EXPERIMENTS ON THE CAUSATION OF THE THREAT POSTURES OF CANADA GEESE

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Summary

A PAIR of Canada Geese hand-rearcd in 1953 were used between 1955 and 1958 to test experimentally the hypothesis that certain display postures of this species are caused by a conflict between tendencies to attack and to flee from an opponent. The geese would follow and stay peacefully with the author if he was wearing a red sweater, corduroy trousers and Wellington boots. If he carried a stick or brush they would flee. If he wore a jacket they would attack vigorously. Thus it was possible to administer attack-evoking and escape-evoking stimuli simultaneously. When this was done the postures previously interpreted as ' threatening' were elicited. When the attack-evoking stimulus was presented behind a fence which the geese had learned they could not get through, some but not all of the postures observed in the attack-flee conflict were seen. The experiments support the original hypothesis, which was based on non-experimental field observations.

Introduction

Most studies of the motivation of the displays of birds are based on observations of free wild birds. Tinbergen (1959) has recently reviewed the analysis of field observations and "natural experiments." Several nonexperimental investigations have supported the hypothesis that in natural situations "threat displays" arise when the bird is in a state of conflict, tending at the same time to attack and to flee from an opponent. To verify this hypothesis and, at the same time, the interpretative methods that gave rise to it, it is necessary to be able to stimulate the tendencies to attack and to flee both separately and simultaneously. On the 'conflict' hypothesis, simultaneous presentation should evoke threat postures but the separate stimuli should not. Though such an experiment is extremely simple in principle, it is rarely practicable, so that it seems worth reporting some experiments of this kind with Canada Geese *Branta canadensis*.

Hostile behaviour in wild Canada Geese

Between 1950 and 1956 I had been watching free-living feral Canada Geese in the field, and had become familiar with their displays and other behaviour throughout the annual cycle.

Hostility (attack and avoidance) is shown when territory holders meet, and in winter flocks when different pairs or family parties meet or come close together. Certain postures also occur in these situations. Those most commonly seen are named and described below. They are only a small part of the repertoire of the species but are by far the commonest both in natural quarrels of captive and wild birds and in the experiments.

1. **Bent-necked** posture. The head is lowered and held close to the breast, and the neck is doubled back on itself. The bill is usually pointed towards the opponent.



2. Forward posture. The head is lowered and held far in front of the body with the neck more or less nearly straight. Intermediates between these two are seen, and the forward often develops out of the bent-necked posture by a forward thrust of the head. Although it is usually practicable to classify a posture as one or the other they are grouped together for the purposes of this paper. They are usually accompanied by a quiet grunting call (mostly with bent-necked) and loud, rapid honking (usually with forward), and sometimes there is a flicking movement of the closed wings with the forward posture.



3. Erect posture. The head and neck are held erect and the body is also tilted into an erect position. Feathers on the body and neck are raised, often very strongly, and sometimes the bird hisses and makes trampling movements with its feet.

4. **Head-pumping.** The head and neck are held erect but the neck is repeatedly bent and straightened, lowering and raising the head each time in a vertical bobbing movement.

In their recent paper Collias and Jahn (1959) describe head-pumping, bent-necked and forward postures and interpret their motivation on the basis of their similarity to actual attack and alarm positions. My own interpretation, from general observation of free-living birds, without quanta-

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tive analysis, is that all four postures occur when there is reason to believe that the bird is simultaneously motivated both to attack and to flee from its opponent, e.g. in situations where the bird often attacks or retreats from another goose. A goose in the erect posture (and at any time with erect feathers) is relatively more likely to flee and less likely to attack than one in the bent-necked or forward postures. Geese performing bent-necked and forward are more likely to attack than to flee. A goose doing the forward posture seems more strongly motivated than one doing bent-necked in that if it attacks it fights more vigorously. However, Klopman (pers. comm.) finds that bent-necked more often precedes actual attacks than does forward.



Head-pumping

Experimental arrangements

The opportunity for experiments on the conflict between attacking and fleeing was provided by a pair of Canada Geese hand-reared in 1953. When adult these birds would uninhibitedly attack and fight with people whom they did not see often, and with familiar people dressed in an unfamiliar way. They were quite unafraid of the author and his parents when dressed in their habitual gardening clothes and would follow them or stay peacefully with them but if we carried a stick or brush we could chase the geese away and make them run in front of us. (The geese learned this response in their first year, probably as a result of being pushed out of the house with a brush, but ontogeny is irrelevent here). Otherwise it was only possible to make the geese move by walking away and calling, whereupon they would follow.

Thus a familiar person wearing strange clothes and carrying a brush moving towards the geese constituted a simultaneous stimulus to attack and to flee. To check whether the fleeing tendency played any greater part than just preventing attack, in one series of experiments the intruder advanced

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towards the geese behind a wire-netting fence which the geese had learned they could not get through but which they never avoided or fled from.

The experiments made use of five situations: non-hostile (control), attack - evoking, flee - evoking, attack - and - flee, attack - prevented. The occurrence of attacking, fleeing, bent-necked and forward posturing or other behaviour was recorded, but usually with little reference to how frequently each was shown during the trial. Thus the quantitative records consist of comparisons between the numbers of trials in which an activity was seen and those in which it did not occur.

Results

1. Non-hostile situation: I would go to the geese wearing Wellington boots, corduroy trousers and a red sweater. Usually they would watch me come, greet me briefly (with postures that *superficially* resemble the 'threat' postures) then prepare to follow me or else resume their previous activities until I went, when they would attempt to follow. A complete record of the number of these encounters was not kept, as the behaviour was so consistent.

2. Attack-evoking situation: I would go to the geese wearing a jacket instead of the sweater. They would see me, raise their heads rapidly, then run towards me calling, with their heads held low in front of them. They would then peck and take hold of me with their bills and begin to beat me with the carpal joints of their wings. Beating would continue until I broke away and ran off too quickly to be caught. The geese would give chase but then stop and come no nearer. Line b. of Table I shows the frequency of attacks in this situation. Comparison with the control (line a) shows that the intruder plus jacket evokes significantly more attacks than intruder without jacket. Fighting does not give way to posturing (Table I, line e); so one can also say that the stimulus evokes fighting more readily than, or preferentially to, posturing.

 TABLE I:
 Responses of Canada Geese to intruder in experimental situations, described in text.

Frequency of attacks	Attack and fight	Do not attack
 a. intruder in familiar sweater (control situation) b. intruder in jacket c. intruder in jacket, and carrying brush d. in jacket, and separated by fence 	2 24 5 3	54 5 18 23
Frequency of posturing	Bent-necked or forward posture	No posturing
e. intruder in jacket f. in jacket, and carrying brush g. in jacket, and separated by fence h. in familiar clothes, carrying brush	7 21 25 3	22 2 1 c.300

The comparisons between rows in the table which are referred to in the text have been tested using X^{2} and all found to be significant beyond P=0.01.

3. Flee-evoking situation: I would go to the geese wearing familiar clothing but carrying a brush or stick. They would watch me. As I got near they would turn and walk or run away, depending on how quickly I approached and whether I waved the weapon at them or not. A complete

record of such visits was not kept. They were very numerous and their effects nearly constant.

4. Situation combining stimuli to attack and to flee: I would go to the geese wearing unfamiliar clothing (e.g. a jacket, or shoes instead of boots) and carrying a brush or large stick. They would see me, rapidly raise their heads, then run towards me calling and with heads lowered. Near me they would stop and stand, continuing to call and posture, changing from one posture to another very often and perhaps wing-shaking and preening. When I withdrew they might chase after me, still posturing. Lines c and f of Table I record the frequencies of attacks and of posturing and show that there were fewer attacks but more posturing to the intruder in a jacket when he carries a brush.

Postures adopted while the geese were running towards the intruder are excluded: so the comparison shows effect of the brush, not the remoteness of the intruder. If postures during approach are included the difference between responses to with-brush and brushless situations is less marked, showing that fear of the brush, though it determines whether posturing or attack occurs once the geese have reached the intruder, has little influence on whether or not they 'threaten' while running towards him.

5. Situation in which attack is prevented by a fence: the geese would be first shut in a fenced paddock. Later I would go to them wearing unfamiliar clothes and stand by the fence. They would approach rapidly, as in situations 2 and 4, then stop by the fence, continuing to call and posture. Sometimes they would walk up and down trying to find a way through the fence or just push against it, usually for only a short time. Lines d and g of Table I record the frequencies of attacks and of posturing in this situation. There was significantly less attack and more posturing to an intruder in a jacket when he was behind a fence.

The prevention of attack by the fence increases the occurrence of 'threatening' postures in just the same way as the brush, *i.e.* a physical barrier has the same effect as the conflicting tendency to flee. Though this seems to be true for the bent-necked and forward postures it is probably not true for some others (notably the erect) which seem to occur only when a tendency to attack and a strong tendency to flee co-exist.

6. Comparison of effect of intruder with and without jacket, within the thwarting situation: If threat postures are partly caused by a tendency to attack, stimuli which evoke attack should also increase the likelihood of threat postures occurring. Fighting and threatening do not occur simultaneously. It is therefore best in looking for the effects of attack-stimuli on posturing to consider a thwarting situation, in which fighting does not occur. Line h, derived mostly from occasions when the geese were being shut up for the night, contrasts greatly with line f: strange clothes enhance the likelihood of the intruder evoking threat. I have no records of the 'control' situation with normal clothes and the fence between me and the geese, though there were many such occasions. Posturing was certainly not at all common in this situation.

Discussion

The experiments show that the same stimulus evoked both attack and bent-necked and forward postures. Two questions arise from this. The first

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is whether it is only stimuli which evoke attack that produce these postures. Since these two postures appeared markedly absent from situations where there was no attack evoking stimulus it was not thought important to pursue this question. But ideally it would be necessary to compare the attack-flee situation with another approach-avoidance situation (e.g. feeding or flocking against fleeing) to show that the postures were related to the attack tendency and not to the approach tendency which it involves. Casual observation of various blocked approach or locomotion situations revealed no bent-necked or forward postures or aggressive calls. In fact the Canada Goose seems to have other special calls given whenever locomotion (to whatever purpose) is blocked.

The second question is what factors determine whether the stimulated bird attacks or does not attack but postures instead? Observation shows that fighting and posturing have a negative relationship with each other in addition to the positive relationship of a shared stimulus. In the attack experiments it was seen that fighting did not give way to threat and that it occurred to the exclusion of posturing. Prevention of fighting by presenting a fleeing-evoking stimulus simultaneously with the attack-evoking stimulus, or by a physical barrier which the birds showed no tendency to flee from, allowed bent-necked and forward postures to appear. One can only conclude that in the causation of these two postures some factor which prevents attack is necessary. A known physical barrier and a conflicting tendency to flee will do this equally well. It is also conceivable that a weakly attackmotivated bird may be prevented from attacking by any conflicting tendency, even just the tendency to continue feeding or sleeping.

Comparison of the fence experiments and the brush (attack-flee) experiments enables one to see whether the fleeing tendency is necessary for the causation of a posture beyond being simply a factor preventing attack. It seems to have no effect in the causation of bent-necked and forward threat beyond preventing aggression. But this does not apply to the erect posture, which did not occur in the fence experiments and could only be evoked in the brush experiments, usually only by waving the brush or approaching very quickly (which were described as strengthening the fleeing behaviour in the control situation). In the causation of this posture the fleeing tendency plays a greater part than just as an inhibitor of fighting. Its effect on this posture cannot be mimicked by a physical barrier to attack, both attacking and fleeing tendencies are essential to it. Head-pumping, also sometimes seen in brush experiments and not in fence experiments, may require only a blocked fleeing tendency but no experiments on this were tried. Clearly experiments with blocking a fleeing tendency by a fence would be worthwhile but again casual observation suggests that only head-pumping might possibly appear in this situation.

It is important that, though the geese fled from the brush when I was in normal clothes and they never fled from me by the fence, they had learned that they could not get through the fence by pushing or walking up and down, and that if they tried to get through the fence they would only threaten on ceasing their attempts to get through. Prevention of attack relies on an "internal decision" within the attack-threat system, a choice between behaviour appetitive to attack (trying to get through the fence) and posturing. It seems that repeated failure to succeed in getting through the fence builds up a block on attacking, and that a *relatively* weak fleeing tendency can have an identical effect. But fleeing differs from inability to get through the fence in that it can vary independently of the attack tendency, and so become relatively stronger than the attack tendency. This seems to be what leads to the occurrence of postures not seen in the fence experiments.

The experiments do not go very far in showing what determines which of the threat postures is performed. Moynihan (1955) has described the importance of various combinations of absolute and relative levels of attackand flee-tendencies. The differences between the fence and brush experiments show not only that the erect posture and head-pumping require a stronger relative fleeing tendency than do bent-necked and forward but that different relative levels of fleeing tendency can have quite different effects on the attack-threat system: 1) merely preventing attack, which can also be done by other factors, 2) some more far reaching effect which can only be produced by a fleeing tendency.

A way in which experimental demonstration of the difference in causation between bent-necked and forward postures is possible is illustrated by a few observations of the following kind. My wearing slightly unusual clothes (e.g. shoes instead of Wellington boots) evoked weak attack on some occasions, and when behind a fence evoked bent-necked more than forward. This contrasts with the jacket (which gets strong attacks nearly every time) getting mostly forward postures when behind a fence. This suggests that within the thwarting situation, when attack is prevented, the choice between bentnecked and forward postures is determined only by the strength of the attack-evoking stimulus, the potential tendency to attack.

The experiments confirm that some inhibitory influence on attack, at the same time as the presence of a stimulus to attack, is necessary for the occurrence of threat postures. They also show that attack-fiee conflict gives rise to threat postures, but that some of them occur whenever attack is blocked while others will occur only when a fleeing tendency conflicts with the attack tendency.

These results make it seem highly probable that the interpretative methods are correct in suggesting that attack-flee conflict is the situation in which threat postures usually occur in nature.

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