 to 1000 meters away from crows territory (Sullivan and Dinsmore, 1990). High vegetation also reduced depredation. However, the height above 20 to 50 cm did not affect depredation. Moreover, crows may base themselves on other cues than the nests to locate them such as watching the nest building (Sullivan and Dinsmore, 1990). However, these investigators found, in a complementary study, that crows were foraging on crop land in more than 50 % of the time (Sullivan and Dinsmore, 1992). Therefore, they believe that crows might not be a as important as it seemed. Similarly, Parker (1984) showed that corvid depredation on willow ptarmigan and black grouse was probably exaggerated (Sullivan and Dinsmore, 1992). However, Ewins (1991) found that

American crows were more important predators of gull eggs and young than expected in gull colonies, contrary to what Sullivan and Dinsmore (1990) found for waterfowl.

Sugden (1987) studied the effect of different kinds of background on crow depredation. He found that with different backgrounds if the eggs were not concealed then no consequences were noticed on depredation rates. However, when the outlines of the eggs were disrupted by the vegetation crows took longer to find the prey (Sugden, 1987).

Montevecchi (1976) investigated the effect of prey size (white eggs), on the predatory behavior of the American crow. The experiment consisted of presenting individual sized eggs, then presenting in a single nest three eggs of the same size and finally three eggs of different sizes (Montevecchi, 1976). The outcome was that smaller eggs were usually more vulnerable than larger eggs. Smaller eggs are easier to carry and cache at a distance. In contrast, the larger eggs are eaten directly on site because they are more difficult to pick up and carry off (Montevecchi, 1976).

Territoriality

Breeding season

Usually crows bond for at least one year and frequently for life (Johnson, 1994). Crows are territorial especially during the breeding season which begins between February and May (in the south, the nesting can start earlier) (Johnson, 1994). Chamberlain-Auger et al. (1990) showed that in Cape Cod the incubation period requires about 23 days and that the incubation occurs during March until June. The young leave the nest after 5 weeks and during the summer forage with their parents (Johnson, 1994).

Territory

In McGowan's (2001) study, crows, both in rural and suburban areas in the state of New York, were defending permanent territories. Crows were defending a breeding territory during the entire year, but outside the breeding season they were leaving the territory to forage and roost (McGowan, 2001). Crows usually roost in fall (even mid-to late summer) and winter (peak in December and January) and the flocks can be as large as a million birds in one area (Gorenzel and Salmon, 1995; Jonhson, 1994).

According to region studied and the density of crows, territory size varies. Parker (1984) mentioned the results of another study where 31 pairs of crows/km^2 were found which was abnormally high compared to the result of his own study which was about 15 times less than that. In 1989, Kilham reported that the size of crow territory was 0.90 km^2 (Kilham, 1989; McGowan, 2001). In Cape Cod, crows defended their territories all year round, averaging 0.42 km^2 (2.4 pairs/km^2; Chamberlain-Auger et al., 1990). The distance between nests of adjacent territories was 0.86 km (Chamberlain-Auger et al., 1990). Sullivan and Dinsmore (1992) found that, in Manitoba, the home range of American crows is about 2.6 km^2 (0.38 pairs/km^2) without any overlapping. They also found that crows flew about and no more than 382 meters from the nest to forage (Sullivan and Dinsmore, 1992). Moreover, their flights were usually not longer than 700 meters, but the longest flight observed was 2.1 km (Sullivan and Dinsmore, 1992). McGowan (2001) found that suburban territory averaged 310 meters in diameter and rural territory averaged 672 meters in diameter. Therefore, in suburban areas 11.5 territories/km^2 were found, whereas 2.6 territories/km^2 were recorded in rural areas (McGowan, 2001).

Cooperative breeding

Family group

It is also important to mention that one territory usually contains more than two crows (the breeding pair) due to cooperative breeding strategy observed in crows. Crows become sexually mature between 2 and 6 years old; the sexually immature individuals help their parents with nest-building, feeding, sanitation of the nest etc. (Chamberlain-Auger et al., 1990; Kilham, 1984-1985; McGowan, 1998). These helpers influence the reproductive success and reduce the effort of the breeding pairs (Caffrey, 1999). Therefore, in one territory it is possible to observe between 2 to 15 crows (including the breeding pair; Chamberlain-Auger et al., 1990; Kilham, 1984; Kilham, 1989; McGowan, 1998).

Intelligence

The corvidae family has been considered to include some of the most intelligent avian species (Angell, 1978; Gill, 1994). Many factors could explain these differences between corvids, and more specifically crows, and other species.

First, crows are generalists and their behavior is highly flexible (Kilham, 1984). Therefore, crows can effectively adapt to many kinds of changes (Kilham, 1984; Savage, 1996). Secondly, crows are social animals and for that reason they have evolved a complex communication system also known as the «intelligence network» (Kilham, 1984, 1990). Their vocalizations (23 different calls have been studied) are considered very complex (Chamberlain and Cornwell, 1971). Therefore, most of the time they forage in groups to optimize foraging efficiency by transmitting information to each others. Their communication system is also important when there is an intruder in the territory, bringing reinforcements by others. Moreover, crows can also communicate using different postures (Angell, 1978).

Having helpers at the nest shows another aspect of sociability in crows. Moreover, gathering by group members has been reported following the death of one of the mates, resembling the behavior of elephants after the death of a member of the group (Savage, 1996).

However, the essential aspect of their intelligence is the fact that they possess an ability to learn and remember. In fact, corvids have large brains relative to their body size (the ratio of body size to brain size is nearly equivalent to humans and dolphins) (Angell, 1978; Savage, 1996). The hyperstriatum (part of the forebrain considered in all vertebrates to be responsible for learned intelligence) was discovered to act as the primary organ of intelligence in birds (Gill,. 1994; Savage, 1996). In addition, it was reported that the larger the hyperstriatum the better the birds did on tests (Savage, 1996). Among corvids, crows have a larger brain and succeeded in tests better than other species of birds (such as doves, chickens and quails) who all had smaller hyperstriata (Gill, 1994; Savage, 1996).

One experiment showed that birds were able to count and solve problems (Gill, 1994). For example, ravens and parakeets were able to find food hidden under a box by counting up to 7 objects in front of this box (Gill, 1994). Crows seem to be able to do comparisons and seemed to know the concept of "more than" and the "same/different" concept (Smirnova et al., 1998; Zorina and Smirnova, 1995).

A high ability of crows in problem solving and in decision making is indicated by the fact that crows can use tools to extract food from dead wood in a way similar to that of primates feeding on termites (Hunt, 2000). Crows also play and can invent games meaning that the others can learn novel behaviors (Savage, 1996).

Finally, crows have an excellent memory. It is believed that once crows have learned something they do not easily forget it (Savage, 1996). For example, they can retrieve caches within 24 hrs (spatial memory). Savage (1996) proposed that birds that can possess the ability to form mental maps have minds (possessing a certain level of intellectual capacities). It is also believed that the information might be retained and stored in search images (Savage, 1996). A search image is when a bird can clearly see and remember the way a certain cryptic prey looks and afterwords can localize the same prey even if it blends with the background (Savage, 1996).

For all those reasons, crows make a suitable predator choice.

Objectives of the present study

Aposematic and conspicuous coloration patterns share similar characteristics (are easy to detect), but there is a clear difference between them. Conspicuous colors are those that contrast with the background. Although aposematic coloration also contrasts with the background it utilizes a combination of specific colors and displays these colors in specific patterns. To my knowledge, there is no previous study that examined the role of all three coloration patterns (aposematic, conspicuous and cryptic) simultaneously. Therefore, I must establish if increased avoidance is associated with aposematic coloration resulting from a truly "warning" nature of that coloration pattern (i.e. resulting from a specific combination of selected colors), or if it is simply a result of greater visibility (conspicuousness) of certain colors. Therefore, the major goal of my project is to examine the effect of warning coloration on the feeding behavior of the American Crow (*Corvus brachyrhynchos*).

First, I want to establish if the avoidance is innate or if it is learned. If the feeding avoidance is innate then all crows should avoid the eggs with warning coloration but not the eggs with conspicuous or the cryptic coloration. However, the avoidance of prey with warning coloration could have a strong learning component. Therefore, if the avoidance has a strong learning component then we would have to establish if different patterns of coloration (warning, conspicuous and cryptic coloration) of unpalatable prey have different effects on the rate of avoidance learning by crows.

To achieve this goal, I trained crows in several series of trials to avoid potential food by offering them an opportunity to learn to associate unpalatable prey with selected coloration patterns. I expected that with repeated exposures to unpalatable prey the predators should learn to associate the coloration pattern of that prey with its unpalatability, eventually resulting in avoidance of that prey. Although I expected that crows should learn to associate any coloration with unpalatability, I predicted that crows should learn faster to avoid eggs with warning coloration than conspicuous prey, and should learn even less rapidly with cryptic prey. Therefore, the depredation rate should be lower for eggs with warning coloration compared to conspicuous and cryptic coloration.

Since conspicuous colors retard the extinction of a learned avoidance, I predicted that the extinction of avoidance response should be affected by the coloration pattern (Roper, 1994). More specifically, I predicted that avoidance should persist longest for prey with warning coloration, but should become progressively shorter for conspicuously colored and then cryptic-colored prey. I tested these predictions through a series of field experiments.

To conclude, the main objective of my study was to examine the learning ability of the American Crow and to test the idea that warning colors are recognized by this predator and that they facilitate acquisition of prey avoidance response. Most research done on the topic concentrated on the role of conspicuous versus cryptic coloration of prey in predator feeding responses. In contrast, my study should be the first one that will examine and compare the effectiveness of cryptic, conspicuous, and aposematic coloration in feeding behavior of crows.

Methods

Study sites

All field studies were conducted in selected open meadows of the Ottawa region on NCC lands in April to June 2002. A total of 12 study sites (Figure 2, map of site location) were selected with at least 2 km separating the neighboring sites (meadows). This distance between sites was selected to avoid any conflicts with different family groups (see introduction; Chamberlain-Auger et al., 1990; Kilham, 1989; McGowan, 2001; Parker, 1984; Sullivan and Dinsmore, 1992).

Sites were chosen according to the following criteria (2 examples; figure 3). First, crows had to be present at all sites. Second, sites were also chosen knowing that depredation rate on ground nests increases in clear-cuts openings and in areas characterized by a reduced vegetative cover. Sites were chosen near forest edges which provide protective cover (De Santo and Willson, 2001; Nicolaus et al., 1989; Sugden, 1987; Timsit and Clergeau, 1998; Yahner et al., 1989; Yahner and Wright, 1985; Ward and Low, 1997). Moreover, it is believed that the depredation rate increases with the fragmentation of forests in agricultural landscape creating forest-farmland edges (Andrén, 1992; Annand and Thompson, 1997; Danielson et al., 1997; Maccarone, 1991). Andrén (1992) also suggested that as the forest becomes fragmented and intermixed with agricultural land the density of corvids increases. Therefore, the American crow is considered to be a forest edge species (Yahner and Wright, 1985; Yahner et al., 1989). From this, most of the sites were chosen based on the presence of forest edges and their proximity to agricultural fields. However, even if open areas were necessary for the purpose of this study, the presence of perches was also an important factor to consider (perch sites allow foraging time to be increased; Yahner and Wright, 1985). Yahner and Wright (1985) suggested that a low density of shrubs and a high frequency of perches in clear-cut areas made nest more conspicuous for avian predators. Therefore, all fields had several dispersed trees offering good perching sites.

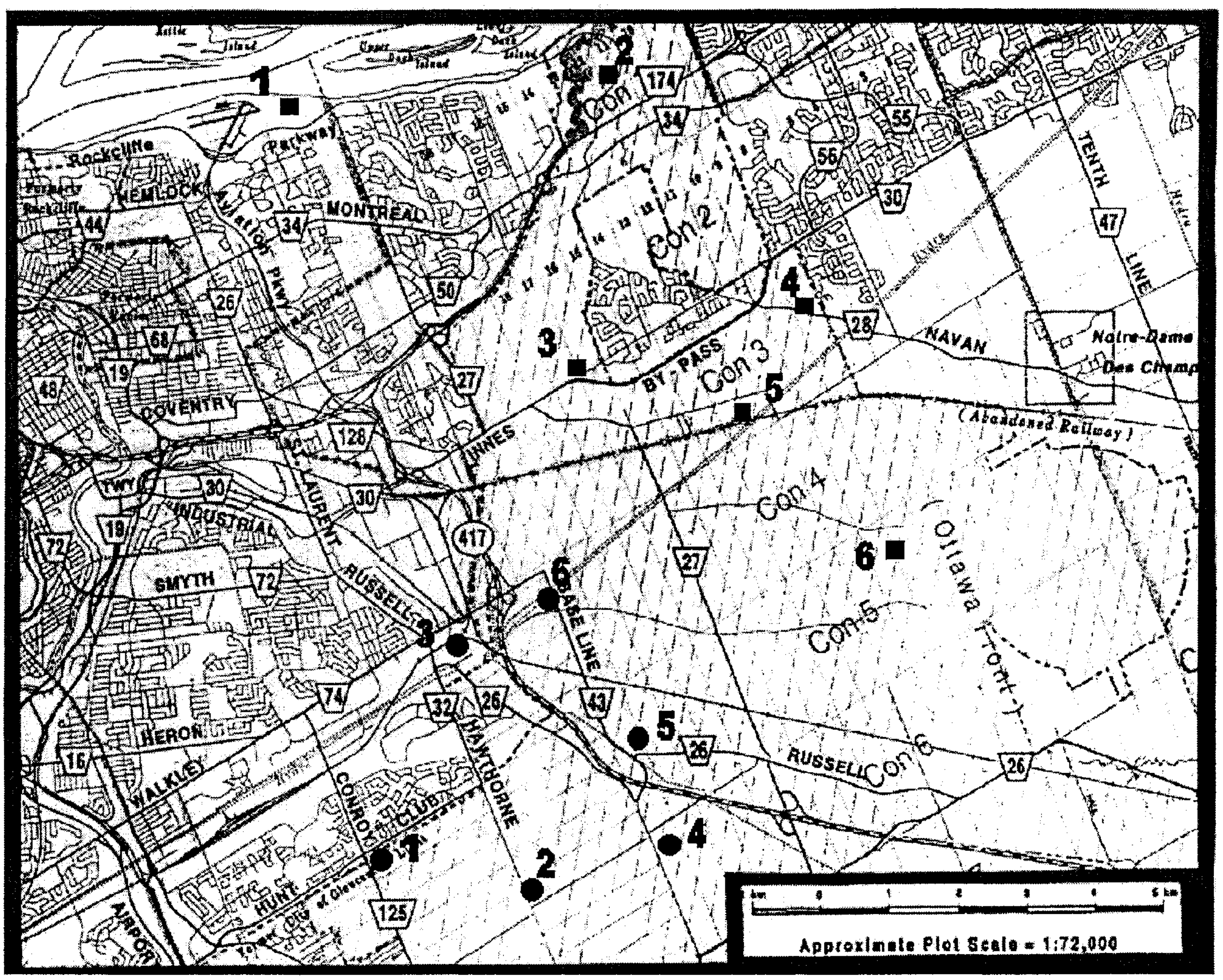
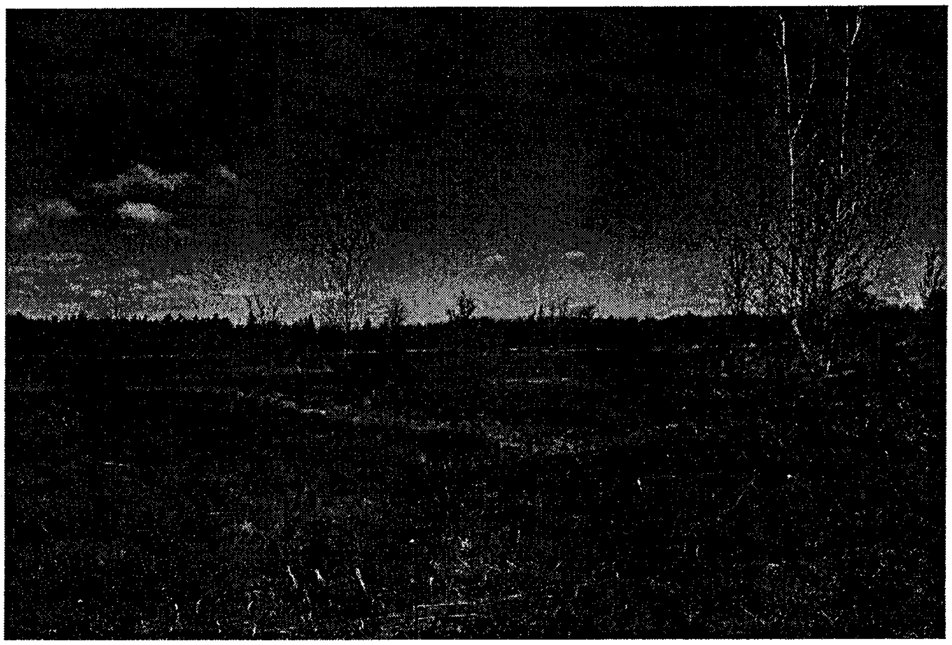


Figure 2: Map showing location of the 12 study sites during the 2 series of experiments. Squares represent sites in series 1 and circles sites in series 2.

a



b

Figure 3: Examples of two study sites. a) Site 2 and b) site 4 during series 1.

Field set up

First, artificial nests are an excellent tool that can be used in studies of various aspects of nest depredation (Götmark et al., 1990; Ohno, 1996; Sullivan and Dinsmore, 1990). However, this technique cannot be used to measure real depredation rates, but can only be used to study pressures exerted by predators in different sites (Timsit and Clergeau, 1998). Each site (30m x 30m meadow) had 6 rows of 6 uniformly distributed stations (a square with 36 stations separated by 5 m). Each station was composed of two dry grass nests (two nests were 20 cm apart), and each nest contained one small chicken egg of a selected color (figure 4). For example, one nest had an egg with warning coloration and the nest beside it contained an egg with conspicuous coloration. Contents of these eggs were either palatable or unpalatable depending on the stage of the experiment (figures 8 and 9). Nests were not labelled, however, since nests were close and half of them contained a conspicuous egg, once crows found one nest they would easily find the rest of nests (Sullivan and Dinsmore, 1990). The eggs were placed in all nests every morning at 6 am and then checked for depredation around noon and then at 7 pm. Depredation occurred when an egg was gone or pecked (Hogrefe et al., 1998; Montevecchi, 1976; Sugden, 1987; Sullivan and Dinsmore, 1990; Ward and Low, 1997; figures 5, 6a and b).

The position of the two kinds of eggs (left or right) was alternated between stations and this position was changed each day to prevent habituation by the crows (Nicolaus et al., 1983). All eggs were removed at the last check to prevent nocturnal depredation mostly by mammalian predators (Sullivan and Dinsmore, 1990).

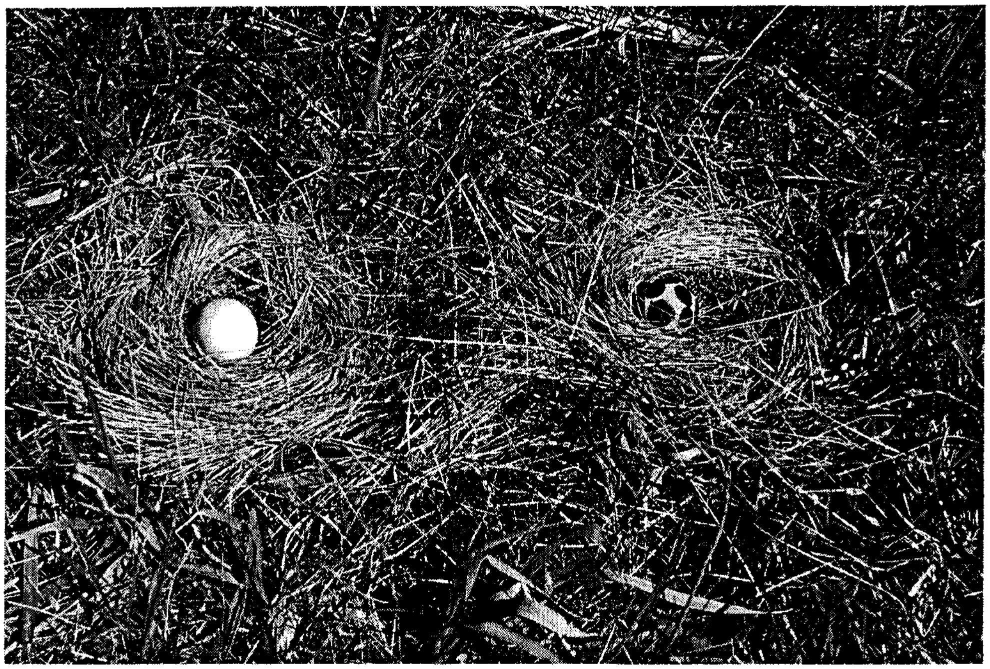


Figure 4: Example of one station composed of two nests. Each nest contains a different colored egg. In this example treatment A (warning versus conspicuous) is shown.

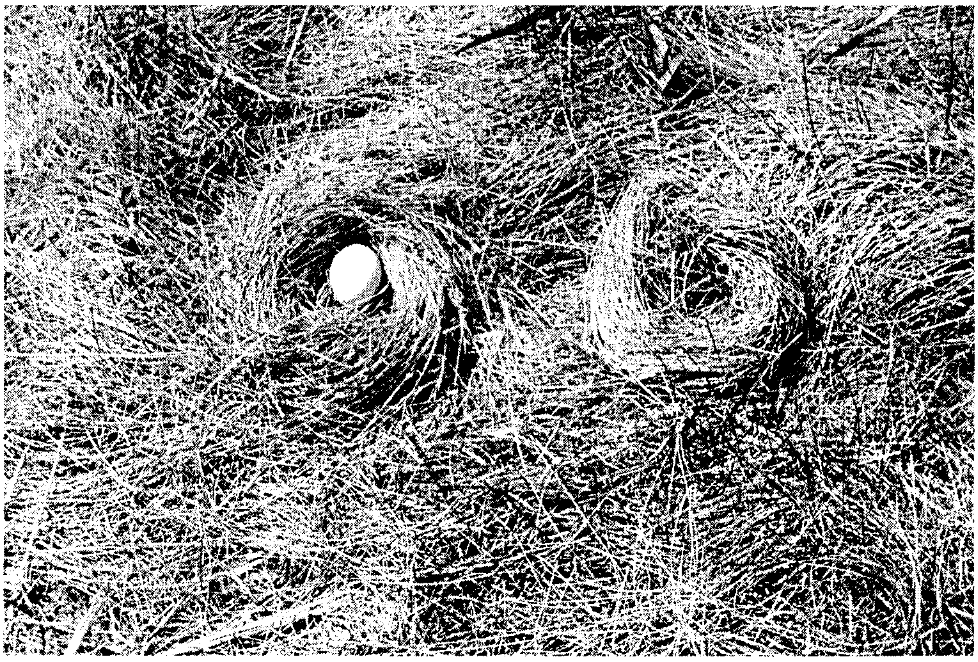


Figure 5: Example of crow's depredation. Egg gone.

Figure 6: Two examples of crow's depredation (eggs were evidently pecked).

Egg preparation

The use of chicken eggs as the prey can be justified by a number of facts. First, crows are effective egg predators (Ewins, 1991; Meilvang et al., 1997; Montevecchi, 1976; Sullivan and Dinsmore, 1990, 1992; Sugden, 1987). Second, Cott (1964) mentioned that some eggs, in nature, can present conspicuous colors and also these conspicuous eggs are in many cases unpalatable. Third, mobility of a prey does not seem necessary since Caldwell and Rubinoff (1983) did obtain an avoidance response towards dead sea snakes. Fourth, chicken eggs are easy to purchase, inexpensive and can easily be manipulated. Small eggs are usually depredated more frequently than larger ones (Montevecchi, 1976). I used small natural brown chicken eggs as the cryptic prey (C). The conspicuous prey (CON) were small white chicken eggs. The warning-colored eggs (W) were small white chicken eggs painted yellow (background) with black dots stamped on the eggs (with non-toxic acrylic paint; see figure 7). The average length and width of the eggs were for a sample of 60 eggs (40 white eggs and 20 brown eggs) was respectively: 54.56 mm ± 2.75 mm and 39.66 mm ± 1.49 mm. The mean volume (0.498 x length x width^2) for the egg sample (60 eggs) was 42.844 cm^3 ± 4.249 cm^3. The mean shape index (length/width) was 1.38 ± 0.07 (also see table 1 in results). A set of control trials for the effect of paint on egg strength was conducted prior to the initiation of the main series of experiments. This control was done using the puncture resistance apparatus to establish if the initial coloration and acrylic paint has any effect on strength of eggshells.

The unpalatability of the eggs was achieved by extracting the egg contents by drilling a small hole in the eggshell (in the blunt pole area) and removing the egg contents with a syringe. The egg contents were then mixed with water, dishwashing soap (non-toxic) and cayenne pepper (40 g of cayenne pepper per 1800 ml of the final mixture, 1/3 of mixture of egg contents (about 600ml), 1/3 of soap (600 ml) and 1/3 of water (600ml)). Cayenne pepper contains capsaicin which is considered to be an effective repellent (Conover, 1984; Hoover and Conover, 1998). The mixture (about 30 ml) was injected back into each emptied egg with a syringe and the hole was then closed with parafilm melted onto the shell around the edges of the opening. The eggs were stored in a refrigerator prior to their use in the field trials.

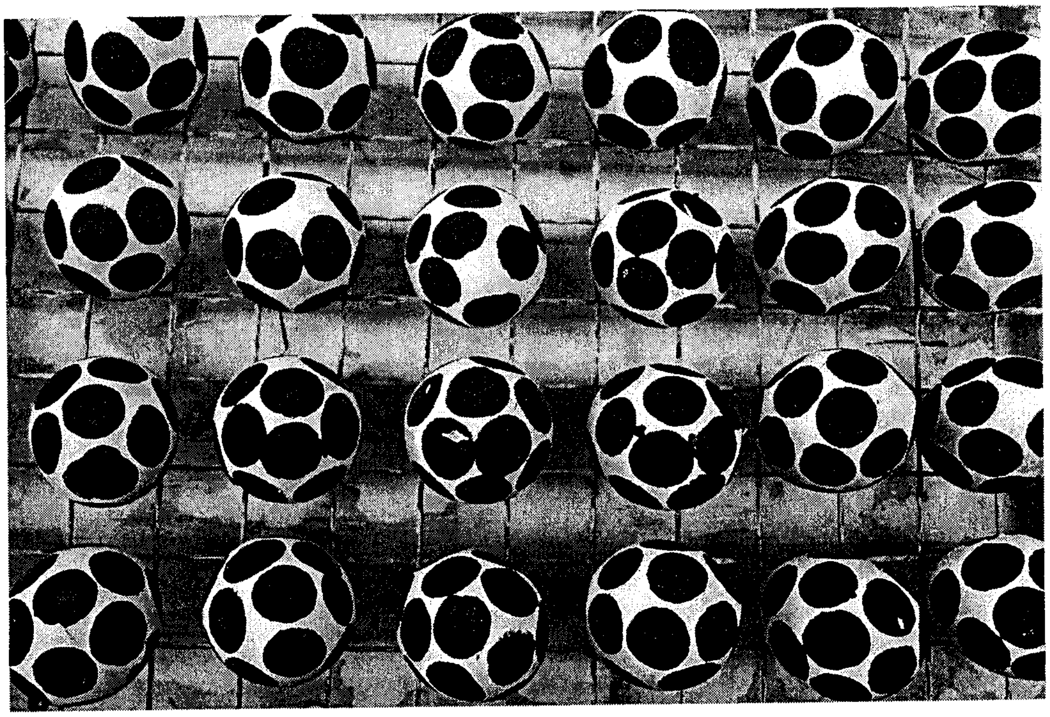


Figure 7: example of eggs with warning coloration.

Experimental design (figures 8 and 9)

Three different treatments have been conducted at six different sites (6 replicates/experiment), each using chicken eggs as the bait (prey).

Treatments involved a choice between two kinds of prey that were offered to crows on individual fields.

Treatment A: Warning-colored eggs vs Conspicuous eggs.
Treatment B: Warning-colored eggs vs Cryptic eggs.
Treatment C: Conspicuous eggs vs Cryptic eggs.

Each treatment was conducted in the following manner:

For each control both egg types were palatable and for experiment 1, one egg was palatable and the other was unpalatable. For experiment 2, the color of the egg that was originally palatable in experiment 1 was then treated to be unpalatable, and the egg that was originally unpalatable in experiment 1 was palatable. Controls were run for 4 days and experiments for 3 days. From now on I will use the following symbols in figures: warning palatable (WP) and unpalatable (WU); conspicuous palatable (CONP) and unpalatable (CONU); cryptic palatable (CP) and unpalatable (CU).

Statistical analyses

First, I used a one-way ANOVA with a Tukey multiple range test to establish if painted and natural eggs were similar in strength, volume and shape.

Analyses of data on depredation rates were done using also analysis of variance

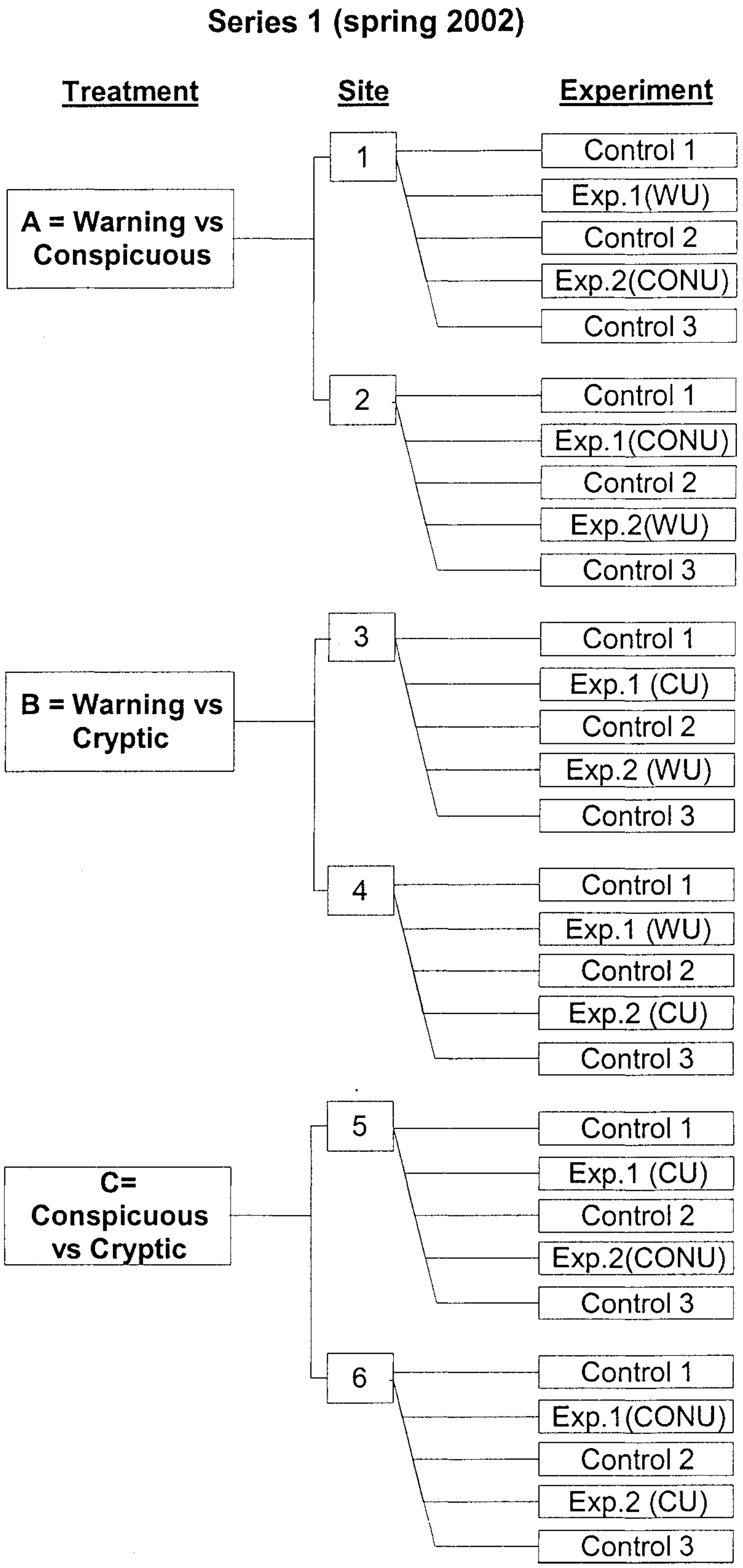


Figure 8: A summary of the experimental design, in series 1, for each treatment. Exp.1 and 2 where one egg is palatable while the other is unpalatable and the latter represented in brackets : WU meaning warning eggs unpalatable, CONU meaning conspicuous eggs unpalatable and CU meaning cryptic eggs unpalatable. During controls 1, 2 and 3 both eggs were palatable.

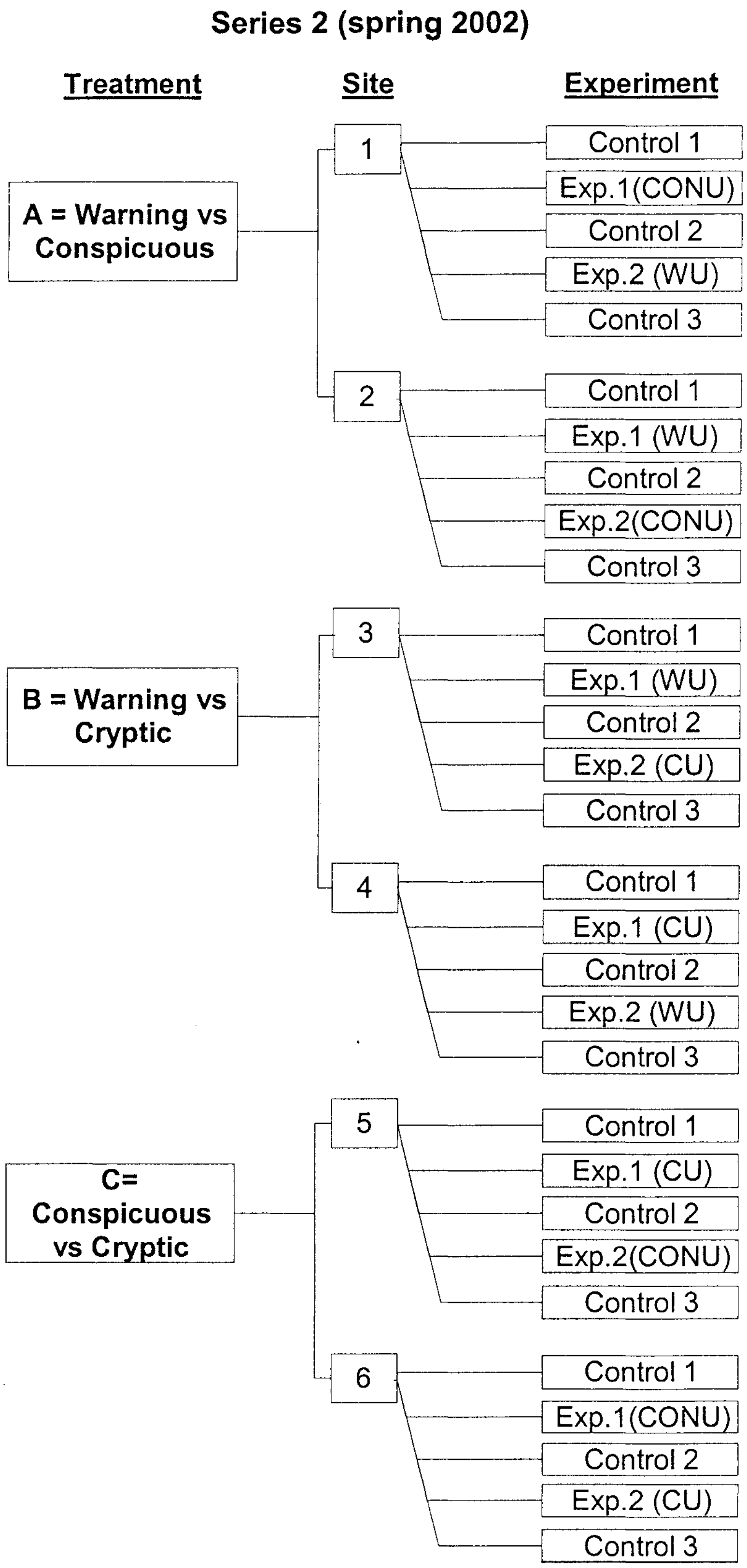


Figure 9: A summary of the experimental design, in series 2, for each treatment. Exp.1 and 2 where one egg is palatable while the other is unpalatable and the latter represented in brackets : WU meaning warning eggs unpalatable, CONU meaning conspicuous eggs unpalatable and CU meaning cryptic eggs unpalatable. During controls 1, 2 and 3 both eggs were palatable.

Results

Observations

Most of the observations were made in the mornings after all sites were set up, although a small number of observations were made prior to noon and during the evening. Crows were the only predator observed at all 12 sites during the entire experimental period. There was no evidence of mammalian depredation, which is usually characterized by crushed eggs.

The number of crows observed at individual sites varied between 2 and 10. However, during series 2, I observed at least 15 crows on site 5 (this group was probably composed mostly of immatures). During the entire experimental period a depredation rate of 100 % was recorded at this site even during experiment 1 and 2, where both palatable and unpalatable eggs were presented. This suggests that this group of crows probably did not have a well established communication system compared to all other groups of crows. Unfortunately, I was unable to identify individual crows because my birds were not individually marked.

On several occasions, I observed crows defending the sites (used for the purpose of the study) against red-tailed hawks (*Buteo jamaicencis*), turkey vultures (*Cathartes aura*), gulls (*Larus delawarensis*) and a raven (*Corvus corax*). Crows tended to gang up and chase the intruders out of sight (see also Kilham, 1989). At two of the 12 sites, gulls sometimes ate leftovers but I never observed any direct depredation on the eggs by gulls (i.e. egg breakage by gulls).

At most sites, crows were waiting for us each morning as Dimmick and Nicolaus (1990) also observed. As soon as we walked towards the field crows started to communicate with each other using vocalizations. Moreover, some even scanned the area, as Heinrich (1988) observed, then perched in trees nearby and waited for our departure to take action.

According to Sullivan and Dinsmore (1992) crows usually forage individually rather than in groups. Ward and Low (1997) observed, for their part, that group members normally arrived together on study sites and departed as a group. Ward and Low (1997) also suggested that in disturbed area, group formation was an important vigilant factor. Most of the time, in the present study, crows foraged in groups. Some individuals were evidently guarding the area (perched in trees around the site performing the sentinel behavior; Kilham, 1990) and other individuals foraged on foot between nests (see also Sullivan and Dinsmore, 1992; Ewins, 1991). Some crows ate the eggs directly on site and others preferred taking the eggs further away from the site (see also Dimmick and Nicolaus, 1990). To transport eggs, crows first pecked the egg creating a hole, then by entering one mandible in the hole could picked up the egg and flew off with it, (see also Montevecchi, 1976). I saw crows leaving the site with an egg in their beak on a number of occasions. However, I was unable to determine if crows cached the eggs. Crows eating eggs directly on site never stayed for a long period of time. The longest time I observed the same crow was about 5 minutes. After foraging, crows flew to nearby trees and then returned again to the site.

I also observed apparent curiosity exhibited by crows during the experimental period. At one site, during the evening check, one crow perched about 5 meters away from me and watched me. When I got too close (about 1 meter) the crow flew to the other side of the transect, perched again and continued watching me before it eventually left and perched in another tree. At the same site, but during the observation period in the morning, one of the crows walked towards the car where I was sitting, then the crow pecked at the road, probably to collect some insect, and then flew off. We were also able to get very close to one crow that was perched on a fence near one of our sites.

However, I also noticed that some of the crows exhibited some fear. On one site, where I was doing my observations early in the morning, crows probably noticed my presence as they flew over me a couple of times and because of this they never depredated on any of the eggs while I was there.

Paint control

A puncture resistance test was performed on 20 white chicken eggs, 20 brown chicken eggs, and 20 white chicken eggs painted yellow and black to establish if paint had any effect on the strength of eggshell. Results of the ANOVA analysis showed that shell coloration and paint had no significant effect on the eggshell mechanical strength (Table 1). Furthermore, I examined if eggs from the three treatment groups differed in size (volume) and shape (Table 1). Egg volume differed significantly between eggs with conspicuous coloration and eggs with warning coloration and a weak significant difference was observed between both eggs with warning and conspicuous coloration and eggs with cryptic coloration.

Table 1 : Summary of data on the outside puncture resistance, egg volume and shape (mean ± SD). Results of one-way ANOVA (using the mean value for all coloration combined) for the egg puncture resistance, volume and shape are also presented (N=60).

Test	**Mean values ± SD**			**ANOVA**	
	Conspicuous (white)	Cryptic (brown)	Warning (white eggs painted)	F	P
Puncture resistance (g)	1892.50 ±430.69	1891.53 ± 360.57	1691.67 ± 94.90	2.49	0.09
Volume (cm^3)	41.36 ± 3.37	42.09 ± 4.76	45.08 ± 3.72	4.86	0.01
Shape	1.38 ± 0.07	1.39 ± 0.05	1.36 ± 0.09	0.78	0.46

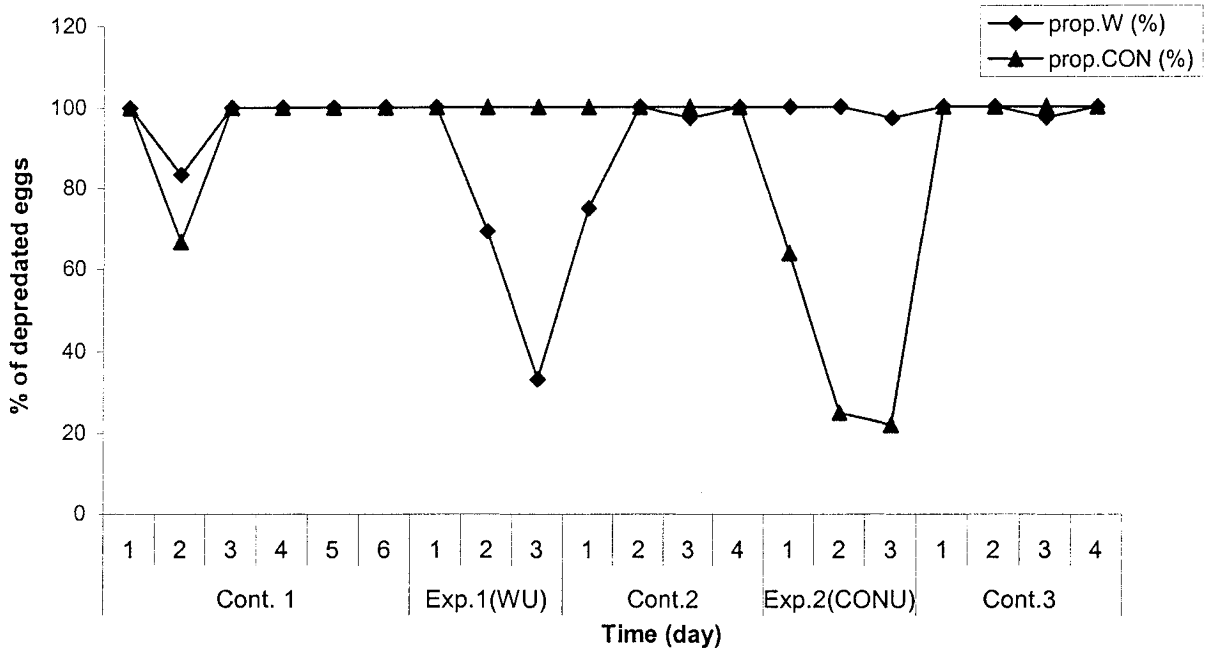
Results for the experimental period

I will use two sites as an example to summarize results obtained during the entire experimental period (figure 10). Results from the remaining 10 fields are shown in the appendix A. In each graph, the percentage of eggs depredated (number of depredated eggs of one type / 36 x 100) is shown for each day during the entire series of experiments (control 1, experiment 1, control 2, experiment 2 and control 3).

For control 1 both egg types were palatable and eggs differed in coloration pattern only. In control 1, both egg types seemed to be depredated at the same rate. At both sites, during experiment 1, the rate of depredation on the unpalatable egg decreased, starting on day 2, although it did not decline completely to 0%.

On day 2, of control 2, depredation rates on eggs that were unpalatable in experiment 1 increased to the initial rate. Again as in experiment 1, experiment 2 resulted in a decrease in the rate of depredation on unpalatable eggs, this time starting on day 1. The rate of depredation on unpalatable eggs again did not decline completely to 0%. Finally, control 3 yielded rates of depredation which were similar for both color types of palatable eggs with the exception of days 2 and 3 on site 2.

In the following section, I combined results from both time series.



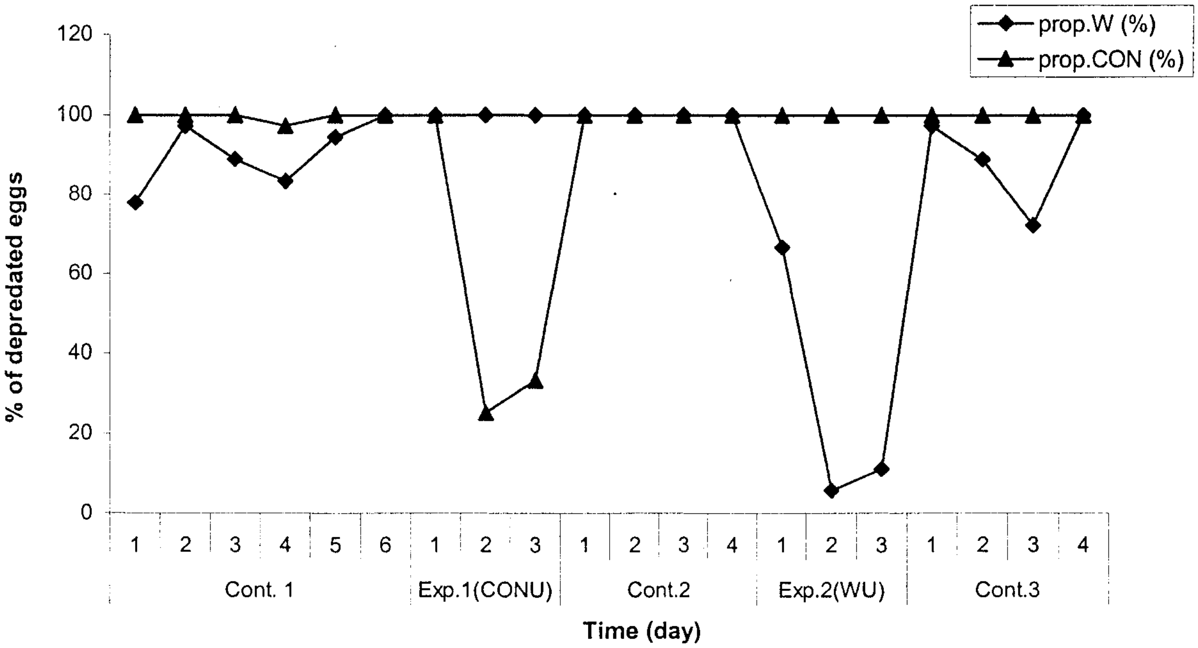


Figure 10: Percentage of eggs depredated by crows each day on sites 1 and 2 (series 1) throughout the entire experimental period. WU and CONU implies warning unpalatable and conspicuous unpalatable, respectively.

To establish the effect of independent variables on depredation rates (proportion of depredated eggs), I used two-way analysis of variance. In an attempt to satisfy assumptions of parametric statistics, I transformed the data using Arcsin square root. Despite this, in some cases, some of the assumptions were not met. Therefore, I also used non-parametric ANOVA. In all cases results of both, the parametric ANOVA and its non-parametric equivalent were similar, here I report results of the parametric analysis of variance only.

Moreover, because all trials were conducted in two time series, series should be considered as a random variable. Therefore, I followed Zar (1984) and recalculated all F-ratio and P values according to his recommendation.

Where the variable series had an effect on results ($P \leq 0.05$), two separate ANOVA analyses were then conducted (one for each time series; the critical level of significance was set at $P = 0.025$). When the ANOVA analysis yielded a significant difference, I used a Bonferonni test for significant difference(s).

Innate avoidance?

Control 1 was designed to test whether crows possess a genetically fixed predisposition to avoid prey with warning coloration (i.e. possess innate avoidance). All types of eggs were palatable and differed in coloration only. Rates of depredation on eggs for each pattern of coloration are presented as a percentage of depredated eggs (number of depredated eggs/N) x 100. The sample sizes are shown in figure 11.

Seventy-eight percent of eggs with conspicuous coloration, 68.3% of eggs with warning coloration and 67.8% of eggs with cryptic coloration were depredated (figure 11). The depredation rates did not differ significantly between the three types of egg coloration patterns (table 2). However, because there was a statistically significant interaction between series and coloration (table 2), I conducted two separate ANOVA analyses, one for each of the series. These analyses failed to yield any significant effect in the two series (table 3). However, both P-values are relatively close to the significance level.

Table 2 : Results of ANOVA testing the prediction of the first hypothesis (i.e. crows do not possess a genetically determined predisposition to avoid eggs with warning coloration). Data from the control 1 were used (N= 108; data transformed using Arcsin square root). F-ratio and P values obtained from the initial ANOVA and the recalculated values for these parameters (as recommended by Zar 1984) are shown. The critical level of significance was set at P = 0.05.

Source of variation	**df**	**F-ratio**	**P**	**F-ratio recaculated**	**Df$_1$**	**Df$_2$**	**P recalculated**
Color	2	2.00	0.14	0.41	2	2	0.709
Series	1	3.83	0.05	3.85	1	102	0.052
Color*Series	2	4.88	0.01	4.90	2	102	0.009

Table 3 : Results of ANOVA for each of the two series concerning the prediction of the first hypothesis (i.e. crows do not possess a genetically determined predisposition to avoid eggs with warning coloration). Control 1 was used (data were transformed using Arcsin square root). F-ratio and P values are shown. The critical level of significance was set at P = 0.025 (see Zar, 1984; N = 60 for series 1 and N = 48 for series 2).

	Series 1	**Series 2**
Source of variation	Color	Color
Df	2	2
F-ratio	3.669	3.388
P	0.032	0.043

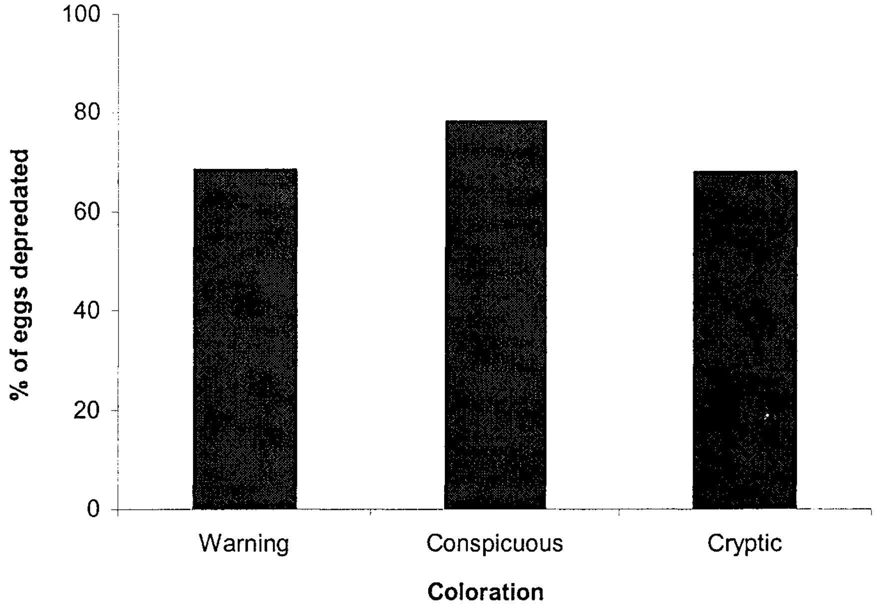


Figure 11: Percentage of palatable eggs depredated by crows during six days (all six days combined) of control 1. Both time series are included. For W: N = 1404 eggs , CON: N = 1260 eggs, and for C: N = 1224 eggs.

Learned avoidance

To test the second hypothesis, I selected data from experiments 1 and 2 (I included eggs with palatable and unpalatable contents for all three egg coloration patterns to establish if warning coloration facilitates avoidance learning). Data are presented as a percentage (number of depredated eggs/N) x 100, and sample sizes are shown in figure 12.

Depredation rates on eggs with the three coloration patterns did not differ significantly (table 4). However, there was a significant decrease in depredation with time (day; see table 4 and figure 12). Further, two evidently ambiguous results were yielded by the statistical analysis. Although the initial ANOVA demonstrated that the predictor palatability and the interaction between day and palatability had a significant effect, these significant effects disappeared once the values were recalculated according to Zar (1984). Series, as a random variable, thus evidently introduced a bias into the initial analysis. With respect to all other factors and all interactions (two-way, three-way, and four-way) between them, there were no significant effects (Table 4).

Table 4 : Results of ANOVA testing the prediction of the second hypothesis (i.e. aposematic coloration facilitates avoidance learning). Data from experiment 1 and 2 were used (N= 144; data transformed using Arcsin square root). F-ratio and P values obtained from the initial ANOVA and the recalculated values for these parameters (as recommended by Zar 1984) are shown. The critical level of significance was set at P = 0.05.

Source of variation	Df	F-ratio	P	F-ratio recaculated	Df_1	Df_2	P recalculated
Day	2	1.528	0.222	30.636	2	2	0.032
Color	2	0.167	0.846	0.076	2	2	0.929
Palatability	1	40.149	0.000	13.783	1	1	0.168
Series	1	0.144	0.705	0.145	1	108	0.704
Day*Color	4	0.172	0.952	1.152	4	4	0.447
Day*Palatability	2	3.579	0.031	10.260	2	2	0.089
Day*Series	2	0.049	0.953	0.049	2	108	0.952
Color*Palatability	2	0.004	0.996	0.009	2	2	0.991
Color*Series	2	2.193	0.116	2.190	2	108	0.117
Palatability*Series	1	2.913	0.091	2.909	1	108	0.091
Day*Color*Palatability	4	0.261	0.903	1.289	4	4	0.406
Day*Color*Series	4	0.148	0.963	0.149	4	108	0.963
Day*Palatability*Series	2	0.348	0.707	0.348	2	108	0.707
Color*Palatability*Series	2	0.487	0.616	0.484	2	108	0.618
Day*Color*Palatability *Series	4	0.204	0.936	0.204	4	108	0.936

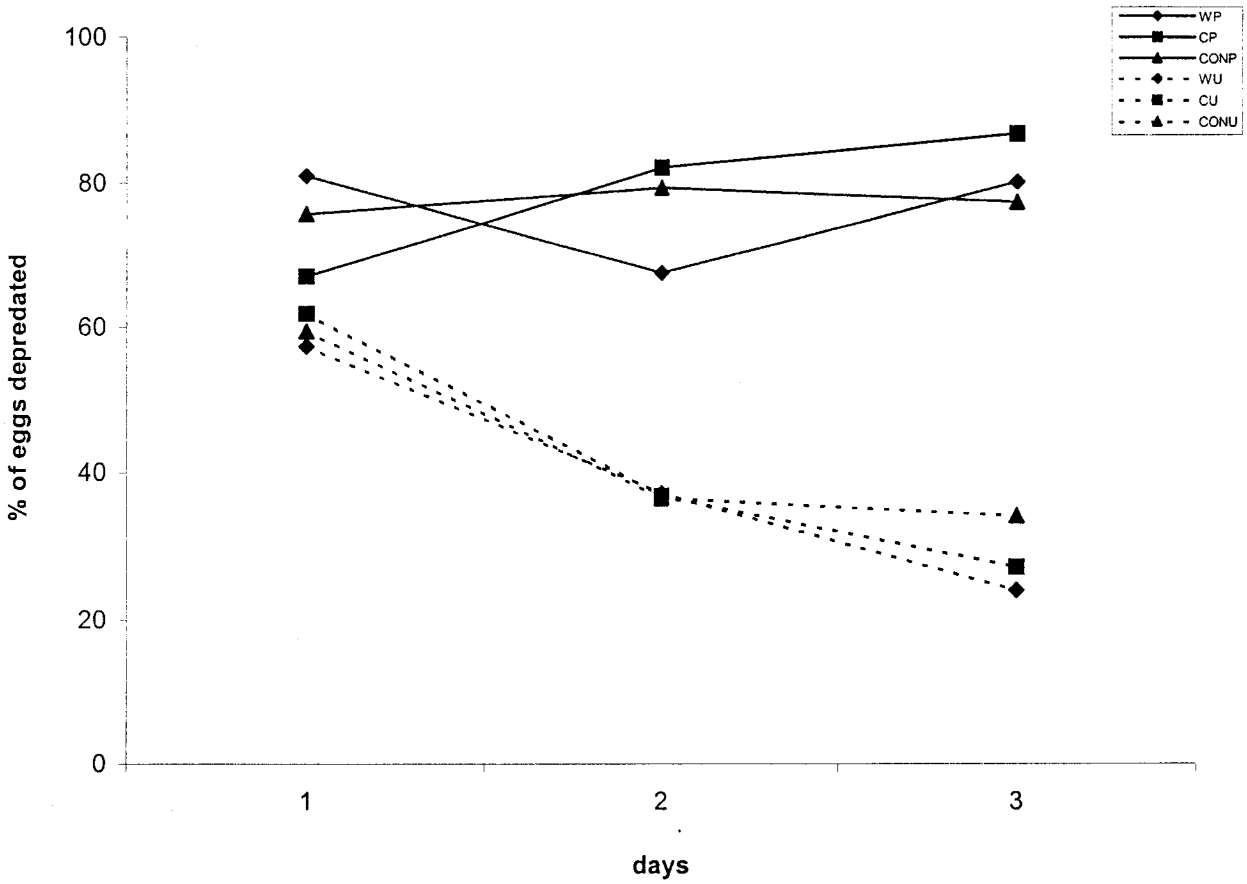


Figure 12 : Percentage of depredated unpalatable and palatable eggs by crows in experiment 1 and 2 during a period of three days (both time series combined). N = 288 eggs for each data point. For abreviation explanation see figure 10 and section methods.

Extinction rate

The rate of extinction of avoidance response is shown in Figure 13. I selected Control 2 only for the purpose of this test. I excluded control 3 because crows are known to experience difficulties with prolonged testing programs (Matyniak et al., 1971). In addition, I selected only those cases where eggs had unpalatable contents in experiment 1. A difference (or change; Δ) was calculated between the proportion of depredated eggs from the last day of experiment 1 and the proportion of eggs depredated each day of the control 2 period. Data are presented as a percentage of depredated eggs (number of depredated eggs/N) x100, and sample sizes are shown in figure 13.

Results of the statistical analyses are ambiguous since there was a significant difference between the three types of egg coloration patterns before recalculating the F-ratio and P values, as proposed by Zar (1984; see table 5). The non-parametric analysis also yielded a significant effect of coloration pattern ($P = 0.02$). A Bonferonni test demonstrated that warning coloration was significantly different from conspicuous coloration ($P = 0.028$), but did not differ from the cryptic coloration ($P = 1.000$). However, when the values were recalculated according to Zar (1984), no significant effect of egg coloration pattern was found (table 5). However, because series had a significant effect, I performed separate ANOVA analyses for each time series (table 6).

In series 1, a significant difference was found between coloration patterns (table 6). The difference lay between warning and both conspicuous ($P = 0.032$; very close to the significance level of $P = 0.025$) and cryptic coloration ($P = 0.039$; also close to the critical level of $P = 0.025$). Unfortunately, this result is ambiguous because of the P-values obtained from this test. However, my data do suggest that the depredation rate on eggs with warning coloration were increasing at a slower rate than those on eggs with conspicuous or cryptic coloration (figure 13).

In contrast to results of the series 1, in series 2, no significant difference was found in the speed of extinction of avoidance response between the three egg coloration patterns. The speed of extinction of the avoidance response was not significantly different between the three types of coloration but there was an indication of differences between warning coloration and both conspicuous and cryptic coloration in series 1(the effect of coloration patterns is close to the significance level; table 6).

Table 5 : Results of ANOVA testing the prediction of the third hypothesis (i.e. crows continue avoiding eggs with warning coloration longer). The cases that were selected for this analysis come from the difference between the proportion of depredated eggs from the last day of experiment 1 and the proportion of eggs depredated each day of the control 2 period. (N= 48; data transformed using Arcsin square root). F-ratio and P values obtained from the initial ANOVA and the recalculated values for these parameters (as recommended by Zar 1984) are shown. The critical level of significance was set at P = 0.05.

Source of variation	df	F-ratio	P	F-ratio recaculated	Df_1	Df_2	P recalculated
Color	2	4.114	0.029	0.688	2	2	0.592
Day	3	0.097	0.961	0.455	3	3	0.733
Series	1	51.876	0.000	51.990	1	24	0.000
Color*Day	6	0.310	0.926	1.391	6	6	0.349
Color*Series	2	5.985	0.008	6.000	2	24	0.008
Day*Series	3	0.209	0.889	0.214	3	24	0.886
Color*Day*Series	6	0.227	0.964	0.223	6	24	0.965

Table 6 : Results of ANOVA for each of the two series concerning the prediction of the third hypothesis (i.e. crows continue avoiding eggs with warning coloration longer. Data (selected from control 2 only) were transformed using Arcsin square root. F-ratio and P values are shown and the critical level of significance was set at P = 0.025 (see Zar, 1984; N = 24 for series 1 and N = 24 for series 2).

	Source of variation	Df	F-ratio	P
Series 1	Color	2	5.880	0.017
	Day	3	0.242	0.866
	Color*Day	6	0.232	0.958
Series 2	Color	2	3.910	0.049
	Day	3	0.031	0.992
	Color*Day	6	0.317	0.916

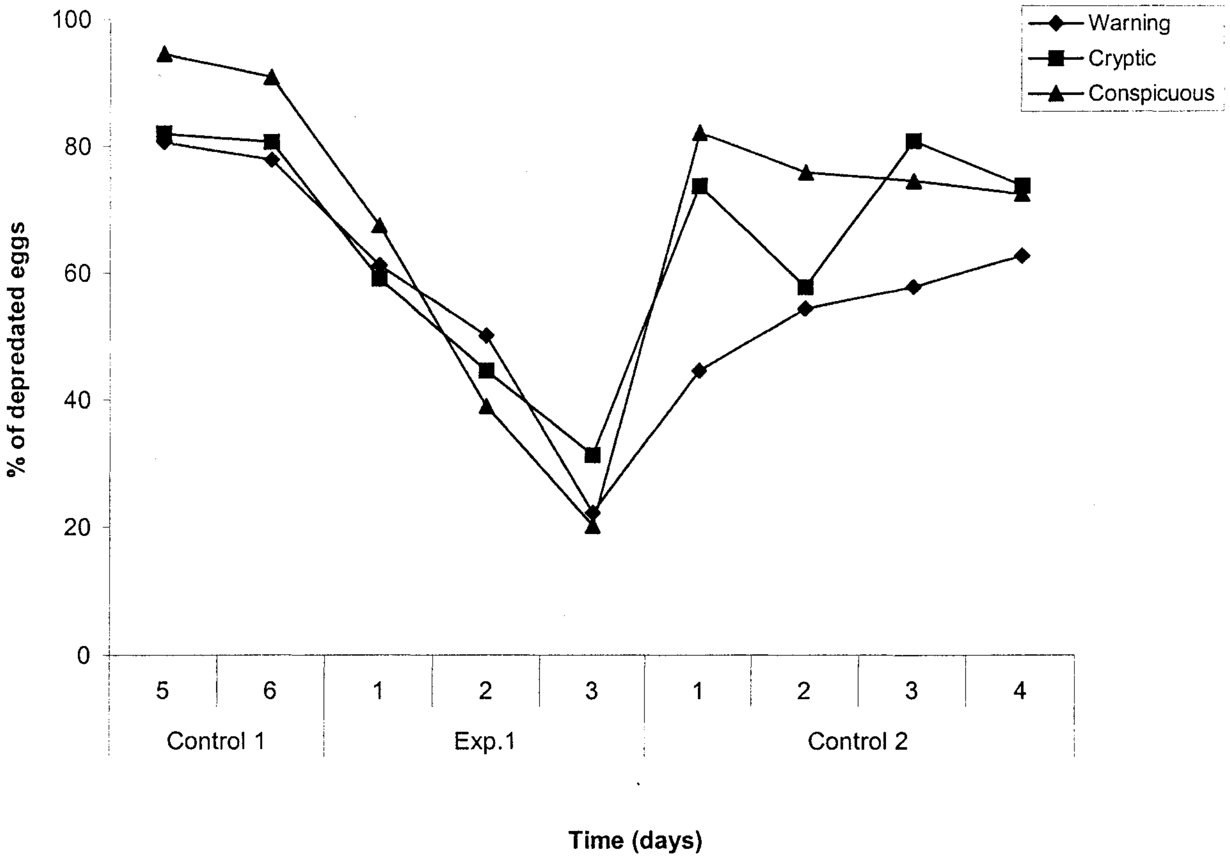


Figure 13: Rate of extinction of the avoidance response after three days of exposure to unpalatable contents of eggs with the three coloration patterns. The two time series were combined (N = 144 eggs for each data point except for conspicuous coloration on day 6 of the control 1, when N= 108 eggs).

Discussion

Three major conclusions may be drawn from this study. First, the avoidance response by the American crows towards eggs with warning coloration does not appear to be an inflexible genetically controlled act, but instead shows high flexibility which demonstrates a strong learning component. The results showed that crows did not avoid, in a majority of cases, eggs with warning coloration during the first encounter. This finding is consistent with those of other studies (Forsman and Merilaita, 1999; Gamberale-Stille, 2000, 2001; Gamberale and Tullberg, 1996; Gittleman and Harvey, 1980; Gittleman et al., 1980; Guilford and Dawkins, 1991; Roper, 1994; Roper and Redston, 1987; Roper and Wistow, 1986; Schuler and Hess, 1985; Servedio, 2000), even though some studies also reported strong innate avoidance (Brodie, 1993; Brodie and Janzen, 1995; Caldwell and Rubinoff, 1983; Lindström, 1999, 2001; Mastrota and Mench, 1995; Roper and Cook, 1989; Rowe and Guilford, 1985; Roper and Cook, 1989; Rowe and Guilford, 1985; Schuler and Hesse, 1985; Smith, 1975).

However, a surprising result was that crows did not learn faster to avoid eggs with warning coloration compared to eggs with conspicuous or cryptic coloration, which is contradictory to what a majority of other studies found (see e.g. Gittleman and Harvey, 1980; Gitleman et al., 1980; Roper, 1994; Roper and Redston, 1987; Roper and Wistow, 1986). My study indicated that the rate of depredation decreased similarly for all three egg types, and that crows were able to learn to avoid them regardless of their coloration.

Finally, the third main conclusion reached is that the extinction of avoidance response occurred, in an ambiguous way, slower for eggs with warning coloration compared to eggs with conspicuous or cryptic coloration. This was similar to what Roper

(1994) observed. Therefore, crows seemed to be able to remember longer the association between unpalatability of prey (egg contents) and its coloration when that coloration was aposematic than when it was cryptic or conspicuous.

Innate or learned avoidance?

Some birds can avoid certain insects that they believe to be unpalatable on the first encounter (Schuler and Roper, 1992). Moreover, it was shown that free-ranging birds (naive or experienced) are sometimes genetically predisposed to avoid certain color patterns (e.g. those including black and yellow patterns; Lindstöm et al., 1999; Roper and Cook, 1989; Schuler and Hesse, 1985; Siemens and Greene, 1995). Therefore, innate avoidance can be adaptive if prey encountered are highly poisonous and hence lethal to predators (Allen and Cooper, 1994; Roper and Schuler, 1992). In such cases, all individuals should avoid prey upon recognition. In this study, based on control 1 (see figure 11), no statistically significant differences were observed between all types of coloration patterns. Therefore, I conclude that crows did not show a strong preference for any of the coloration patterns I tested. Eggs with conspicuous coloration were slightly more depredated (78%, see figure 11) and by separating both time series P-values were still close to the significance level (Table 3). Therefore, color may be important, but perhaps the sample size was inadequate. This result may be explained by the fact that conspicuous colors, such as white, may attract attention of predators first, therefore resulting in a higher depredation rate (Gamberalle-Stille, 2001; Lindström et al., 2001). In addition, other confounding variables might have masked the predicted effects.

Moreover, crows might have avoided eggs with warning coloration at first, but then through sampling found that these eggs were actually edible and started to depredate on them. Unfortunately, observations did not allow me to notice any preference (clearly the use of cameras could have been useful for that purpose). Another possible explanation for this lack of color preference is the fact that adults might associate the shape of eggs with palatable prey (Lindström et al., 1999). In addition, crows are also considered more bold and would have depredated on eggs with warning coloration anyway (Lindström et al., 1999). Moreover, according to Schuler and Roper (1992), compared to mammals, birds are less sensitive to chemicals and react and respond more ambiguously. Schuler and Roper (1992) also suggested that the study of innate responses requires the use of naive individuals. In my case, I do not know how many individuals were affected by prior experience. However, it was found that chicks who had been previously fed on yellow food still avoided black and yellow striped prey (Schuler an Hesse, 1985). Therefore, even with previous experience .concerning specific colors, an avoidance response can be observed. Since crows did not avoid eggs with warning coloration pattern in any of the cases, I conclude that they did not have a genetically fixed predisposition to avoid yellow and black patterns.

It is important to mention that at the very beginning of the study, on two of the sites, the presence of crows was noticed but no depredation occurred on any of the three color types of eggs. These individuals were probably afraid of the eggs regardless of their colors. However, brown chicken eggs are similar in coloration to eggs of ruffed grouse (*Bonasa umbellus*) and wild turkey (*Meleagris gallopavo*; Hogrefe et al., 1998). Therefore, crows could have been afraid of eggs with warning or conspicuous coloration depending on the treatment involved which eventually derived to avoidance of brown eggs also. Since at these two sites crows avoided all three color patterns, early experience with warning colors is not likely the best explanation. Therefore, the best explanation for the observed reaction is probably neophobia. Neophobia refers to fear of novel things and it usually does not persist as long as innate avoidance. Neophobia is also defined as the fear of novel food source rarely consumed or encountered by generalists, such as crows (Jones, 1986; Lindström et al., 1999; Marples and Roper, 1996). Moreover, neophobia usually occurs in small habitats for generalists (Heinrich, 1988, 1995). Neophobia would be adaptive when novel morphs appear in nature and where these novel prey survive because predators avoid them by fear (Gamberale-Stille and Tullberg, 1999; Marples et al., 1998). Therefore, genetically fixed predisposition would not be necessary in the majority of cases to allow the selection of warning colors.

Furthermore, Heinrich (1988) examined the fear of novel food in corvids. He found that corvids, in general, did not peck new food items until 25 to 74 hrs after discovery. Therefore, for the purpose of my study I used two new sites to avoid loss of data. This also explains why control 1 in series 1 (see figure 10) has 6 days instead of 4 like in the original set up.

In any case, these two sites were evidently the exception. On the other hand, neophilia (attracted by new things) was also observed by Heinrich (1995). Heinrich (1995) found that young ravens were more attracted to new objects regardless of their conspicuousness or the degree of unpalatability. Of course, after a while the raven exhibited a preference towards palatable objects. Therefore, all other sites reflected this behavior.

Even when investigators observed innate avoidance, some found that a negative reinforcement is necessary to preserve it (Lindström et al., 1999; Schuler and Hesse, 1985). Even Heinrich (1988) suggested that young hand-reared ravens can display innate avoidance towards novel food items but truly need learning through individual and social experience to be able to identify edible food item. In conclusion, the avoidance response by the American crow in the present study appears to be based mostly on learning.

Learned avoidance

Avoidance of aposematic coloration is often considered to have been acquired through learning (Lindström et al., 2001; Mastrota and Mench, 1995; Schuler and Hesse, 1985). Moreover, individual and social learning are considered very important for birds in establishing edibility of food (Heinrich, 1988; Langen, 1996; Ward and Low, 1997). Predators are known to learn to associate unprofitability or unpalatability of prey with conspicuousness rather than cryptic patterns of coloration (Gittleman and Harvey, 1980; Lindström et al., 2001; Terrick et al., 1995). To my knowledge, no previous studies have been done that would compare the effect of warning, conspicuous and cryptic coloration on the avoidance learning. I designed experiments 1 and 2 to examine this problem.

My results showed that crows avoided similarly the three types of unpalatable eggs, regardless of their coloration. The depredation rates decreased from about 70 % to 25 % for each coloration patterns. However, the rates did not decline to 0 %. This could be explained by crow's continuation of sampling to detect changes in food edibility

(Avery and Decker, 1994; Marples et al., 1994). Thus, it is possible that crows continued pecking the eggs to confirm their unpalatability. Heinrich (1995) hypothesized that birds exposed to a large range of objects in their environment would be attracted to a novel object. This could be a result of exploratory behavior. Therefore, through trial and error, birds would learn to select the appropriate food sources. Schuler and Hesse (1985) also found that chicks approached black and yellow prey and pecked them eventually (after repeated exposure), suggesting that their initial aversion to prey with black and yellow coloration was gradually lost. Furthermore, Allen and Cooper (1994) proposed that learning could occur after the prey has been attacked but not consumed. Schuler and Hesse (1985) found that when chicks were presented with yellow and black prey, they pecked at the prey but did not consume it. In my study, depredation was implied when an egg was pecked. However, consumption may or may not have occured (unfortunately this was not studied). Therefore, similar depredation on eggs with the three color patterns may be a result of a bias caused by the index I used to establish if depredation occured. However, Guilford (1985) reported that chicks attempted to distinguish palatable from unpalatable items before pecking at the prey.

Overall, my results showed that crows did not learn faster with warning coloration compared to conspicuous and cryptic coloration. In fact, crows learned to avoid all unpalatable eggs, regardless of their coloration. These results are consistent with a study cited by Schuler and Roper (1992) where toads were offered a black and yellow striped stick along with a blue stick. Toads learned to avoid both prey types at the same rate. Kawaji (1994) also concluded that depredation rates on artificial nests are not significantly related to egg colors (white and brown). Furthermore, in another experiment (with a similar design as in my study), two groups of predators (chicks) were offered two different prey types: a black and yellow prey and a green prey. The first group was offered unpalatable black and yellow prey and palatable green prey. The second group was given unpalatable green prey and palatable black and yellow prey. Results of this study showed that avoidance learning in chicks was not influenced by coloration, which is similar to my results (see also Schuler and Roper, 1992).

However, my results contradict those of the majority of other studies, which have shown that conspicuous colors contrasting with background are learned more easily than cryptic colors (Gittleman and Harvey, 1980; Lindström et al., 2001; Roper and Redston, 1987). Some of these studies used unpalatable prey only (Gittleman and Harvey, 1980; Roper and Redston, 1987; Roper and Wistow, 1986, Roper, 1994), whereas others included both palatable and unpalatable prey (Gittleman et al., 1980; Alatalo and Mappes, 1996; Lindström et al., 1999). Lindström (1999), therefore suggested that we should be careful when interpreting results of different studies. Moreover, most earlier studies used one or two individuals in a laboratory set up, whereas I used free-ranging crows in their natural environment. In fact, I observed more than two crows at most of the study sites. Therefore, because crows are social animals and possess an information network, this could have lead to a faster rate of learning with all types of coloration patterns affecting the outcome of my study. Because of my experimental design, I believe that my results are more representative of what could be really occuring in a natural environment.

My results are also inconsistent with the finding that birds learn faster with novel prey (Roper and Redston, 1987). Yellow and black eggs were novel prey for crows but this did not affect the speed of their avoidance learning. It is possible, however, that this color pattern might not have been novel for crows in my area. However, I noticed several signs of neophobia in some of the crows which suggests that the coloration pattern was novel for at least those individuals studied. In addition, since generalist predator species are considered to be bolder towards novel prey than specialists, this could explain why some individual crows depredated on eggs with warning coloration in a similar manner as on those with conspicuous and cryptic coloration (Lindström et al., 2001).

Nevertheless, some authors believe that prey coloration in general (including egg coloration) is an important cue facilitating learning in foraging predators, including crows (Clarke et al., 1979; Marples et al., 1994; Mason and Reidinger, 1983; Nicolaus, 1987; Schuler an Hesse, 1985; Sugden, 1987; Verbeek, 1990). Ingalls (1993) suggested that objects possessing bold black patterns produce avoidance reactions in an effective way, but this is obviously not the case in my study.

Lindström et al. (1999) found that weak signals prevented birds from learning to separate unpalatable aposematic signals from cryptic ones. Therefore, according to Lindström et al. (2001), it seems that a certain threshold in conspicuousness signals has to be reached to allow an association between unpalatability and coloration to develop and also to allow predators to learn to avoid such prey. Even if a slight difference appears between the color of prey and the background, this might influence predators (Lindström et al., 2001). Therefore, there is a possibility that cryptic eggs might not have been that cryptic after all. Hence, crows could have learned to avoid eggs with cryptic coloration in a similar manner as those with conspicuous and warning coloration patterns. On the other hand, eggs with warning coloration might be considered as cryptic from a distance (due to disruptive coloration) but as conspicuous at a closer distance (Gamberalle-Stille, 2001).

Furthermore, the knowledge of color preferences is important since birds use visual cues to select suitable food items and avoid unpalatable ones. Therefore, Roper and Marples (1997) concluded that depending on the method of presentation of bait (with liquid or solid food), the color preference is likely to be affected. However, these authors used only small bait such as seeds, crumbs and grains, which is very different from eggs used in the present study and from field conditions where food is mostly scattered (Roper and Marples, 1997).

In addition, preference for certain colors could be biased by the fact that parents teach their young what is beneficial to eat and do not teach them necessarily what to avoid (Lindström, 1999). Thus, crows might have been taught that any eggs are good and that egg coloration was never associated with unpalatability. On the other hand, it is believed that color preference could allow young naive predators to avoid aposematic prey during their first encounter (Lindström, 1999). Hesitation may have occurred, but color biases may have allowed sampling or may have favored the avoidance learning (Lindström, 1999). Therefore, it is more likely that crows did sample the eggs and then established that eggs with warning coloration were palatable during control 1. This could explain why crows did not exhibit a genetic predisposition for avoidance of warning coloration and considered the three types of eggs as equal at the start. The high level of behavioral flexibility in crows is also reflected in the avoidance learning later on in the experiments. This contradicts Lindström's (1999) finding concerning the preference for brown prey compared to yellow prey at the very beginning of their experimental procedure.

Lindström (1999) also proposed that the use of artificial prey (i.e. the use of symbols) offers a useful tool allowing researchers to examine the role of color preference and prey conspicuousness. In contrast, Schuler and Roper (1992) argued that artificial objects in laboratory studies would not be useful for the examination of color preference. However, the prey I used in my study (eggs) represents a real prey. Because an egg is not a live prey, it cannot exhibit flexible behavioral responses. Live prey, such as insects, tend to use multimodal displays with odors, sounds and different behaviors which could influence outcomes of a study (Lindström, 1999). Mappes et al. (1999) suggested that efficiency of depredation may vary according to learning and visual capabilities of predators involved, their early experience, the complexity of their environment, and different prey types. Different prey types could include prey of varying degrees of edibility, crypsis and signal characteristics (kind and strength of signal; Mappes et al., 1999) or even prey possessing multimodal displays (Rowe and Guilford, 1999).

Smell rather than coloration, might be responsible for the association with unpalatability in avoidance learning. However, Marples et al. (1994) found that color was the most effective cue and smell the least effective one (birds failed to associate the smell of a seven-spot ladybird with unpalatability). On the other hand, Roper and Marples (1997) found that birds can use odors in taste-avoidance learning and that in some cases they can be more effective than visual cues. It is known that not all odors act equally (Roper and Marples, 1997). Moreover, it was shown that only a certain proportion of avian species can detect a wide range of odors (Roper and Marples, 1997).

The eggs used in the present study were not filled completely with the unpalatable mixture, reducing the possible effect of odor. Moreover, the level of repellency could have influenced the rate of learning. The unpalatable mixture was prepared in the same way each time, which eliminates the possibility of having prey with varying degrees of edibility. In addition, the repellency of the mixture was effective since the depredation rates on unpalatable eggs decreased significantly with time, regardless of coloration patterns. It is important to remain cautious because if the repellent used was too aversive, the learning response could be too fast to be useful in studying the effect of coloration (Schuler and Roper, 1992). Brett et al. (1976) concluded that taste cues were more effective than color cues for red-tailed hawks (*Buteo jamaicensis*). In contrast, several other studies reported that taste was less effective than color but that it still facilitated the association of unpalatability with coloration (Clarke et al., 1979; Franchina et al., 1993; Westbrook et al., 1980).

It appears that crows may not possess a good color vision. Color patterns, such as yellow and black coloration used in the present study, include contrasting light and dark patterns and even predators lacking good color vision could learn to avoid such patterns (Terrick et al., 1995). However, birds, in general, are known to possess excellent color vision (Lyytinen et al., 2001; Osorio et al., 1999). It was also established that some birds are able to see in the near-ultraviolet light (320-400 nm; Lyytinen et al., 2001; Majerus et al., 2000; Osorio et al., 1999). Furthermore, several recent investigations were designed to establish if prey apparently cryptic to a human eye could appear conspicuous to birds in the UV light. However, Lyytinen et al. (2001) found that warning signals based on UV signals are not effective. These authors concluded that the studied birds did not have the predisposition to learn to distinguish between unpalatable and palatable objects on the basis of UV light (Lyytinen et al., 2001).

Crows did not exhibit any predisposition to avoid warning coloration as predicted. Crows also learned to avoid unpalatable eggs of different coloration similarly, contrary to what was predicted. However, did they retain the avoidance of eggs with warning coloration longer as reported previously (Roper, 1994)?

Extinction of avoidance

Predators, in a majority of cases, learn to associate unpalatability of prey more easily when it is conspicuous (Lindström et al., 2001). However, this was not the case for crows in the present study. Earlier studies established that predators also tend to retain the avoidance response for a longer period of time when prey coloration is conspicuous (Gamberalle-Stille, 2001; Roper, 1994, Roper and Marples, 1997; Roper and Redston, 1987). Controls 2 and 3 were designed to verify this observation in crows. However, because crows apparently experience difficulties with respect to learning during prolonged behavioral testing programs (Matyniak et al., 1971), I excluded control 3 from the following test.

Results from control 2 are ambiguous and suggest that the extinction of the avoidance is similar for all types of coloration patterns. However, if we take into consideration only series 1, there is a weakly significant difference between warning and both conspicuous and cryptic coloration. The examination of the trends in figure 13 leads to a conclusion that the extinction rate was slightly slower for eggs with warning coloration than for eggs with conspicuous or cryptic coloration. Even series 2 provides weak evidence (P value very close the the level of significance) that warning coloration is remembered longer (see table 6). Therefore, I conclude that crows do remember to avoid warning colors longer than conspicuous and cryptic colors. However, a larger sample size or a more powerful experimental design addressing this problem would provide a more definite answer.

According to Guilford and Dawkins (1991) many factors could contribute to the association between different events, such as coloration and edibility, and how long this association will be retained. These factors could include the intensity of the signal (contrasts), novelty of the signal and if there is any reinforcement involved (punishment or reward). In my study, crows seemed to remember longer to avoid warning colors (at least in series 1). However, the effect of contrast is probably not sufficient to explain why crows remembered longer to avoid eggs with warning coloration since eggs with conspicuous coloration (white eggs) were also considered as a highly contrasting prey. In this case, the pattern and a combination of specific colors may be more memorable than conspicuousness itself. Osorio et al. (1999), who studied memory of visual signals in chicks implied that different aspects of a stimulus might play separate roles (while color contrast may attract attention, a specific combination of colors may play the role in retaining information). However, these authors found that chicks possess a good memory for coloration but not necessarily for patterns which attract attention. If this was true for all species, then crows in my study should have exhibited a slower extinction of avoidance for eggs with both warning and conspicuous coloration patterns. Furthermore, novelty of the prey could have influenced the retention of the aversion, thereby introducing noise into my results. However, as I stated earlier, yellow and black coloration patterns might have not been that novel for at least some of the crows studied.

Implications of results for the evolution of warning coloration

According to Lindström (1999) and Allen and Cooper (1994) there are three major hypotheses that partly explain how conspicuous morphs could have evolved. These hypotheses are based on predator psychology (and not on the prey's point of view) and concentrate on the benefits of unpalatable conspicuous prey compared to cryptic prey. The first hypothesis is that predators should learn faster to avoid conspicuous unpalatable prey (Allen and Cooper, 1994; Gittleman et al., 1980; Lindström, 1999). The second is that predators should remember longer to avoid conspicuous prey (Allen and Cooper, 1994; Gittleman et al., 1980; Lindström, 1999). Finally, the third hypothesis proposes that predators should make fewer recognition errors when prey is conspicuous (Allen and Cooper, 1994; Gittleman et al., 1980; Lindström, 1999). Moreover, to establish if conspicuous coloration is more advantageous compared to cryptic coloration a comparison should be made between unpalatable conspicuous prey and unpalatable cryptic prey (Lindström, 1999). Thus, my study followed this suggested model.

Explaining the evolution of warning coloration based only on avoidance learning is not really sufficient since crows in my study did not learn faster with warning coloration. It was shown earlier that birds tend to learn faster with conspicuous colors and therefore populations of conspicuous color individuals could be maintained this way (Marples et al., 1998). However, conspicuousness brought one problem in explaining the evolution of warning coloration since the novel conspicuous morph would attract the attention of predators who would attack and hence potentially remove it from the population (Marples et al., 1998). Results of Marples et al. (1998) showed that blackbirds (*Turdus merula*) and robins (*Erithacus rubecula*) vary in their responses towards yellow, red and green baits where some took longer to eat the baits. This study suggested that prey with aposematic coloration did not necessarily suffer higher depredation than the cryptic ancestors (Marples et al., 1998). This has been also shown in the present study during control 1. Furthermore, responses of predators could have been altered by evolution. Therefore, it was suggested that the increased domestication in chicken, for example, resulted in a decreased intensity of the response towards prey with warning coloration (Schuler and Roper, 1992). It might be possible that crows that have been exposed to an increased urbanization responded in a similar way as chicks with increased domestication, thereby possibly explaining the lack of a significant effect of coloration on avoidance learning. The evidence that a learned avoidance is adaptive is weak according to some authors and requires further research (Schuler and Roper, 1992).

Finally, crows did remember longer to avoid eggs with warning coloration compared to eggs with conspicuous or cryptic coloration as expected from prior reports (Gamberalle-Stille, 2001; Roper, 1994, Roper and Marples, 1997; Roper and Redston, 1987; Schuler and Roper, 1992). The evolution of aposematic coloration could be influenced by the rate of learning by predators and also by the way they remember to associate color with unpalatability (Guilford, 1990; Guilford and Dawkins, 1991; Servedio, 2000). Moreover, according to Servedio (2000), the effect of forgetting would have more importance than learning since it was also shown that predators can learn to avoid unpalatable cryptic prey. More studies are necessary to verify if crows really remember longer or not. This demonstrates that conspicuous coloration may not be necessary to enable the association between palatability and color (Guilford, 1988). Therefore, conspicuous coloration may not have an aposematic role (Guilford, 1988).

However, all three hypotheses were not directly tested (including the recognition error hypothesis not tested in the present study) but still could be used to explain the evolution of warning colors. The mechanisms implied by the three hypotheses could have contributed to the evolution of warning colors and cannot be mutually excluded from one another. Caution in interpretation as to be applied as for the implications of these results for the evolution of conspicuous morphs. Thus, my study was based on a frequency of 50 %-50 % for two different colorations (like a majority of studies) depending on the treatment involved at a specific site (Lindström, 1999). However, since conspicuous morphs are considered prey evolved from a cryptic ancestor and were initially rare, this might influence the real implication of conspicuous and warning coloration. On the other hand, it is also hypothesized that in the ancestral population conspicuous morphs could have already been represented in high densities if degree of crypsis varied between individuals of the cryptic population (Allen and Cooper, 1994). No clear answer exists and the evolution of warning coloration is an amalgam of hypotheses and theories that still need empirical evidence.

General trends

I will discuss some general trends from the experimental design which is a series of 5 experiments (control 1, experiment 1, control 2, experiment 2, control 3) and three combinations of colors (W vs CON; W vs C and CON vs C). Therefore, I predicted that during controls (1, 2 and 3) there would be no significant difference between the rate of depredation on both color types involved at least at the end of the control periods. The prediction for the two experiments was that the unpalatable eggs should be less frequently depredated than the palatable eggs regardless of the color pattern involved. Overall, the predictions were supported by results of the study (figures 10 and 14 to 18).

Marples et al. (1998) studied the responses of blackbirds (*Turdus merula*) and robins (*Erithacus rubecula*) towards novel colored prey in their natural environment. They used red, yellow (aposematic prey) and green baits (cryptic prey). The results showed higher depredation rates on red and yellow prey than on prey with green coloration. These results were inconsistent with a majority of studies. Compared to results of laboratory studies, they found a much greater variation between individual birds in the response to differently colored prey. Moreover, Marples et al. (1998) even found variation between individuals sharing the same territory. Because my study was conducted directly on crow's territories, some variation in their responses is to be expected.

A possible explanation for some of the noise in data obtained from the 12 different sites is the fact that 6 sites were studied in series 1 (earlier in the season) and the other 6 sites were studied in series 2 (later in the season). The rate of depredation by crows decreases later in the breeding period (Sullivan and Dinsmore, 1990). I also observed a slight decrease in depredation by crows, which occurred towards the end of the second series of the experimental period, which represents the end of the breeding season (Sullivan and Dinsmore, 1990). Moreover, through statistical analysis I found that the factor series influenced some of the outcomes. Therefore, the rate of egg depredation could be affected by seasonal shifts in foraging habitats, or it could reflect a change in the nutrient requirements (Maccarone, 1991; Sullivan and Dinsmore, 1990). These two different periods thus may have represented different nesting stages. If the breeding crows are not in the same stage of nesting, then their energy requirements are likely to be different. The decrease in the depredation rates might also be due to the crow's confusion after the experimental period and not necessarily due to different time frames. Moreover, eggs provided during the course of the study might have been only a supplementary food source. Therefore, the depredation rates observed on study sites were probably not really representative of the crow's real energy demands. On the other hand, Yahner et al. (1989) noticed that artificial nests were more depredated than natural nests because of the greater conspicuousness of artificial nests. In this case, the eggs could have been the primary source of food for some of the groups of crows studied. These possibilities might explain why depredation rates varied significantly between sites.

It is also known that crow's food resources may vary between seasons according to insect cycles and agricultural cycles (Maccarone, 1991). Because the study started in April (colder temperatures) and finished in June (warmer temperatures), these two types of cycles have likely changed and this may have influenced results. However, crows are known to adapt to many kinds of changes. For example, it is possible that crows preferred the experimental eggs and influenced the depredation rates if a change in their usual food supply availability appeared during the course of the study. Maccarone (1991) also observed that crows maintained similar foraging patterns and experienced relatively stable food supply throughout their breeding season. Yahner et al. (1989) also observed that depredation on avian nests by crows did not vary with time (May to July for their study). Therefore, I conclude that the two experimental periods (time series) that were included in my study probably did not affect the depredation rates. However, the factor series is still considered to be a random variable and the best way of designing the experimental period would have been to use 12 sites in one series only. Unfortunately, due to the amplitude of the study this was not feasible. To deal with the problem, I transformed data as was suggested by Zar (1984).

Another possible explanation for the variation observed between sites concerns differences in temperature and weather conditions (Kilham, 1990, Ward and Low, 1997). Luginbuhl et al. (2001) showed that with even light rain the depredation rates by corvids on artificial nests decreased significantly. In the present study, day 2 of control 1 (series 1), for example, was a rainy and windy day and the depredation rate seemed to decrease at that point for most of the sites. However, a significant effect of temperature was not observed for each site (see figures 10 and 14 to 18 in appendix A). Therefore, depending on the site and the proximity to protective cover, temperature could have affected some crows more than others (Ward and Low, 1997). Moreover, it is also important to mention that snow covered the nests for two consecutive days, explaining the greater duration of control 1.

The depredation rates could have been influenced by occasional sampling (Dimmick and Nicolaus, 1990). Depredation was implied when an egg was gone or pecked but a puncture did not necessarily represent complete depredation since the content was not in all cases entirely consumed. This technique, called occasional sampling, can be adaptive in the presence of mimics (Marple et al., 1994). Thus, predators can detect changes in prey quality and therefore eventually detect mimics (Marple et al., 1994). In the present study some crows might have been sampling more than others.

Another explanation for fluctuations and noise in data is that a large number of individuals or members of some family groups might have increased the number of individuals per site usually encountered. However, I did not observe more than 10 individuals per site. Thus, since a family group can include up to 15 individuals, the probability that there were two family groups at some study sites is weak. Moreover, if two or more different groups were present, I would probably have observed conflicts between individuals which I did not (Kilham, 1985, 1990; Stouffer and Caccamise, 1991). Caccamise et al. (1997) also suggested that food sharing is probably an important factor in social bonds such as in cooperative breeding. Crows were most probably sharing food and were presumably not competiting for it. Moreover, group size could also increase vigilance in foraging crows (Ward and Low, 1997). Therefore, sites with higher disturbance caused, for example, by cars or human activities, were usually represented by larger groups which could have influenced depredation.

Furthermore, Ward and Low (1997) suggested that group size is related not only to protective advantages, but also to social learning, leading to increased foraging efficiency. Even with large number of individuals, if they have a well established communication system necessary to transfer foraging information, crows should learn to avoid unpalatable eggs. Thus, in most sites, where large numbers of individuals were observed, a high rate of learning was observed since crows did learn quickly to avoid unpalatable eggs (Kilham, 1990; Langen, 1996). Moreover, it was shown that large groups of individuals tend to have less food available in their territories compared to single nesters (Shank, 1986). Therefore, larger groups could have been depending on eggs more than smaller groups. This could have further affected my results.

According to Savage (1996), younger crows tend to be more gregarious. Therefore, age of individuals should also be considered as a factor affecting depredation rates. Groups of immatures probably do not have a well established communication network, and they are certainly not at the same level as adults in the learning process. Site 5 (series 2; see figure 18), for example, might represent this situation since all crows ate everything (complete depredation) including unpalatable eggs, without learning to avoid them.

Arrival of new individuals in the middle of the experimental procedure, on some of the study sites, might have also introduced noise into the results. This could be explained by the fact that most avian predators use random search to find food sources and nests, and once found, memorize the location (Andrén, 1992; Heinrich, 1988; Götmark et al., 1990). Some authors even believe that crows might form a search image for different nest sites (Kilham, 1990; Yahner and Wright, 1985). Moreover, since eggs contribute only 1% to corvids food requirements, it has been suggested that crows probably find nests by chance (Andrén, 1992). Therefore, the relative importance of predators might be affected by the abundance of individuals of different species and their searching efforts (Andrén, 1992). Crows searching more intensely might have discovered the nests quickly, whereas others discovered nests later in the experimental period. It seems that crows could have learned to use the presence of experimenters in finding nests (Götmark et al., 1990). However, the field workers were present at all sites for each of the depredation checks, thereby creating the same bias at all sites.

Location of the study sites directly on a territory or near the boundary of territories could have also affected my results. It was shown that nests placed in the crow's breeding home range were more frequently depredated than nests placed outside the home range limits (Sullivan and Dinsmore, 1990). This could explain why some sites experienced a higher depredation rate. Kilham (1985) noticed encounters between groups of crows along territory boundaries. However, based on literature, the 2 km distance between sites seemed adequate. No conflicts between different group members were observed. As I mentioned in Methods, the choice of location for study sites was based on several factors, such as proximity to farmland, forest edge, protective cover and the presence of perches. Not all sites had exactly these characteristics. Some sites were closer to roads, further from forest edges, or some were situated between several forest edges. Some sites were closer to farmland than others which could have resulted in a larger number of crows because crows prefer foraging on agricultural fields (Andrén, 1992, Yahner and Wright, 1985). All sites had perches and were at least located near forest edges, near forest-farmland edges or near farmland edges. Yahner et al. (1989) showed that depredation on artificial nests by crows did not vary between different degrees of edge contrast. It was shown that distance from edge had no effect on the depredation rate of artificial ground nests (Danielson et al., 1997; Hogrefe et al., 1998). Selected sites represented good quality foraging areas.

Another aspect for the selection of sites was vegetation cover. It is known that ground nests located in areas characterized by high vegetation cover are less frequently depredated by American crows than those in low vegetation (Kawaji, 1994; Sullivan and Dinsmore, 1992; Yahner et al., 1989; Yahner and Wright, 1985). Crows searching on foot found more artificial nests in sparse and short grass and also when nests were close to each other (Sullivan and Dinsmore, 1990). For this reason, I chose fields with low vegetation cover, and nests were placed at a reasonable distance from one another. However, the height of vegetation cover increased during the course of the season for each series of experiments, but the sites did not change. Sullivan and Dinsmore (1992) noticed that once crows locate a nest through aerial searching, an increase in vegetation growth (height) above 20 to 50 cm did not affect depredation rates. Sugden (1987) found that, even with different complexity of background, if eggs are entirely exposed the depredation rates will not be affected. It might be possible that some eggs were more concealed and not entirely exposed, therefore slightly affecting depredation rates on some of the sites. Crows can find nests and can remember their location (Götmark et al., 1990), once they are discovered, differences in height of adjacent vegetation would not influence the depredation rates. In my study, crows carried the eggs away and ate them along the roadside which allowed them to watch for predators (Sullivan and Dinsmore, 1992).

Crows were observed at all study sites and were considered to be the primary predators. However, other species are known to appreciate the taste of eggs, and therefore, these other predators could be considered as one of the causes for noise in data. I removed eggs each night from all sites to prevent nocturnal depredation by nocturnal predators such as skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), squirrels (*Tamiasciurus hudsonicus*) and owls (Hogrefe et al., 1998). Furthermore, I never encountered raccoons, squirrels, snakes, foxes or even black bears (*Ursus americanus*) on the study sites when doing nest checks. Although once I saw a skunk early in the morning, before eggs were placed in nests, I am positive that it did not came back later for eggs based on the depredation signs. Blue jays (*Cyanocitta cristata*) are also effective egg predators; however, blue jays prefer shrub nests to ground nests (Danielson et al., 1997). Jays are usually considered to be a forest species and not a forest edge species, such as crows (Andrén, 1992). Jays were heard a couple of times near some of the sites, but I never saw them on the sites. I also noticed the presence of a red-tailed hawk (*Buteo jamaicencis*) on two of the sites, but crows chased them out of sight, as Kilham (1984, 1989) also often observed. A red-tailed hawk passed near my head as it was flying down to one of the sites but it attacked a group of young starlings (*Sturnus vulgaris*) and not the eggs. I also observed turkey vultures (*Cathartes aura*) near some of the sites, but they seemed to be searching the area for road kills.

Finally, egg size might have influenced the efficiency of depredation (Montevecchi, 1976). However, Montevecchi (1976) showed that small eggs were more effectively preyed upon than larger eggs since they are easier to carry. Smaller eggs are usually carried away and cached or eaten further from study sites, whereas larger eggs are pecked and eaten directly on site (Montevecchi, 1976). I only used small sized chicken eggs in my study. Of course, size may vary from egg to egg and larger eggs were eaten on site (table 1). It can be argued that spoiled eggs could also influence predatory behavior but according to Kilham (1990) different degrees of spoilage in hot weather would not make a difference since crows already eat rotten foods such as road kills.

Many causes of noise described above are likely weak, but if they act in concert this could explain the large amount of variations observed throughout the experimental period.

As for the design of the experiment many factors were impossible to avoid. For example, the conditioning of crows with time throughout the entire series of experiments was inevitable. As mention earlier the variable "series" was considered as a random variable (I was unable to avoid it due to feasibility-related problems). F-ratio and P values were, however, recalculated as suggested by Zar (1984) taking into account this variable. The original design was to prevent confusion, and two colorations of eggs were, thus, presented at each site. Eggs varied in size because they were laid by hens from different breeds of chicken. A pseudoreplication was also inevitable since the number of crows could not have been controlled, and individual crows were responsible for a varying number of depredation events. However, the design dimished this possible effect. Finally, the number of factors involved and the complex interactions between them complicated the intrepretation of results. Although there are many problems associated with the design of the experiment in the crow's natural environment, the results from this study are still likely to be more relevant and representative of what could really be happening in a natural environment.

Future research should establish if the use of different concentrations of a repellent (i.e. different degrees of repellency) could affect the outcome of foraging trials.

In addition, it would be interesting to test if the reacquisition of a lost aversion is faster or slower with warning colors as some of the earlier studies tested with taste aversion (Hart et al., 1995). To do so, only one color prey should be used on one study site throughout the entire experimental procedure. In any case, the efficiency of depredation is likely to depend on the predator and the prey involved, and the environment in which the study would take place. It is, therefore, impossible to generalize with respect to the effect of conspicuous colors on the avoidance learning to all bird species.

Conclusion

In the present study, I examined if the food avoidance by crows was based on their learning or if crows possess a genetically fixed predisposition to avoid warning coloration patterns. First, my data suggested that avoidance of eggs with warning coloration is not genetically fixed but that association learning is involved. However, the use of free-ranging adult birds may have prevented me from an effective study of their real innate responses. It was shown, in other predator species, that innate avoidance diminishes with age and that the strength of responses also varies with the predator's dietary history (Schuler and Roper, 1992). Alatalo and Mappes (1996) also suggested that inexperienced predators could possess an "inherited cautiousness" towards conspicuous prey but that they still do learn to avoid unpalatable conspicuous prey. Therefore, the use of naive crows in future studies could be useful. However, it may be impossible to have an absolutly naive predator (Schuler and Roper, 1992).

The avoidance of unpalatable prey by crows appeared to be based mostly on learning. However, since crows did not learn faster with warning coloration, we must be cautious when comparing results of laboratory studies with those of studies conducted under natural conditions (Conover, 1984; Marples et al., 1998). This implies that coloration in laboratory studies may not be necessarily perceived by a predator in the same way as in studies conducted in a natural environment (Gamberalle-Stille and Tullberg, 1999). Moreover, the use of different bird predators might also influence the outcome of a study. Schuler and Roper (1992) further suggested that the order of testing can be yet another confounding variable when the same individual is presented with a choice between two colors. Therefore, it is difficult to make any generalizations with respect to the effect of coloration pattern on the feeding responses of predators.

In addition, crows are considered generalists that can easily adapt to many changes. This could also be reflected in the depredation rates on the three types of eggs. Moreover, crows appeared to continue sampling which could have helped their learning process, regardless of prey coloration. Young crows could also learn from their parents that all eggs are edible (associating the shape of eggs with edibility). It was shown that crows can pass foraging information on to other members of their family group. This behavior could have affected the avoidance learning by crows during my study.

Finally, crows seemed to remember longer to avoid eggs with warning coloration than eggs with conspicuous or cryptic coloration, as expected from prior reports (Gamberalle-Stille, 2001; Roper, 1994, Roper and Marples, 1997; Roper and Redston, 1987; Schuler and Roper, 1992). The trend in the predicted direction was significant in series 1 only (and close to the level of significance in series 2). The results on speed of extinction of coloration patterns are somewhat spurious and require more data or a more powerful experimental design. Moreover, my results also showed that there was a difference between warning colors and conspicuous colors since crows did not react in a similar way for both coloration patterns during the extinction of avoidance.

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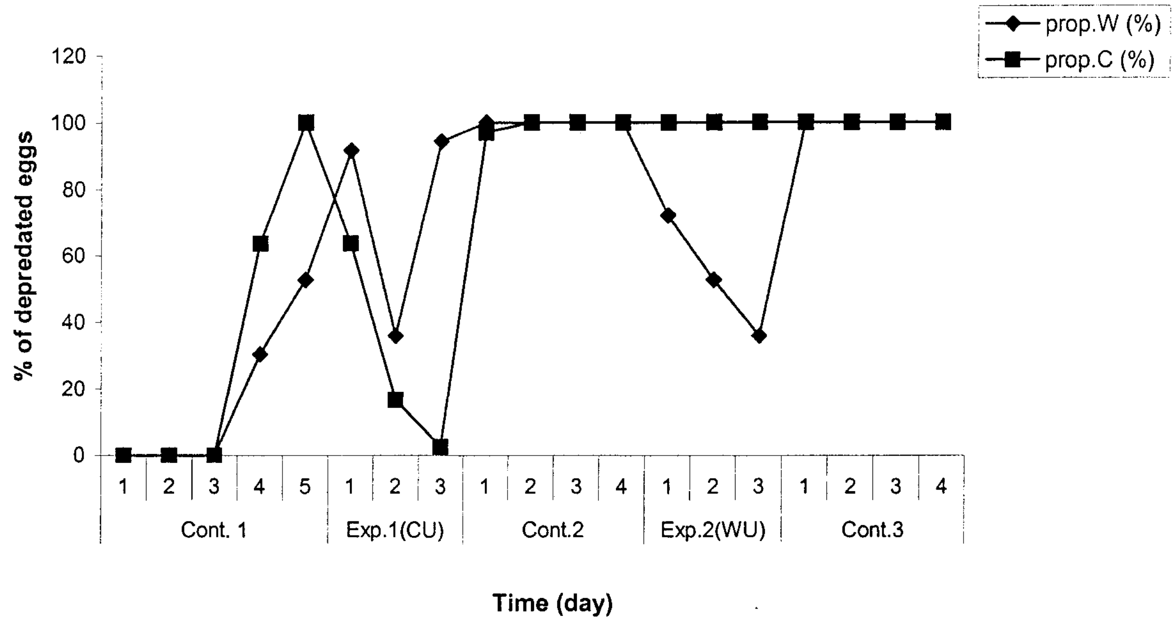
Appendix A

Graphs for the 10 other sites presenting the entire experimental period.



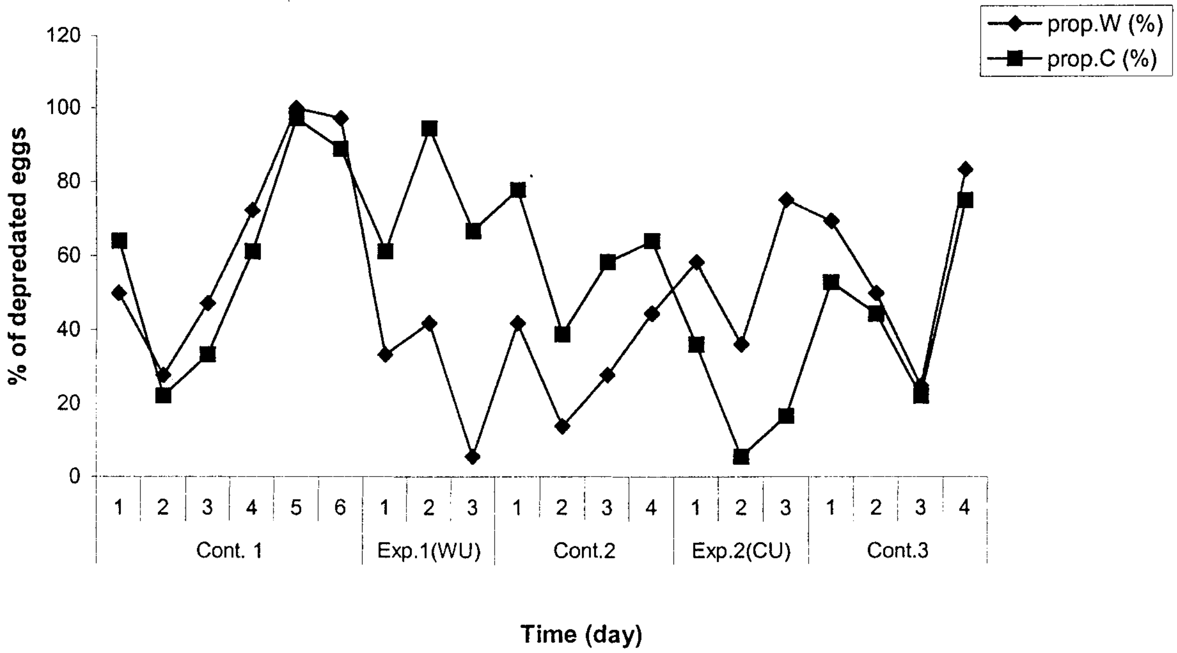


Figure 14: Percentage of eggs depredated by crows each day on sites 3 and 4 (series 1) throughout the entire experimental period. WU and CU implies warning unpalatable and cryptic unpalatable, respectively.

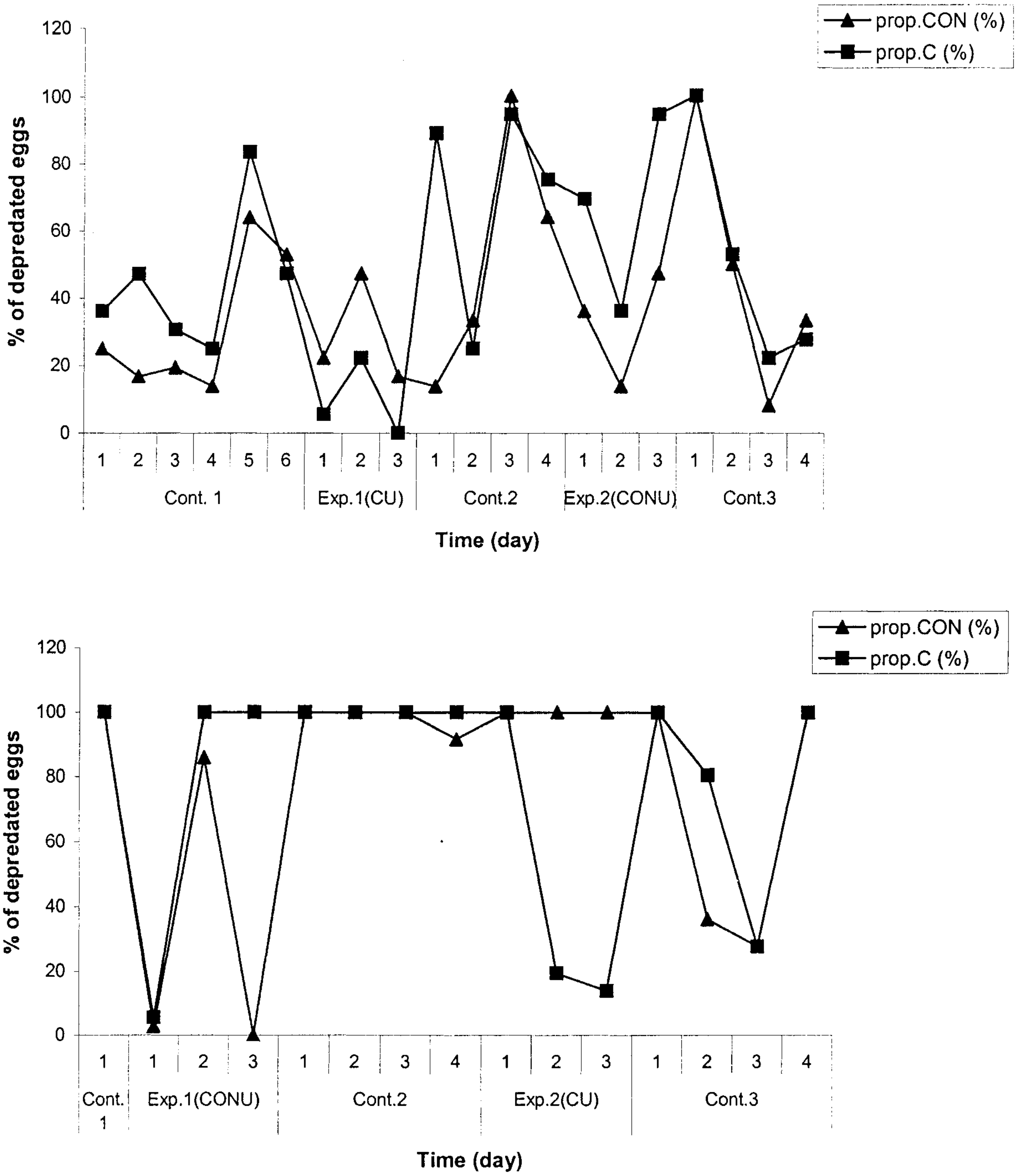
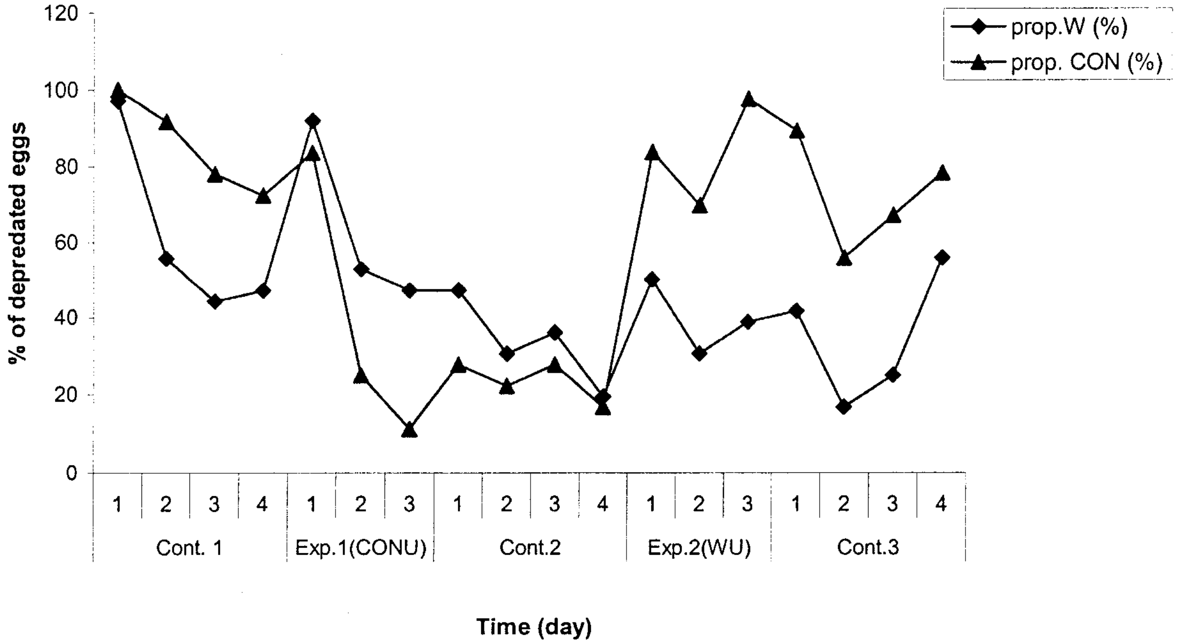


Figure 15: Percentage of eggs depredated by crows each day on sites 5 and 6 (series 1) throughout the entire experimental period. CONU and CU implies conspicuous unpalatable and cryptic unpalatable, respectively.



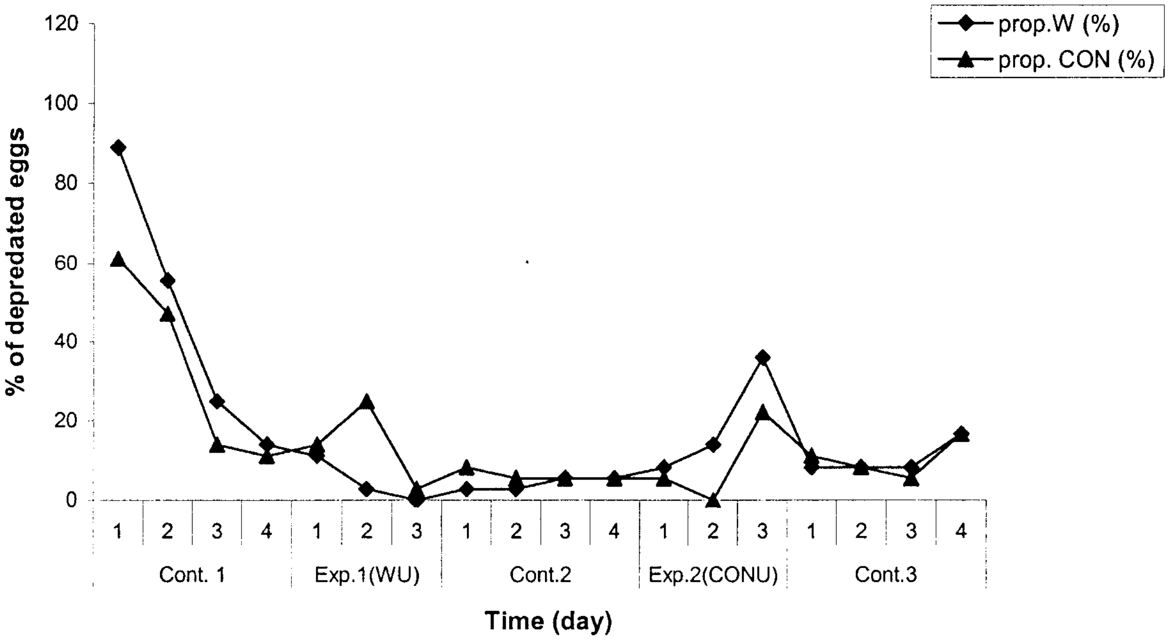
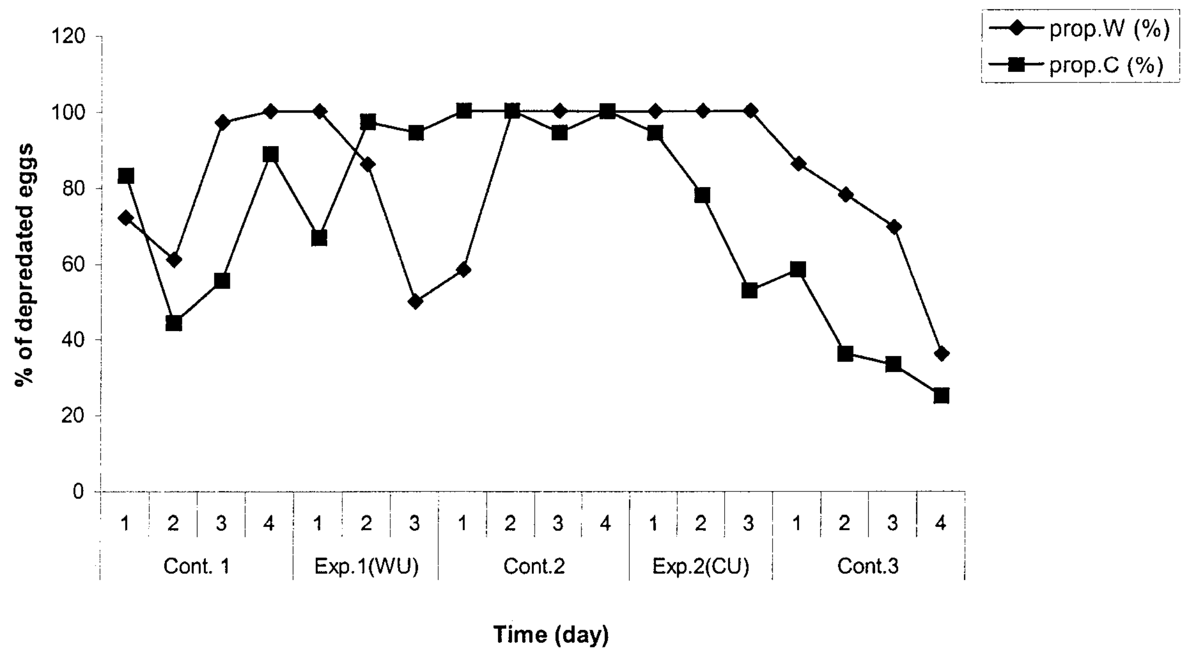


Figure 16: Percentage of eggs depredated by crows each day on sites 1 and 2 (series 2) throughout the entire experimental period. WU and CONU implies warning unpalatable and conspicuous unpalatable, respectively.



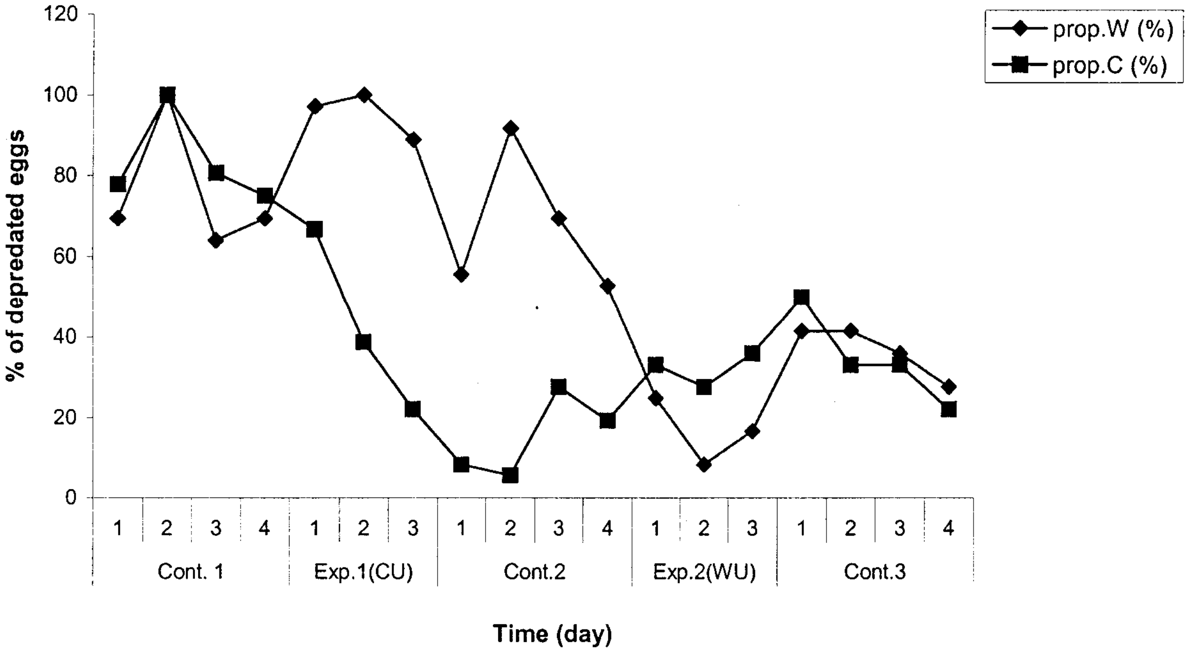
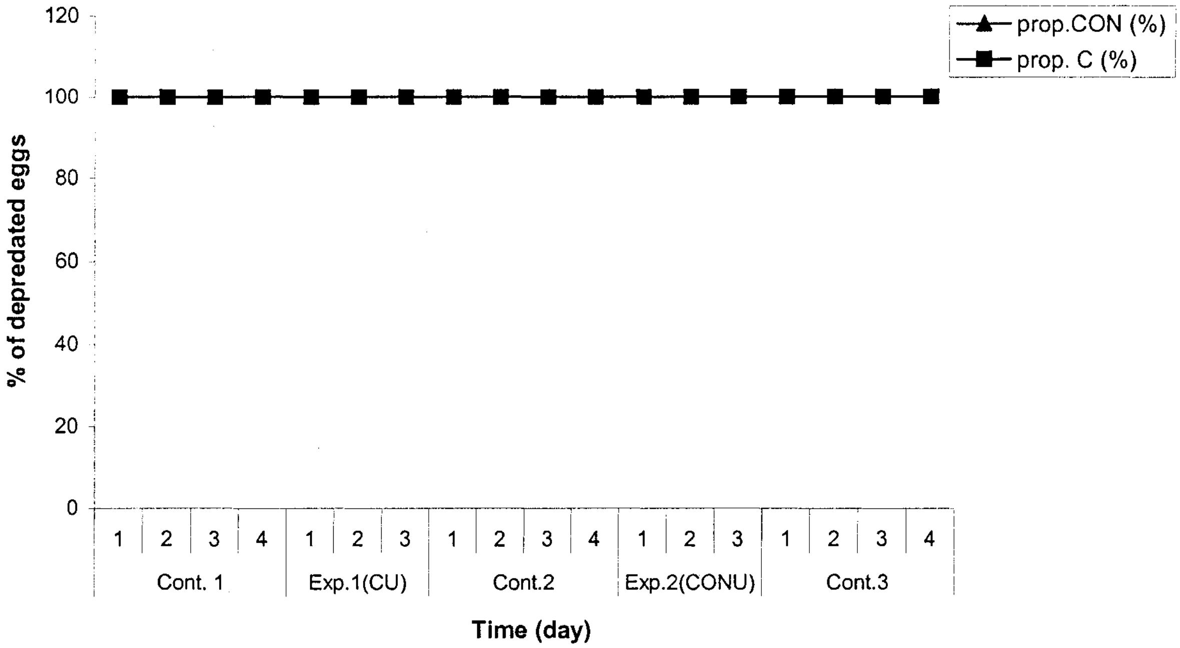


Figure 17: Percentage of eggs depredated by crows each day on sites 3 and 4 (series 2) throughout the entire experimental period. WU and CU implies warning unpalatable and cryptic unpalatable, respectively.



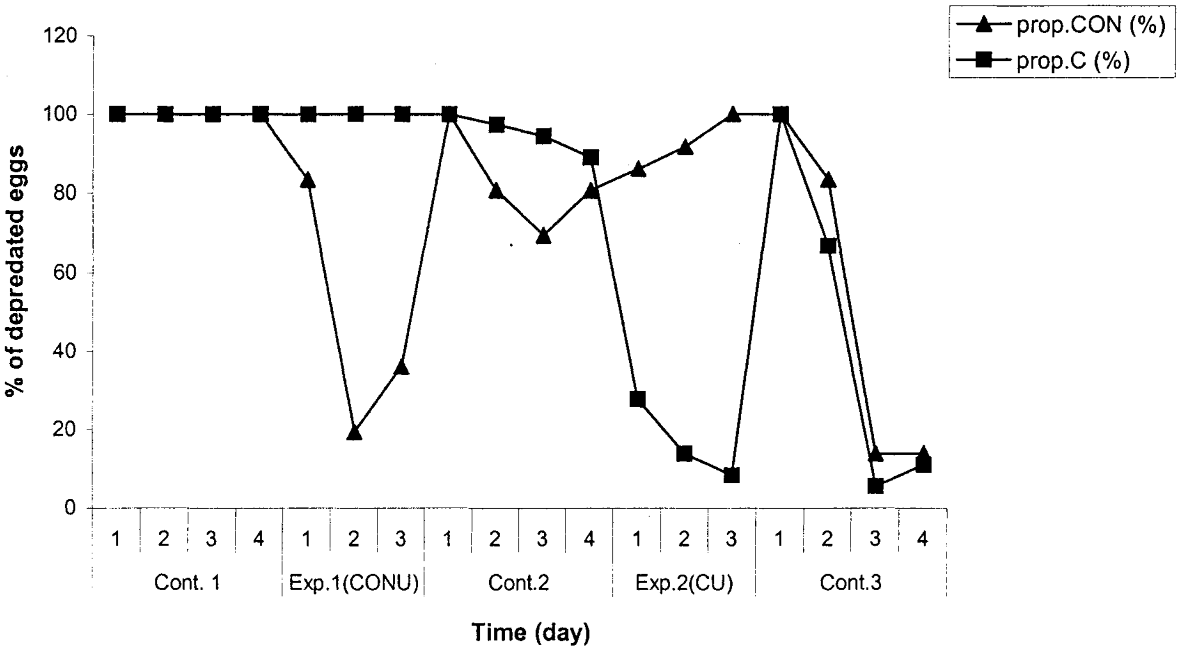


Figure 18: Percentage of eggs depredated by crows each day on sites 5 and 6 (series 2) throughout the entire experimental period. CONU and CU implies conspicuous unpalatable and cryptic unpalatable, respectively.