

## ROLE OF CONTEXT IN IMPRINTING

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**ABSTRACT:** Pekin ducklings (*Anas platyrhynchos*) were exposed either to a white or harlequin duck model. When tested for their preferences with both models simultaneously present, the harlequin was more often preferred. If tested in the presence of another strange object (a stuffed barn owl, *Tyto alba*), the harlequin-trained ducklings more often deviated from choosing their training model than did the white-trained ducks, i.e., a reversal of effects. Apparently, the context of the test interacts with the characteristics of the model in a way that confounds predictions.

### INTRODUCTION

Imprinting denotes a rapid process whereby a stable preference for an object is formed, usually a parent or social companion. The process is most vividly exemplified by geese and ducks, whose young acquire their social preferences shortly after hatching (Heinroth, 1910; Lorenz, 1935). In these and other precocial avian species, the hatchling tries to follow the first moving object it encounters (given that certain developmental conditions are met) and this may then become the object onto which many future social responses become fixated (Hess, 1973). Current theory distinguishes between variables which are important to the elicitation of initial responsiveness and those that enhance or constrain the formation of the subsequent "template". The former have been described in general terms (size, color, rate of movement, degree of articulation, etc., Gottlieb, 1971; Hess, 1973); it is to the latter that this study is addressed, and, in particular, a paradoxical and still unexplained finding of some years past.

The paradox is this: it is well known that not every model used to elicit the following response in imprinting experiments is equally effective. Ducklings (and other subjects, too) cannot be considered *tabula rasa*. But, even among equally effective models, subsequent differences in their "imprintability" exist. Indeed, Klopfer (1967) previously identified three classes of models (Table 1): among the first class, if one model was presented to the duckling and following elicited, that model was indeed subsequently preferred (i.e., followed in deference to the others.) For models of the second class, one model was preferred regardless of the type of model presented in training. For the third, whatever model was used in training, none were

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preferred over any other at testing. In none of these classes were there differences in the effectiveness of the models in initiating following.

**Table 1**  
**Classes of Imprinting Models Identified by Klopfer (1967)**

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Class I:	if A, then A if B, then B
Class II:	if C, then C if D, then C
Class III:	if E, then E or F if F, then E or F

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We suspected that these results might not be due solely to the effect of the model but to an interaction between the model and the context in which the experiment was performed. Specifically, we wished to know whether a heightened degree of arousal would lead to the ducklings ignoring all but the more familiar model.

This study replicates the Class II conditions described in Klopfer (1968) and then repeats the experiment with the imprinted ducklings tested in the presence of a presumably frightening object (a barn owl). It was expected that the fearfulness (or at least arousal) induced by the owl would cause the ducklings either to follow their imprinting model more closely or, alternatively, if the degree of fright were too great, to become less discriminating (Schleidt, 1961).

## MATERIAL AND METHODS

The subjects were 150 Pekin ducklings, a domesticated and inbred form of *Anas platyrhynchos*. Eggs were obtained daily from the Duke flock and incubated in force draft incubators at  $37.5 \pm 0.5^\circ\text{C}$  and relative humidity of 80-90%. Hatch rates ranged from 80-90%. Hatching was in the dark.

Within four hours after hatching, each bird was placed in a cardboard box measuring about 250 cm<sup>3</sup>. The individual boxes were then placed in a plywood brooder, kept at 30°C, which was impermeable to most external sounds (80 db  $\pm$  10). A fan within the brooder effectively masked sounds produced by the ducklings.

The training apparatus was a circular table 180 cm. in diameter with vertical sides 30 cm. high. The interior was painted a flat black. In the center of the table was a 20 cm. high black ring, 40 cm. in diameter, which meant the ducklings had to confine their movements to a circular track 70 cm. wide. This ring was removed during testing. The models in the training and test sessions consisted of adult-sized duck decoys made of papier mache, one white, the other multicolored ("harle-

quin"). The models were suspended from overhead, by means of a "T", and were 3 cm. above the arena floor. The model moved intermittently along the periphery of the arena, moving 15 sec. at a rate of about 580 cm. per minute and pausing for 10 sec. The decoy emitted a recorded sound of a male human voice repeating "kom, kom, kom" at a constant rate of about 2 phrases per sec.. Overhead illumination was provided by one 120 watt fluorescent and two 150 watt overhead incandescent lights. Observations were made from an adjacent room through one-way glass.

Each bird was individually trained in the circular training apparatus at 12-24 hrs. post-hatch and 27.5-28.5 days developmental age.

Testing occurred at  $24 \pm 1$  hour after the start of training. The tests took place in the training apparatus and entailed 20 min. simultaneous exposure to the two silent, moving models.

In training and testing, the subject was scored as "following" if it moved with a model and within 20 cm. of its rear or 10 cm. of its side. A cumulative record of the time each subject followed a particular model was kept on electric timers. Controls were handled exactly as the experimentals, except that no models were present during their training period; the sound was presented to them through a speaker beneath the apparatus. In the second series, each duckling was tested with the same pairs of models but between them a stuffed barn owl (*Tyto alba*) was mounted, with outstretched cardboard wings, about 15 cm. above the apparatus floor. The sequence of models was randomly altered. The same number of experimentals were trained to each model and controls were run with each batch.

## RESULTS

The results of the first series of trials (no owl in test arena) replicated, in a fashion, the results obtained earlier by Klopfer (1967); white and harlequin models were equally effective in eliciting following by ducklings at training, but, when presented with both models simultaneously at testing, white-trained ducklings spent significantly less time following the "correct" (training) model than did harlequin-trained subjects (Figure 1 and Table 2). Harlequin-trained ducks spent less time following the incorrect model than did white-trained ducks, though the difference was not significant. Six of 13 white-trained birds followed the harlequin model to at least some extent during the first series of trials; three of 15 harlequin-trained birds followed the white model at some time ( $X^2=2.132$ ,  $df=1$ ,  $P>0.1$ ). When presented with both models simultaneously, white-trained subjects spent more time running about the test arena uttering distress cheeps and less time following either model than did subjects trained to the colored model. Thus, while the present study did not find a dramatic *qualitative* difference between white and colored models in their effectiveness in eliciting following at testing, we have replicated at least a *quantitative* difference consistent with earlier studies using these models. Controls scarcely followed at all, and thus are not further considered.

**Table 2**  
**The Effect of Context at Testing and Training**  
**Model on Following Behavior of Pekin Ducklings: Kruskal-Wallis**  
**Probabilities for Given Contrasts.**

Contrast (N)		Dependent Variable		
		TFT	CFT	IFT
OW(17)	OH(18)	.78	.30	.21
CW(13)	CH(15)	.006	.007	.17
OH	CH	.08	.01	.03
OW	CW	.08	.15	.89

Letter codes indicate context condition (O=owl present; C=owl absent) and training model (W=white; H=harlequin). Variables analyzed are total following time (TFT), following time of correct model (CFT), and following time of incorrect model (IFT).

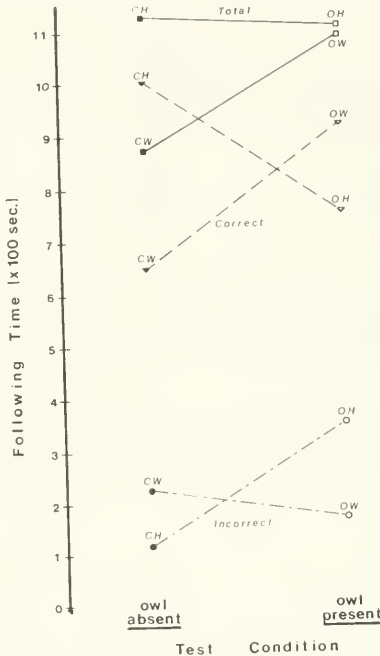
The magnitude and significance of the effects of the owl model on the following of white and harlequin-trained ducks are presented in Figure 1 and Table 2. When the owl was present in the test arena, *no significant difference* was found in the cumulative time white or harlequin-trained subjects spent following models of either type (Total Following Time); white-trained ducklings followed *marginally significantly* better when the owl was present than when it was absent. The opposite effect was found for harlequin-trained birds: their Total Following Time declined when the owl was present, though here, too, the difference was just shy of significance.

When the owl was present, ducklings trained to white models spent more time following the correct model than when the owl was absent, though the difference *was within the realm of chance* ( $p=0.15$ ). Harlequin-trained ducklings, in contrast, followed the correct model much less consistently when the owl was present than when it was absent. White-trained subjects exhibited no strong tendency to follow the incorrect model less when the owl was present than when it was absent, but harlequin-trained subjects erred significantly more when the owl was present than otherwise. Eleven of 18 harlequin-trained birds followed the incorrect model at some point during testing; eight of 17 white-trained subjects did likewise ( $X^2=0.664$ ,  $P > 0.5$ ). More harlequin-trained birds made errors when the owl was present than when it was absent (Fisher's exact  $P=0.020$ ); no such effect was apparent for white-trained subjects (Fisher's exact  $P=0.626$ ).

Because of the interaction between model and context (see Figure 2), context alone had no significant effect on the following behavior of the ducklings (Kruskal-Wallis tests,  $P > 0.18$  for all contrasts). Overall, the

Figure 1

Effect of context at testing and training model on following behavior of Pekin ducklings: mean following times for each context and training model condition are plotted for the three dependent variables described in Table 2.



ducklings showed a slight increase in their Total Following Time when the owl was present, but this effect was entirely due to the behavior of white-trained birds.

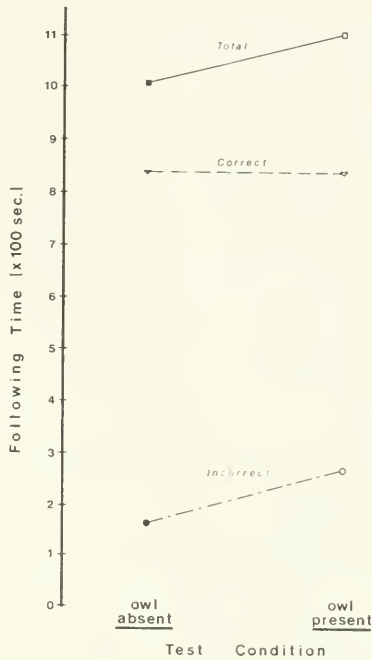
## DISCUSSION

The presence of a stuffed owl, though it did not elicit obvious fear responses (distress-calling or freezing) did alter the behavior of the ducklings. The change, however, was one we had not anticipated. We had expected that in the situation "strange or fearful object present" the ducklings would either adhere more closely to their imprinted ("correct") model, or, if unduly distressed, perhaps become less discriminating. If the presence of the owl was inconsequential we would not expect any change from the behavior seen in its absence. In fact, none of these outcomes were obtained.

Traditionally, imprinting is believed to consist of the formation of a stable internal template during a brief developmental "window" in which

**Figure 2**

Effect of context at testing on the following behavior of Pekin ducklings: plot of mean following times for each of the three variables given in Figure 1, ignoring training model.



the characteristics of the imprinting stimulus are retained in memory (Bateson, 1978; Staddon, 1983). Later behavior is then determined by the degree to which stimuli from the environment match the template. Heredity may bias the imprinting process, causing certain characters to be emphasized in the template and others deemphasized (Johnson and Gottlieb, 1981; Kovach, 1971). Thus, though two ducklings from the same parents may have been exposed to different models during their imprinting "window", some degree of resemblance may exist between their respective templates due to similar hereditary influences.

Probably the most common means researchers employ to determine the characteristics of a subject's imprinted template is to simultaneously present the subject with two different moving models and then compare the amounts of time the subject follows one or the other model. The model followed more is then presumed to resemble the template more closely. The usual interpretation of the results of Klopfer's (1968) study and its replication here would thus be that the characteristics of the imprinted template of Pekin ducklings more closely resembles the multicolored harlequin duck model than the uniform white model, since ducklings

exposed to either model followed the harlequin model at testing more than expected. Klopfer's results were more dramatic than those we found in the present study, though the difference may be attributable to differences in the sources of the ducklings used. Birds in the earlier study were obtained from a commercial source, while our birds came from an unrelated population maintained at Duke University since 1979.

The usual interpretation of following may have to be reassessed, however. In the presence of a barn owl, ducklings exhibited behavior just the opposite of that seen in the owl's absence: harlequin-trained ducklings showed less fidelity to the harlequin model and white-trained ducklings showed more fidelity to the white model. These results suggest that following need not indicate the characteristics of the imprinted template itself. Instead, the context in which previously imprinted stimuli are presented may in some sense modify the animal's interpretation of the template, emphasizing or diminishing the relative importance of particular characteristics. Our results suggest further that context need not modify all templates in the same fashion. Context and templates interact such that the effect of one context and a particular template cannot be predicted from the knowledge of the effect of the same context on another template.

It can be fairly concluded that the characteristics of the test situation do have an impact upon the response of imprinted ducklings. What the relevant influences actually are and how they operate remains a puzzle.

In summary, white-trained Pekins were less prone to follow any model during testing in the absence of the stuffed owl than were harlequin-trained birds, and they followed the correct model less well than did harlequin-trained birds. The owl's presence caused harlequin-trained birds to err more and spend less time following the correct model than when the owl was absent from the test arena. In contrast, the owl's presence did not cause the white-trained birds to make more mistakes, but did cause them to follow the correct model more closely.

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