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SEASONAL VARIATION, SEX DIFFERENCES AND HABITUATION OF TERRITORIAL BEHAVIOUR IN *CYGNUS OLOR*

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Introduction

Among Old World immigrants resident around Long Island Sound, none is more striking than *Cygnus olor*. In spring, sometimes upwards of 50 birds gather on the bays, inlets and estuaries. Some will leave their flock to find a pond or secluded cove to breed. Others may disperse to find an area uninhabited by mated swans. In the past few decades, however, this swan has undergone a population explosion and uninhabited areas have become uncommon. As a consequence *C. olor* has

spread south to Maryland and New Jersey and north to Massachusetts and Rhode Island.

The reason for this success appears to be the swan's lack of competition with other species, its general aggressiveness and the fact that it is highly territorial. Territories vary in area from 0.2 to more than 4 ha and may be maintained for several seasons or longer (Scott 1972). Flocks of swans intruding on a territory are driven out, frequently by both members of the mated pair and territorial boundary disputes are not uncommon. Generally, threat behaviour is all that is necessary to drive out trespassers.

The threat behaviour has been described in general terms by Heinroth (1910) and Johnsgard (1965). The author has examined the graded nature of the threat display and the sequential order of behavioural postures leading up to and following an attack (Demarest 1980a, 1980b) and in this paper explores several parameters of territorial defence.

General method

The studies were carried out between 1973 and 1977 at sites in eastern New York on the north shore of Long Island in an area known as Setauket Harbour and in New Jersey at Wreck Pond on the Atlantic shore. Territories were defended by four mated pairs at the New York study site, only one mated pair at the New Jersey site. The territorial birds were named after the body of water they inhabited, ie Van Brunt's Cove, Harbour Cove, Little Bay North, Little Bay South and Wreck Pond. All areas were estuarine waters connected to a larger bay, in generally residential neighbourhoods. Each pair of the New York swans shared at least a portion of their territorial boundary with another pair. However, these birds rarely crossed into another's precinct. Trespassers were almost always unfamiliar birds.

The behaviour of the swans was collected by direct observation, recording the observations on protocols with a concurrent time base. Some sessions were recorded on videotape. Models were used to simulate territorial intruders since actual confrontation was infrequent and was typically brief with a quick retreat by the intruder. The models had the added advantage that they could be presented systematically for fixed periods, at specific locations and their 'behaviour' was consistent. The models were white polyethylene imitations of swans, 57 cm in length and 20 cm in diameter. The wings and neck were shaped into a Busk posture (see Fig 1B) and each model was weighted with 7 kg of sand to achieve stability and a natural waterline.

Seasonal variation in the threat display

The threat display of *C. olor* is a graded series of wing and neck postures indicative of different intensities of threat (Demarest 1980a). Five of these postures are

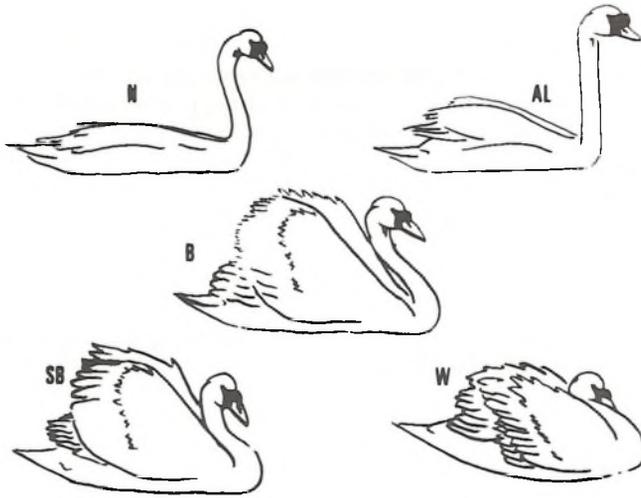


Fig 1. A graded series of postures used to signify increasing intensity of threat in *Cygnus olor*.

(N) Normal posture, (AL) Alert threat, (B) Busk, (SB) Strong Busk and (W) Wedge posture.

shown in Fig 1. The least threatening Normal posture (N) is in the upper left-hand portion of the diagram and the most intense threat, the Wedge (W), is in the lower right-hand corner. Alert threat (AL), Busk (B) and Strong Busk (SB) are intermediate intensity threats. A more intense display, not shown here, is the Zig-Zag Dance (ZZ), most often observed during boundary disputes between territorial males. In general, the most frequent threat display performed is the Busk, and it is usually sufficient to drive away territorial intruders at any time.

Method

In order to assess seasonal variations in the strength of territorial defence, the model was presented to each mated pair in the New York population ($N = 4$) once a month from March 1973 to March 1974. The model was always anchored 2 m from the shoreline approximately 100 m from the swans. During the incubation period the model was placed 100 m from the nest. Each test lasted ten minutes and every 30 seconds the type of display posture and the distance between each swan and the model was recorded. Since spatial distance between defender and intruder is inversely related to the intensity of the threat display (Demarest 1980a), only threat display data are considered here.

Results and discussion

The number of 30-second intervals in which either the male or female performed a Busk threat or more intense threat display was tabulated for each pair. These data were combined over two-month periods and averaged across pairs of birds. Fig 2 shows the mean amount of time threatening the model during each of the six two-month seasons of the year. Threats were most often observed from March to June, the period of nest building and incubation. The frequency of display dropped off in July and August but increased again in late autumn. The lowest incidence of threat display was found from November to February. In fact, almost all of the displays elicited in the first two months of the year were from the February test and coincided with the first appearance of threat behaviour by first-year juveniles in some of the families. This seasonal onset of display in the young suggests very strongly that the threat display is at least partly under endocrine control.

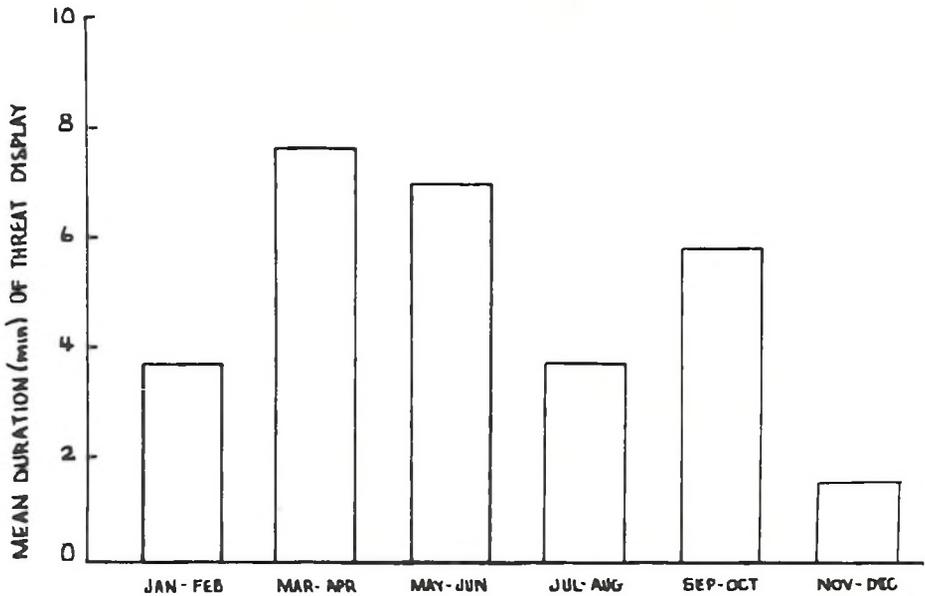


Fig 2. Seasonal variation in the mean duration of the threat display (ie B, SB, W or ZZ) directed to the model.

Independent of the tests with the model, records were kept of the number of intruders observed in each territory each month. These records were not entirely systematic; they were made haphazardly at semi-random times of the day, typically two or three times a week from 1973 to 1974, and emigrant swans most often invaded only two of the four territories studied. The total number of swans observed in all the territories in two-month periods was tabulated and averaged over the number of observations made during each period. This gave the mean

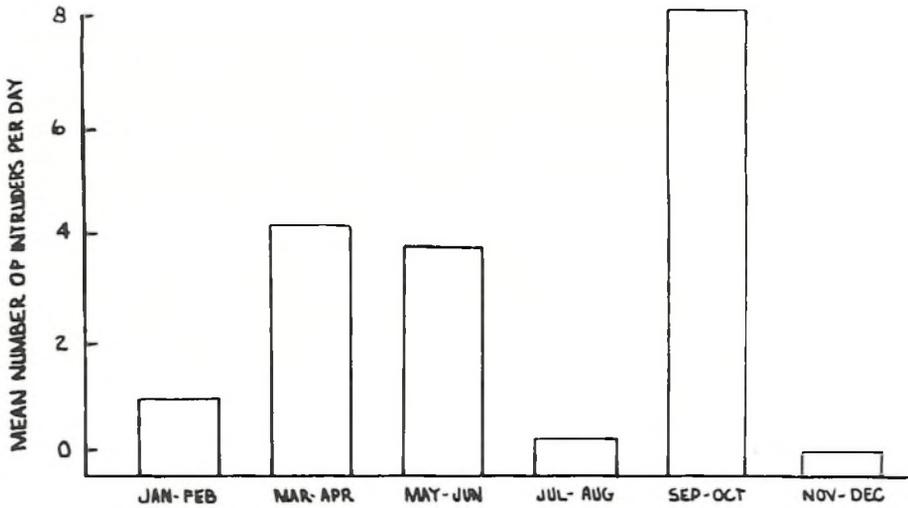


Fig 3. Seasonal variation in the mean number of alien *Cygnus olor* entering the Setauket Harbour area each day.

number of swans in Setauket Harbour each day. Subtracting the number of swans that had territories gives the mean number of intruders a territorial *C. olor* could expect to confront on a given day (Fig 3). The figures undoubtedly underestimate the actual numbers since small groups of three or fewer intruders were typically expelled from an area in ten to 20 minutes, and observation periods were sometimes no more than spot checks lasting from five minutes to half an hour. Despite the deficiencies of the procedure, the results provide an interesting backdrop for the seasonal variation in threat display. Territorial trespassing appeared to peak in early spring and again in late autumn, the periods when the probability of threat display is highest. Interestingly, intrusion was rare during July and August when incubation came to an end and the young cygnets began to hatch and leave the nest. It may be that the original flocks of birds observed in March and April secure a territory or temporary feeding ground for the next few months.

Territorial defence by the male was most evident during the May to June incubation period. This behaviour is undoubtedly under strong selection pressure since a safe and ready access to food and feeding sites would appear necessary to sustain the female who remained on the nest most of the day, occasionally leaving to feed for short intervals only.

Sexual diethism in the threat display

Because of the essential differences between the sexes in parental investment (Trivers 1972), polygamy and promiscuity would seem to be the mating systems

most preferred by males. Among birds, however, monogamy is the most common system (Lack 1968) and swans, in particular, are believed to mate for life (Johnsgard 1965). Monogamy usually correlates with near equality in parental investment by both mates and is expected when successful reproduction requires the co-operation of two committed adults (Barash 1977; Orians 1969). In the white swans of the Old and New Worlds the males do not seem to take part in incubation but they may now and then stand over the eggs to guard them (Heinroth and Heinroth 1958; Scott 1972). The male and female do co-operate in nest building, however, and both animals may defend the territory against intruders, especially early in the spring (Boase 1959; Heinroth 1910; Huxley 1947). Threat displays in male and female *C. olor*, however, appear to differ in intensity and the male appears to take the greater risks. This was examined in a series of experiments on model-elicited territorial aggression.

Methods and results

Preincubation test: Model tests were administered prior to incubation in three pairs from the New York population in 1974 and one pair from New Jersey in 1977. All tests were initiated in March. The model was presented once a day for seven days, two hours after high tide at a point 2 m from the shoreline and 100 m from the swans. Each test session lasted 10.5 minutes and every 30 seconds the type of display posture and distance between the swan and the model was recorded. Each bird's behaviour was therefore recorded a total of 147 times. The analysis included the behaviour of both the male and the female.

The total number of recorded threat postures were grouped into four categories representing different intensities of threat display. The complete absence of any display was Level 1. Level 2 included Alert-threat and Busk displays, Level 3 the Strong Busk and Wedge postures, and Level 4 incorporated all episodes of Zig-Zag Dance and Attack. Totals for male and female are shown in Table 1. Males performed the most intense displays more often than any other display, while females failed to threaten almost half the time. Females, in fact, never performed a Zig-Zag Dance and never attacked the model. A Chi-square test performed on the group totals indicated that the sexual diethism is highly significant ($\chi^2 (3) = 317.5, p < 0.001$).

In addition to intensity of the threat display, the spatial relationship of male and female swans with respect to a territorial intruder appears to differ. Mean distance for the male swans and for the female swans as a function of time from the introduction of the model into the territory is averaged in Fig 4. A repeated measures analysis of variance performed on these data indicated that the birds approached the model more closely as time progressed ($F (11, 146) = 63.6, p < 0.001$), and that the rate of approach for a male was more rapid than for a female ($F (11, 146) = 3.57, p < 0.001$). No female ever got as close as its mate but the females from two territories (Little Bay North and Van Brunt's Cove) each

Table 1. Sexual diethism in the frequency of different intensities of threat display elicited by a model.

	Territory	Intensity of threat display			
		Level 1	Level 2	Level 3	Level 4
Male	Van Brun't's Cove	29	26	49	43
	Harbour Cove	43	38	27	39
	Little Bay North	3	44	33	67
	Wreck Pond	11	30	70	36
	Total	86	138	179	185
Female	Van Brun't's Cove	76	49	22	0
	Harbour Cove	97	41	9	0
	Little Bay North	45	64	38	0
	Wreck Pond	69	36	42	0
	Total	287	190	111	0

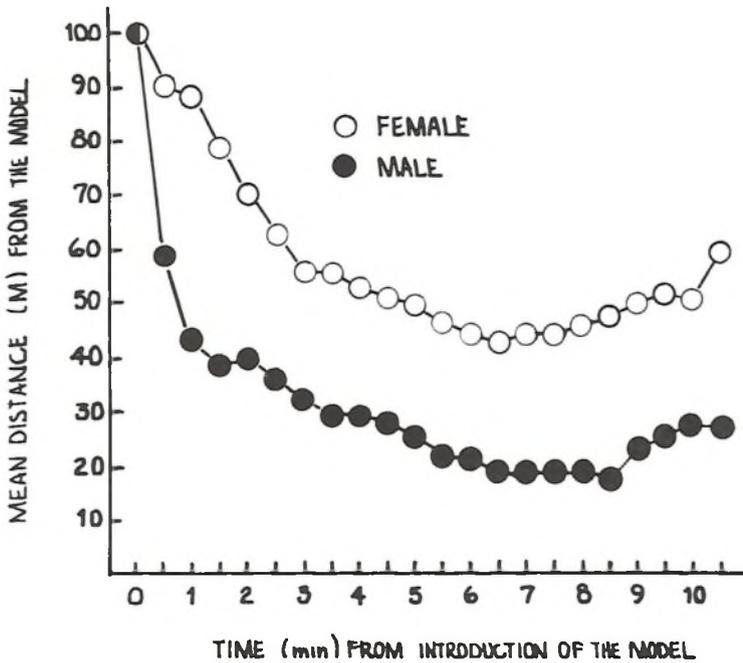


Fig 4. Gender differences in the mean distance between a territorial swan and the model, computed at 30-second intervals from the time the model was placed in a territory.

approached the model more closely than did the males from Harbour Cove and Wreck Pond.

Incubation test: Model tests were resumed seven days after the first egg was found in the nest and were continued every day for 20 days. During incubation the female generally ceased responding to the model. Only three pairs of swans produced successful nests and of these only two continued to respond to the model. The Harbour Cove male failed to react after the fifth day of testing and the experiment was terminated for this bird after five more days.

The testing procedure during the incubation period was the same as in the previous section except that the model was always placed in the same location in the territory, 100 m from the nest. Records were made of the behaviour and distance from the model of each member of a territorial pair. On each trial the observer indicated whether the animal spent most of the test interval on the nest, threatening the model, or engaged in some other activity (eg feeding, preening). If an animal did more than one of these, the activity that was performed most often was counted. Although each trial lasted 10.5 minutes, it was unusual for an animal to change its behavioural response.

The total number of trials on which the animal was scored as threatening, incubating or engaged in some other behaviour is shown in Table 2. Males spent

Table 2. Sex differences in the activities typically performed during the incubation period.

		Activity engaged in					
		Sitting on the nest		Threatening the model		Other	
	Territory	N	%	N	%	N	%
Male	Little Bay North	3	15	17	85	0	0
	Wreck Pond	1	5	19	95	0	0
	Harbour Cove	1	5	4	40	5	50
	Total	5	10%	40	80%	5	10%
Female	Little Bay North	15	85	3	15	2	10
	Wreck Pond	14	70	0	0	6	30
	Harbour Cove	7	70	0	0	3	30
	Total	36	72%	3	6%	11	22%

little time on the nest and most of the time threatening the model. Females spent almost all their time either on the nest or preening nearby. Occasionally the female would threaten the model but, except for one trial, this was always performed as

the bird was swimming to feed near the test area. As has been reported previously (Boase 1959; Heinroth 1910; Huxley 1947) males never actually incubated the eggs, rather they stood on the side wall of the nest, usually engaged in preening.

One pair attempted several nests during this season, none of which was successful. The first nest was poorly constructed and completely washed away after 17 days. One egg had been laid but had not been incubated until day 12. On day 20 the pair began building a new nest which was again destroyed by the tide. Over a 25-day period the male threatened the model on 21 sessions and the female displayed on 19 of these sessions. Two of the days on which they ignored the model were times when both birds were engaged in nest building. The female remained on the nest during four of the sessions. Differences in defence motivation between the male and female of this pair are thus not as dramatic as in incubating birds. Indeed, the first two times the model was introduced into the territory both birds threatened and, upon its removal, performed the Triumph Ceremony (Johnsgard 1965). Furthermore, the female in this pair was as likely to threaten the model (76%) as were the males from the nesting pairs of swans (80%). Thus there does not appear to be a significant gender difference in the motivation to defend the territory in non-incubating birds. The male did, however, continue to threaten at a closer distance to the model.

Post-incubation test: After hatching, the tests with the model were resumed for seven days. Two males stopped displaying altogether and stayed with the female and cygnets as they moved from one place to another in the territory. The third male, from Little Bay, did not respond to the model on the first two days after hatching and responded somewhat unevenly over the next five test days (Table 3).

Table 3. Sex differences in the activities typically performed after the young have hatched.

Activity engaged in	Sex of the parent			
	Male		Female	
	N	%	N	%
With the cygnets	11	52	21	100
Threatening the model	4	19	0	0
Other activity	6	29	0	0
Total	21	100	21	100

Territorial defence by the male dropped from 80% of its activities during incubation to 19% after hatching. Male hostility in several species of *Anatidae* has been shown to wane with the hatching of the young (Lorenz 1959; McKinney 1970) and subsequent studies on different territorial pairs of *C. olor* verified the

reduction and almost complete lack of response to the model upon hatching of the young and their exodus from the nest.

The female, on the other hand, spent all of her time with the cygnets. This close bond continued throughout the summer and winter months. Indeed, juveniles were still following their mother at eight months of age. The male, in each case, was close to the family group but usually remained spatially distinct and never actually initiated group movement from one place to another.

Discussion

Wilson (1975) has argued that monogamy may serve to facilitate defence of a scarce and valuable resource. This hypothesis is certainly compatible with the *C. olor* situation since the population explosion in the northeast United States has placed a premium on satisfactory nesting habitats. However, while both the male and female engage in territorial behaviour prior to the onset of incubation, after incubation this activity is predominantly the role of the male. Johnsgard (1962) and Kear (1970) have discussed evolutionary trends in waterfowl breeding systems and they suggest that differences in defence motivation favouring the male and/or differences in incubation drive favouring the female could result in gender differences such as those observed in this study. These motivational differences are very probably under the control of a complex interaction between stimulus conditions and endocrine state (Silver 1977; Stokes 1974) and can probably be better understood as threshold differences (Hinde 1966; McKinney 1961). Abundant evidence shows that, in vertebrates, increases in aggression parallel the growth of the testes, are eliminated by castration and can be induced by injections of male gonadal hormone (Beach 1948; Collias 1950; Guhl 1961). Androgens, for example, lower the threshold for aggression in many species. Often this lowered threshold is accompanied by an increase in the distance at which the eliciting stimuli are effective and a tendency for aggressiveness to become linked with environmental references such as a territory. The implication for swans is that females shift from territorial behaviour to nest building and incubation to care of the young with changes in hormonal and contextual stimulation, and in the same sense, males shift from territorial defence to defence of the nest to a strategy of defending the young. Furthermore, defence of the young may shift back to territorial behaviour when environmental and endocrine states are suitably altered. In two consecutive years males with young began to threaten their offspring for the first time at approximately eight months of age, in January and February. In each case the threats resulted in the emigration of the young from the territory several weeks later. Changes in length of day, in the size or plumage colour of the juveniles and possibly other characteristics (Norman 1978) may have influenced this behaviour.

We might also consider these gender differences in terms of current evolutionary theory. Triver's (1972) treatment of parental investment implies that the sexual diethism of swans must be constrained to the extent that monogamous couples

should have an equal investment in rearing their young. In the tests described here, both sexes participate in territorial behaviour prior to nesting. When nesting starts, roles begin to differ. Nest building is shared equally but incubation is primarily a female activity. Defence is primarily a male activity. From Table 2 we can determine that males are responsible for about 93% of all territorial defence and only 12% of the incubation activities. Females, on the other hand, are responsible for 88% of the incubation activities and only 7% of the territorial defence. The mean investment for males in these two activities is approximately 53%, while female parental investment is slightly less, 47%.

The female, however, has the greatest energy investment in egg production (Daly and Wilson 1978; Williams 1975). In *C. olor* the average egg weight is 300 g and the average clutch size is six eggs (Scott 1972). Each season a female produces gametes weighing approximately 1800 g, almost 20% of her body weight. Males, however, invest virtually none of their energy resources in egg production. Females also appear to assume most of the rearing activities. Cygnets selectively follow the female and are frequently seen riding on her back. The close mother–infant relationship usually lasts eight or nine months. This asymmetry of parental behaviour is unexpected in a monogamous species, especially one with a prolonged period of infant dependence (Wilson 1975) and may be difficult to reconcile with our expectation of equal investment by the parents. On the other hand, it may be a contributing factor to the evolution of sexual diethism in territorial defence with greater risk to the male during non-reproductive periods of the year.

Habituation of the threat display

Several workers have suggested that habituation is the most fundamental form of adjustment to environmental change available to an organism (Thompson *et al* 1973). It is thought to be the simplest type of learning and a process which is similar in all animals (Thorpe 1963; Wyers *et al* 1973). Studies of habituation in a natural setting indicate that the process is important to adaptation (Petrinovich 1973) and that it probably accounts in part for a number of significant social phenomena (eg the 'dear enemy' phenomenon, Wilson 1975; sexual satiation, Marler and Hamilton 1966; the establishment and maintenance of territories in birds, Falls 1969).

Animals confronted by stimuli and situations which neither facilitate survival and reproduction nor interfere with these processes eventually come to neglect these features. Rouse (1905), for example, reported that pigeons, exposed to what he referred to as 'significant' sounds, continued to attend to these stimuli while habituating to 'meaningless' sounds. Thompson (1969) also demonstrated that male buntings *Passerina* exhibited continued territorial response in the field to playback of their own species song in contrast to song playback of two other species of bunting. Furthermore, stuffed dummies elicited virtually no reaction from territorial birds, whose attention was given to threatening the loudspeaker.

Auditory stimulation does not appear to be an important feature of *C. olor* territorial behaviour (Demarest 1980a). One might expect that reactivity to visual cues in this species is more 'significant' and that these responses ought to be resistant to habituation. However, even species-meaningful stimuli eventually cease to elicit selected responses with repeated presentation (Petrinovich 1973; Petrinovich and Patterson 1979). The September to October 1973 increase in territorial intruders (see Fig 3) was concentrated at the eastern sector of Setauket Harbour, adjacent to Van Brunt's Cove. Over a period of three to four weeks a flock of 12 to 16 birds gradually worked their way into the cove to feed and preen. Initially the mated pair inhabiting the cove threatened and chased any swan that breached the territorial boundary. By mid-October, however, the mated swans were feeding side by side with these trespassers and few threats were seen. It would appear then that habituation of territorial behaviour is possible under natural conditions and that it could play a role in determining which swans will mate and find a place to live.

Method

In order to determine the course of behavioural habituation to territorial encroachment, the males' data from the incubation phase of the 1974 model tests were examined over successive daily presentations. Omitted, however, were the data from the Harbour Cove male, which habituated unusually fast, failing to respond to the model after day 5.

Each bird was administered 20 test trials with the model placed in the water 100 m from the nest. On day 21 a dishabituation test was given in which the model was placed 20 m from the nest. This was followed by three more trials with the model located 100 m from the nest. Testing was discontinued for six days and on day 31 a test for spontaneous recovery was administered. The type of display and distance between the test bird and the model was recorded at 30-second intervals, for ten minutes, at which point the model was removed from the territory. Observations were continued at one-minute intervals for ten minutes after removal of the model.

Results

The first measure, intensity of threat, was found by first grouping each of the 20 daily recorded threat postures of an animal into one of the four levels (see page 215). A daily threat intensity score was calculated by multiplying the frequency of responses in each level by the number value assigned (ie 1 to 4). The daily threat intensity score could thus vary from a low of 20 (ie 20 observations of Level 1 response) to a high of 80. These scores were then divided by 20 to yield the mean daily threat display of each swan and group averages were computed from the products. These data are shown in Fig 5A for each of the 20 days of testing, the dishabituation test on day 21, the following three rehabilitation days (ie days 22 to 24) and the spontaneous recovery test on day 31. A repeated measures analysis of

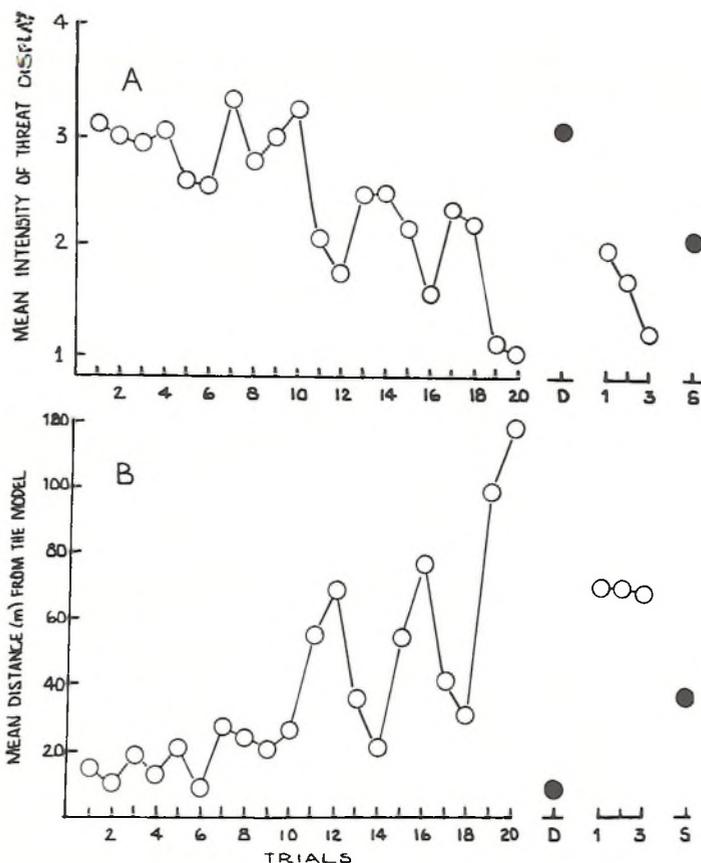


Fig 5. Habituation, dishabituation (D), rehabituation and spontaneous recovery (S) of the *Cygnus olor* threat behaviour over a 31-day period.

The mean intensity of threat display is shown in A and the mean distance between a territorial swan and the model is shown in B. The model was moved to a new location in the territory on the dishabituation trial and spontaneous recovery was assessed after a six-day rest.

variance computed on the first 20 days yielded a significant habituation effect ($F(19, 38) = 6.84, p < 0.001$). At the end of 20 days the swans were no longer reacting to the model. On the dishabituation test, with the model placed only 20 m from the nest, all three birds resumed their threat display activities. In fact, the reactions were as intense as the first day of testing. The male from the Little Bay territory responded even more aggressively on this test than during most days of the habituation test. When the model was reintroduced for three days at the original test site, 100 m from the nest, the threat behaviour rapidly diminished in intensity. On the last test, seven days later, however, all three swans exhibited partial recovery of threat activity. The typical intensity of display was only about

half as great as during the initial days of testing or during the dishabituation test, but there was no overlap in the range of scores on the spontaneous recovery test when compared with either the last two days of original habituation or the last day of rehabilitation:

The distance measure shown in Fig 5B represents the group average distance between the swan and the model on each day of testing. These data were found by computing mean daily distance scores for each swan from the 20 observation intervals and averaging these individual means together. The resultant figures are somewhat misleading because a test always began with the territorial swan approximately 100 m from the test area and individual scores therefore partly reflect the speed at which each bird approached the model. Much of the variability in the individual scores, in fact, was found in the behaviour from the initial five minutes. Despite this, the data show that swans failed to react and approach the model as testing continued. On the last two days no response occurred at all and only token approach responses occurred on several other days (eg days 11, 12, 15 and 16). A repeated measures analysis of variance performed on these data yielded a highly significant habituation effect ($F(19, 38) = 6.09, p < 0.001$). On the dishabituation test, all animals approached the model closely; in fact, two of the three birds spent most of this test performing the Zig-Zag Dance within 1 m of the model. The mean distance scores from days 22 to 24, on the other hand, do not provide clear evidence of a decrement in approach behaviour as might be expected of rehabilitation. However, the variability in these data mask one otherwise consistent finding. Two of the three birds consistently remained over 80 m from the model, while the male from the Little Bay area continued to approach the model. His mean daily distance, however, increased from 6.9 m to 12.8 m to 20.6 m over the course of these three days. The large amount of variability in the distance scores for rehabilitation should be contrasted with the smaller variability in the intensity of threat display over the same period. Finally, the spontaneous recovery test after a six-day reprieve from testing produced closer spacing to the model in all three swans.

Discussion

Thorpe (1963) defined habituation as 'the relatively permanent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement. It is specific to the stimulation and relatively enduring' (p 61). Additional characteristics have been outlined by Thompson and Spencer (1966) and include spontaneous recovery as a function of time since stimulation, more rapid habituation with weaker stimulation and dishabituation to a novel stimulus. The present study found evidence for a gradual decrement in approach and intensity of threat display to a model, dishabituation to the same model placed in a new location, and spontaneous recovery after a six-day interval without stimulation. In addition, a more rapid response decrement has been demonstrated with a black model (ie 'weak' stimulus) in comparison to a white model with these birds

(Demarest 1980a). These data, then, provide clear evidence that territorial threat behaviour can undergo habituation under repeated invasion of a territory. This habituation does not result merely from sensory adaptation; if it did, one would not find dishabituation with a novel stimulus. It could be argued, however, that the model placement on the dishabituation test was actually a 'stronger' stimulus since it was closer to the nest. If sensory adaptation means that the threshold for elicitation of a response is raised, then a stronger 'dishabituating' stimulus might be expected to restore the threat response. The present design does not clearly distinguish between these mechanisms.

Petrinovich (1973) has recently reviewed naturalistic studies of habituation concluding that the process is slower to species-significant stimuli but that response decrements do occur, even to territorial invasion (Mulligan and Verner 1971; Petrinovich and Patterson 1979; Petrinovich and Peeke 1973; Thompson 1969). Falls (1969) has suggested that habituation might be involved in the establishment and maintenance of territories in birds and this is consistent with the field observations described here. A persistent mated pair of birds may, through repeated intrusion into another's territory, gain a small area for themselves. With continued habituation on the part of the original territorial bird, this new pair could enlarge their 'safe' area and begin to defend it. Eventually the area will become sufficiently secure for a nest to be built and young fledged. The author has been witness to such a sequence of events over the years in both the Van Brunt's Cove swans and in the Little Bay South swans, although the latter pair have yet to fledge young.

Furthermore, habituation of territorial behaviour would help to account for the dear enemy phenomenon (Fisher 1954; Wilson 1975). When a recording of a neighbouring conspecific is played to any of several songbirds, the birds do not exhibit a reaction. A recording of a stranger's song, however, elicits aggression and territorial defence. This distinction between strangers and neighbours apparently serves to reduce injury and energy expenditure in agonistic encounters at territorial borders and may also serve some mutual stimulation function (Fisher 1954). In *C. olor*, too, habituation of territorial behaviour toward neighbouring or familiar birds would seem to conserve energy and reduce risk. Furthermore, there is reason to believe that at least some territorial neighbours are related to one another (D Norman, pers comm 1978); thus the dear enemy phenomenon may serve to increase inclusive fitness.

General discussion

Previous studies examining the information available in *C. olor* territorial display (Demarest 1980a, 1980b) have shown that the displays are highly predictive of an animal's impending behaviour. Threat displays prior to an attack, for example, have been shown to follow a sequence which is adequately described by a first-order Markov chain model, if repetitions of acts are ignored. The probabilistic relationship of acts after an attack was also found to be dependent upon the

animal's immediate preceding display and in some instances was absolutely predictable from the preceding behaviour. Smith (1977) has argued convincingly that this sort of relationship between display posture and future behaviour is a message in animal communication. The message is the information that a signal makes available about its sender. It tells what the signaller is likely to do at any moment and hence what it will probably do in the next instant if the situation does not change.

Among *C. alor* the signal value of a given display provides information about the outcome of future interactions. For an animal that finds itself in unfamiliar waters, even a moderately threatening display by the territory owner ought to signal the possibility of attack and injury. As the present results show, however, the messages vary in frequency and ease of elicitation as a function of the time of the year, the sex and reproductive status of the territory owner and the number of previous encounters with the territory owner.

Habituation may not only lead to a 'taming' effect of one animal upon the other but it may also produce familiarity and, as a result, a finer reading of the message in the other bird's display behaviour. A mild threat display which is actually inhibitive of attack (cf Table 3 in Demarest 1980a) might produce an avoidance response from an intruder unfamiliar with the territory owner but no reaction from an intruder from a neighbouring territory. Furthermore, familiarity tends to produce attraction and attachment (Zajonc 1971) and a lower probability of danger for the birds involved. It makes sense that something that stays around for a long time without causing harm is probably part of the favourable environment (Wilson 1975). Threats to the favourable environment are wasted energy and may, in fact, be counter-adaptive. For example, one invasion of Setauket Harbour by five swans in 1973 resulted in intergroup co-operative defence by the Harbour Cove male and both swans from the Little Bay South area. At one point, all three territorial birds postured three abreast in a Wedge display and together chased a single intruder from the area. Although this was the only time I have witnessed intergroup 'co-operative' defence by territorial swans, individual defence by birds from two or more neighbouring territories would certainly reduce the probability of injury to any one bird (Wilson 1975). Individual recognition of neighbours and an ability to interpret the message of a neighbour's display based on familiarity with this animal's behavioural tendencies in various environmental contexts, including seasonal variation and changes in reproductive status, would serve to enhance the adaptiveness of this behaviour.

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Summary

Territorial behaviour was observed in mated pairs of *Cygnus olor* in eastern New York and New Jersey from 1973 to 1977. The frequency of threat display varied seasonally, as a function of the number of territorial intruders. Territorial intrusion reached a peak in early spring and again in late autumn, and was infrequent during the incubation period. Defensive behaviour was studied during the incubation period by the introduction of an artificial model into the territory. The male is almost exclusively responsible for territorial defence. When a female does threaten an 'intruder' (the model), the displays are less intense, of a shorter duration and are performed further from the model. The intensity and duration of display bouts habituated with repeated exposures to the model and decreased abruptly the day that the cygnets left the nest. Introduction of the model into a different part of the territory produced dishabituation. The importance of habituation and familiarization with the threat displays of neighbouring swans is discussed regarding the establishment and maintenance of territories.

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