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## Evolutionary origin, proximate causal organization and signal value of the whistle-shake-display of male shelducks (*Tadorna tadorna*)

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**EVOLUTIONARY ORIGIN, PROXIMATE CAUSAL  
ORGANIZATION AND SIGNAL VALUE OF THE  
WHISTLE-SHAKE-DISPLAY OF MALE SHELDUCKS  
(TADORNA TADORNA)**

by

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**Summary**

This paper focusses on the phenomenon of emancipation in the Whistle-shake, an epigamic display of male shelducks. A comparison with other motor patterns and vocalizations indicates, that the Whistle-shake is a combination of the comfort movement Body-shake, with integrated elements of another display: Bill-tipping with trill. Between Whistle-shake and Body-shake almost no differences exist in total duration, duration of the sub-units they have in common, and in the number of shaking elements.

Artificial rain experiments revealed that the Whistle-shake is not emancipated from the original causal factor, typically influencing the present occurrence of the Body-shake: All males predominantly produced Whistle-shakes when sprayed with water. In addition social factors influence the occurrence of the Whistle-shake. The percentage of shakes consisting of a Whistle-shake was higher in dominant than in subordinate birds. Furthermore, by confronting territorial pairs in spring with either a whistle-shaking or a body-shaking male or an empty neighbouring cage we found that the whistle-shaking male released more Whistle-shakes in the test-males than the body-shaking male. In contrast the test-females, which predominantly produced Body-shakes, did not show any changes in their shaking behaviour in response to the different shaking stimuli presented. Therefore it seems likely

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that the Whistle-shake and the Body-shake share causal comfort factors but differ in their sensitivity for social stimuli. Context analyses demonstrate that the Whistle-shake shows a sequential association with aggression in dominant males and with escape behaviour in subdominant males. Therefore, the occurrence of the Whistle-shake is not restricted to a specific balance between the activation of motivational systems for aggression and fear.

The dual function of the Whistle-shake (comfort and social function) is discussed.

## Introduction

In many animal species intraspecific communication is expressed in conspicuous, stereotyped postures, movements and vocalizations, so called 'displays'. In his conflict hypothesis Tinbergen (1952) proposed a possible origin, evolution and proximate causation of these motor patterns: Based on similarities in form, context, and temporal sequence of displays with other motor patterns, he postulated that displays are derived phylogenetically from intention movements and displacement activities which occur when different incompatible motivational systems are simultaneously activated in social interactions (for a review see Baerends, 1975). During the evolutionary process of ritualization these motor patterns changed into stereotyped conspicuous species-specific displays, which serve communication function. Concomitant with ritualization Tinbergen postulated that the causal factors of displays may gradually become independent of the original causal factors. This evolutionary change was called emancipation. Tinbergen himself was not very explicit about the possible proximate control of displays. However, the use of the present day's context and temporal sequence of displays as arguments to support the conflict hypothesis indicates that displays are thought not to have completely emancipated from their original causal factors. These causal factors are almost always thought to be motivational factors of aggression and fear. However, manipulation of these factors in order to get insight into the causal control of the display is difficult. Furthermore, data collection on the association of display performance with aggressive and fear behaviour is hampered by the complexity of the context, in which the behaviour of the responder influences the behaviour of the displaying animal (Bossema & Burgler, 1980; Nelson, 1984). Moreover, it can be challenged whether the causal organization of social displays can be satisfactorily explained by assuming that these motor patterns are under the control of two motivational systems, one controlling the

tendency to attack and the other to flee. This challenge can be made based on both the causal analysis of behaviour (*e.g.* Groothuis & Ros, in press) and, from a functional point of view, on the game theoretical approach (Maynard-Smith, 1974, 1982; Caryl, 1979; for reviews and discussion see van Rhijn, 1980; Hinde, 1981; Wilson, 1992; Boinski *et al.*, 1994).

In order to study emancipation but to avoid the above mentioned difficulties that are linked with threat-displays we chose the Whistle-shake, an epigamic display of male shelducks. Previous comparative studies suggest that in anatidae most social and courtship displays have been derived phylogenetically from comfort movements (Lorenz, 1941; McKinney, 1965; Kaltenhäuser, 1971). This might hold true for the Whistle-shake display as well. In sheldrakes, for instance, the Whistle-shake and the comfort movement of Body-shake alternate in a yearly rhythm: In spring the Whistle-shake is the mainly occurring form and reaches its highest frequency. Thereafter a gradual regression to Body-shaking takes place. During moult (July/August) males predominantly produce Body-shakes. In autumn the Whistle-shake is gradually restituted via intermediate forms (Ratermann *et al.*, 1990; Ratermann, 1991). In contrast to other presumed phylogenetical precursor patterns of postural displays comfort movements are easy to manipulate by specific external factors affecting plumage condition in many species. Therefore, in order to test the extent of emancipation experimental investigations on the causation of displays that are derived from such comfort movements can relatively easily be carried out.

This paper starts with an analysis of the form of the Whistle-shake. It compares the display with other motor patterns of this species in order to examine similarities in form. We then address the question to what extent the Whistle-shake is still under the influence of factors controlling the present day's occurrence of one of its presumed phylogenetical precursor patterns. Finally, experiments on the signal value of the Whistle-shake were carried out to get insight in the social functions of this display.

### **Form analysis**

In this section the form of the Whistle-shake is compared with the form of other motor patterns of the shelduck in order to get insight into the possible evolutionary origin of the display.

### Methods

Twelve pairs and 6 single males of adult shelducks were housed in 6 groups of 5 individuals. Thus, each group included 2 pairs and a single male. All groups were placed in cages of 5.25 m<sup>2</sup> with water basins of 1 m<sup>2</sup>. The groups could hear but not see each other. In such a group composition males form a clear social hierarchy (see Patterson, 1982), which guarantees the occurrence of the Whistle-shake and other shaking patterns (see below). For individual recognition all birds were colour banded. The ducks were fed with grain and dry pellets for duck and goose farms; the water was refreshed almost daily.

Spontaneously occurring shaking patterns were recorded by video-tape and afterwards analysed in detail. The recordings were taken from a hide at 5 m distance between the ducks and the camera. The following aspects have been used to characterize differences and similarities between the different shaking patterns:

- the position and movement of tail, bill and neck,
- the duration of the different behaviour patterns as well as of their sub-units,
- the presence and sonographic structure of the accompanying vocalizations and their similarities with other calls.

### Results

The Whistle-shake display (Fig. 1c) starts with an intention posture, which is characterized by slightly raised body feathers. Thereafter the movement continues with introductory tail-wagging, followed by shaking of the body and subsequently of head and neck. The latter two are simultaneously moved forward and downward. After reaching the lowest point of the downward movement, head and neck are raised until the neck is stretched vertically and the bill points almost vertically upward. In this position the bird utters a whistling trill. While returning to the normal body position, the display ends with another tail-wagging.

Like the display, the comfort movement of Body-shaking (Fig. 1a) consists of the sub-units of intention posture, introductory tail-wagging, head-neck-shaking and final tail-wagging. However it lacks the upward and downward head-neck component as well as the vocalization accompanying the display. Adult male shelducks are able to produce different transitional forms between body-shaking and whistle-shaking. Ratermann *et al.* (1990) distinguished the Deep and High intermediate form. In contrast to the Whistle-shake both forms are not accompanied with a conspicuous call. In the Deep intermediate form the head-neck-shake component has a slightly larger amplitude in the vertical plane than in the Body-shake. The High intermediate form (Fig. 1b) is more similar to the Whistle-shake display but lacks the tossing of the head and the accompanying call.

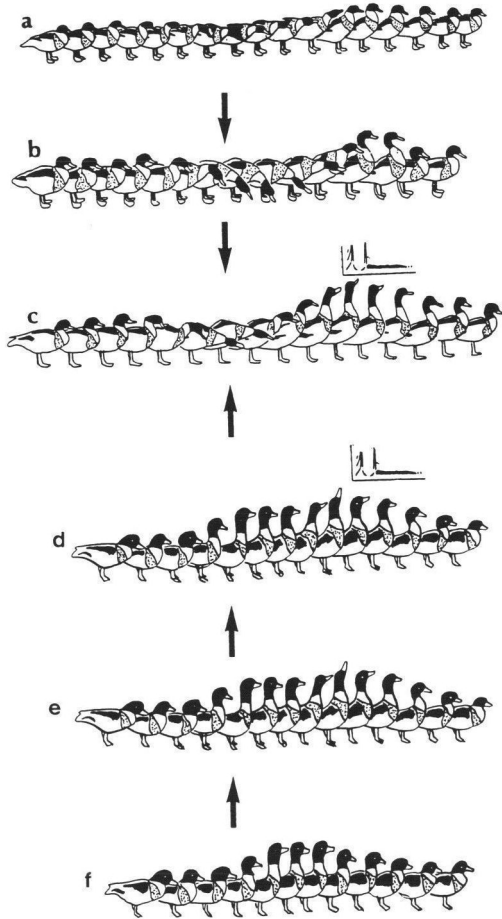


Fig. 1. Form similarities between the Whistle-shake display and other behaviour patterns in male shelducks; a = Body-shake, b = High intermediate form, c = Whistle-shake display, d = Bill-tipping with trill, e = Bill-tipping without trill, f = Alert posture. For further details see text.

We could not find differences in the number of shaking elements in the sub-units of introductory tail-wagging and head-neck-shaking between the different shaking patterns (Whistle-shake, Body-shake, Intermediate forms). However, the final tail-wagging component contains significantly more shaking movements in the Whistle-shake display and therefore lasts somewhat longer (Table 1). The mean durations of the introductory tail-

TABLE 1. *Comparison of the duration and shaking elements in four different shaking patterns as well as their sub-units*

Parameter	Shaking pattern				Significance
	bs ( <i>N</i> = 108)	imd ( <i>N</i> = 108)	imh ( <i>N</i> = 108)	whs ( <i>N</i> = 108)	
Total duration (s)	3.79 (±0.06)	3.80 (±0.25)	3.85 (±0.23)	3.89 (±0.40)	<i>p</i> = 0.84
Duration of introductory tail-wagging (s)	2.04 (±0.07)	1.96 (±0.17)	2.07 (±0.17)	1.89 (±0.23)	<i>p</i> = 0.22
Duration of head-neck-shaking (s)	0.99 (±0.05)	1.07 (±0.03)	1.09 (±0.05)	1.57 (±0.04)	<i>p</i> = 0.00
Duration of final tail-wagging (s)	0.97 (±0.08)	1.03 (±0.09)	1.02 (±0.10)	1.30 (±0.10)	<i>p</i> = 0.004
Number of elements in introductory tail-wagging	44.7 (±1.99)	42.5 (±3.03)	45.2 (±2.14)	41.2 (±4.13)	<i>p</i> = 0.13
Number of elements in head-neck-shaking	7.91 (±0.94)	8.75 (±0.55)	8.34 (±0.61)	8.47 (±0.71)	<i>p</i> = 0.11
Number of elements in final tail-wagging	21.8 (±1.59)	22.9 (±2.00)	23.2 (±1.68)	30.4 (±3.32)	<i>p</i> = 0.007

bs = Body-shake; imd = Deep intermediate form; imh = High intermediate form; whs = Whistle-shake.

The data were collected from 4 subadult males. Statistical analysis was carried out by One-way-ANOVAs.

wagging component of the different shaking patterns are statistically indistinguishable, whereas the head-neck-shake component lasts significantly longer in the Whistle-shake display (Table 1). Despite these differences the total duration did not differ between Body-shaking, Whistle-shaking and Intermediate forms. This is due to a different arrangement of the sub-units: In the Body-shake the sub-units occur more or less successively, whereas an overlap of the components head-neck-shaking and final tail-wagging takes place in the display (Fig. 2).

The main difference between the Whistle-shake and the Body-shake is the head-neck component. The head-neck component of the Whistle-shake, which is accompanied by a conspicuous trill, looks rather similar to another display of male shelducks, the so called Bill-tipping with trill (see Patterson, 1982). This display is characterized by an erect posture, followed by tossing of the head and a conspicuous call (Fig. 1d). The main difference

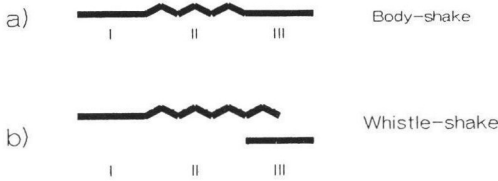


Fig. 2. Arrangement of the subunits of introductory tail-wagging (I), head-neck-shaking (II) and final tail-wagging (III) in the comfort movement of Body-shaking (a) and the Whistle-shake display (b).

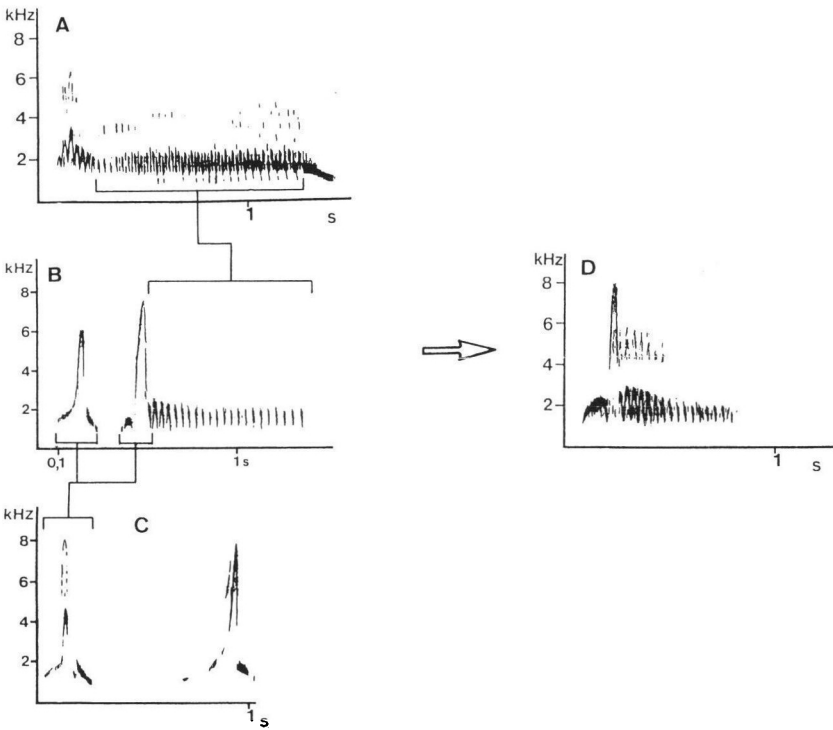


Fig. 3. Form similarities between the whistle-shake trill and other calls of male shelducks; a = aggressive trill, b = bill-tipping trill, c = setju-call, d = whistle-shake trill. For further details see text.

between the Bill-tipping call and the Whistle-shake call is that the former is regularly preceded by a single note, which sounds like 'setju' (Timcke, 1992; Fig. 3b). This single note can also be produced independently in



the alert posture (Figs 1f, 3c). During ontogeny Bill-tipping with trill emerges gradually via Bill-tipping without trill (Fig. 1e) from the alert posture (Fig. 1f) (Düttmann *et al.*, in prep).

The corresponding elements between the Whistle-shake call (Fig. 3d) and the Bill-tipping call (Fig. 3b) consist of a short introductory note of 1.33 kHz on average, followed by a shortlasting higher pitched element. This introductory part is followed by a prolonged series of notes in rapid succession, which sound like 'terrrr' (Timcke & Bergmann, 1994; Fig. 3d). The terrrr-element shows resemblance to the so called 'aggressive trill' (Fig. 3a), whereas the introductory part in Whistle-shake and Bill-tipping call (Fig. 3b, d) is more similar to the setju-call (Fig. 3c).

### *Conclusion*

The results indicate that the Whistle-shake display is a combination of the comfort movement of Body-shaking and the motor elements of Bill-tipping with trill. With regard to the latter several authors report a strong association of Bill-tipping, when performed as a separate display, with alertness and escape behaviour (Beintema, 1969; Bauer & Glutz, 1979; Patterson, 1982; Riebesehl-Fedrowitz & Bergmann, 1984). In alarm situations in the field this motor pattern seems to be regularly produced before birds fly off (Beintema, 1969; Patterson, 1982). However, a detailed context analysis with regard to similarities and differences between Bill-tipping with trill and Bill-tipping without trill is still lacking. The above presented evidence indicates that the conspicuous call accompanying the Whistle-shake movement contains elements of other calls of this species, namely the aggressive trill and the setju-call. The contexts of the latter are largely unknown. It has been claimed that the aggressive trill is associated with overt attacks (Riebesehl-Fedrowitz & Bergmann, 1984). Our own observations on captive birds point in the same direction: In territorial males, which were confronted with male intruders during the reproductive time in spring, aggressive trills were regularly combined with overt attacks. The same call is also produced when male shelducks protect their ducklings against approaching predators or humans. As in the former situation the aggressive trill is associated with overt aggression (see also Beintema, 1969; Riebesehl-Fedrowitz & Bergmann, 1984; Engländer & Bergmann, 1990). Although empirical studies are lacking it seems that the setju-call

is mainly produced in mild alarm situations and is often followed by escape behaviour (Timcke, 1992; Bergmann, pers. comm.). Therefore it seems that the Whistle-shake call is a combination of elements associated with aggression and elements associated with escape. However, because detailed context analyses for both presumed precursor calls are lacking, further investigations are necessary.

### **Experiments on the proximate causation of Whistle-shaking and Body-shaking**

The form analysis presented in the previous section showed that the Whistle-shake shares important elements with a comfort movement, the Body-shake. Consequently stimuli inducing comfort behaviour, in particular shaking, have very likely been part of the original causal factors of this display. Therefore we investigated whether the Whistle-shake is still under the control of factors influencing shaking behaviour.

#### *Methods*

During the reproductive phase in spring, when adult males frequently perform Whistle-shakes, 3 groups, each consisting of two pairs and one single male, were housed separately in cages described previously (see foregoing chapter). In such an arrangement birds form a clear hierarchical rank order within a few hours. Only one male in each group attacked the other males. This one was classified as the dominant bird and the others as subdominant birds. To test, whether the Whistle-shake is still controlled by factors influencing the present occurrence of the Body-shake, single males within each group were sprayed with water for 2 s from a hide just outside the cage and observed subsequently for 3 min. Previous experiments in females showed that this induced Body-shakes consistently. All birds were sprayed randomly in a series of 3 trials for 7 times in total. In pilot-tests it turned out that in adult birds each spray normally induces only one shake. To prevent possible confounding influence of bathing the water basins were covered by wooden panels one hour before the experiments started. Type and frequency of shaking patterns were recorded. The occurring forms were classified according to Fig. 2.

In addition to these experiments the same birds under the same housing conditions were observed to analyse the social context in which spontaneous Whistle-shakes and Body-shakes occur. As in the artificial rain experiments the water basins were covered one hour before the observations started in order to exclude the influence of bathing on form and frequency of the occurring shaking patterns. Observations were carried out in spring, when birds perform mainly Whistle-shakes, as well as in summer when birds almost exclusively perform Body-shakes. The observation sessions were carried out from a hide next to the cage for 2 h per day and for 6 days in total. During the observation we continuously recorded the occurrence of overt aggression, overt escape and the shaking patterns of each

bird. Overt aggression included rapid movements of head and bill directed to the other bird (biting and intention movements to bite; stationary threat displays were excluded) and chasing. Overt escape was defined as moving away from the opponent, induced by aggression of that opponent. Afterwards we analysed the temporal sequence of the shaking patterns with aggression and escape behaviour. To exclude the possibility that shaking patterns preceded by overt attacks or overt escape behaviour are caused by comfort stimuli due to a disarrangement of the feathers during the interactions, we only took those data into consideration in which opponents had no physical contact.

## *Results*

### Artificial rain experiments

Birds reacted very often with shaking behaviour when sprayed with water but subordinate individuals shook less than dominant ones (*t*-test;  $p < 0.002$ ; Fig. 4). Interestingly, all males performed the Whistle-shake display frequently when sprayed with water, a non social stimulus. In addition, although the Whistle-shake was the predominant pattern in all birds, subordinate males produced significantly fewer Whistle-shakes than dominant males (*t*-test;  $p < 0.01$ ; Fig. 4).

### Sequential analysis of Whistle-shake and Body-shake with other behaviours

The association of overt aggression and escape with the Whistle-shake differed according to the social status of the birds during the reproductive time in spring (Table 2). In dominant males 44 Whistle-shakes were preceded by overt aggression (Whistle-shakes followed by aggression hardly occurred). These birds did not perform overt escape so their Whistle-shakes were never preceded or followed by overt escape. In subordinate birds the situation was the reverse. These birds never performed aggression and 49% of their Whistle-shakes were found to be preceded by overt escape behaviour (these shakes were almost never followed by escape) (see Table 2).

In summer none of the males performed overt aggression or overt escape behaviour nor Whistle-shakes. Body-shakes were almost exclusively performed during preening sequences.

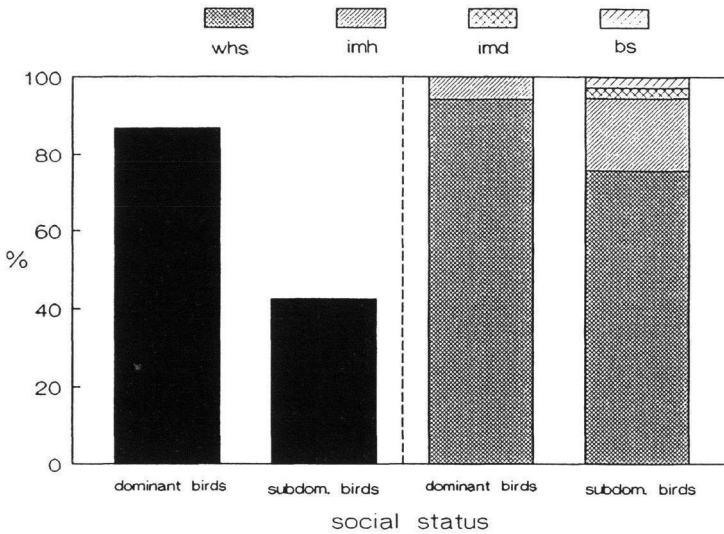


Fig. 4. Shaking behaviour of adult male shelducks in spring in response to artificial rain stimuli and in relation to the social status of the birds. Left: Percentage of artificial rain tests to which dominant or subdominant birds responded with a shaking pattern. Right: Percentage of different shaking forms released by artificial rain in subdominant or dominant birds; whs = Whistle-shake, imh = High intermediate form, imd = Deep intermediate form, bs = Body-shake.

TABLE 2. *Sequential association of the Whistle-shake display with overt aggression and escape behaviour in dominant and subdominant male shelducks, when kept together in a small cage in spring*

Patterns	Social status	
	Dominant birds	Subdominant birds
Overt attack ( <i>N</i> )	62	0
Overt escape ( <i>N</i> )	0	55
Whistle-shake ( <i>N</i> )	41	49
Overt attack → Whistle-shake ( <i>N</i> )	20	0
Overt escape → Whistle-shake ( <i>N</i> )	0	26
Whistle-shake → overt attack ( <i>N</i> )	2	0
Whistle-shake → overt escape ( <i>N</i> )	0	5

### *Conclusion*

In the present study no evidence for emancipation of the presumed original causal factor for shaking was obtained for the Whistle-shake display. Like its presumed precursor pattern, the Body-shake, it is still under the control of factors affecting feather condition. Furthermore the Whistle-shake shows a sequential association with aggression in dominant males and with escape behaviour in subdominant males. Therefore, the occurrence of Whistle-shakes is not restricted to a specific balance between the activation of the motivational systems for aggression and fear as it is assumed in the conflict-hypothesis (see Moynihan, 1955). Rather, it can occur when either aggression or escape is predominantly activated.

### **Experiments on the signal value of Body-shake and Whistle-shake and their sensitivity to social stimuli**

It seems likely that the special form of the Whistle-shake serves a communication function which is lacking for the Body-shake. Furthermore, although both motor patterns are under the influence of comfort stimuli they may differ in their sensitivity to social stimuli. To test these ideas we analysed the behaviour of territorial pairs in spring when they were confronted with either a whistle-shaking male, a body-shaking male or no male at all in a neighbouring cage.

### *Methods*

#### Design

During the reproductive time in spring 5 adult pairs were confronted with either a body-shaking or a testosterone-implanted whistle-shaking male or an empty cage. Each of the experimental pairs (test-pairs) was housed in a cage of 4 m<sup>2</sup> and separated from the stimulus-bird by wire. The latter was placed in a cage of 1.25 m<sup>2</sup> next to the test-pair one hour before the experiments started. In the experiments the stimulus-male was sprayed with water ten times in succession each seventh minute to release Body-shakes or Whistle-shakes. Form and frequencies of displays, aggression and comfort movements of the test-pairs were recorded on video tape from a hide at 5 m distance of the cage. Afterwards we analysed the frequencies of different display patterns and overt aggression produced by the test-pairs in relation to the different stimuli presented. The confrontation with both males and the control observations were carried out in a balanced order.

To obtain a body-shaking and a whistle-shaking stimulus-male two adult birds were castrated. One of these was afterwards implanted with testosteronepropionate. For im-

plantation we used a silicone tube of 3.5 cm length (inner diameter: 1 mm, outer diameter: 3 mm), which contained 30 mg of the hormone. Under the local anaesthesia lidocaine, this tube was implanted subcutaneously in the neck region. Previous studies showed that in male shelducks social displays, bill-knob height and bill-colour are testosterone-dependent (Düttmann *et al.*, in prep.). As both stimulus-birds should differ in their shaking behaviour alone and not in morphological characters with a presumed signal value, the bill of the implanted male was painted in the colour of the non-implanted castrated male. Differences in the bill-knob height remained small and amounted to 3.7 mm at most at the end of the experiments. We think it unlikely that this difference in bill knob height has influenced our results, given the much bigger difference in bill knob height that exist between birds in spring and in summer (more than 15 mm: Ratermann *et al.*, 1990). The form of the shaking behaviour of both stimulus-males was analysed by a completeness-index, which was defined as follows:

$$C = (N_{\text{imd}} + 2N_{\text{imh}} + 3N_{\text{whs}}) / \{3(N_{\text{bs}} + N_{\text{imd}} + N_{\text{imh}} + N_{\text{whs}})\}$$

in which:

$C$  = completeness-index

bs = Body-shake

imd = Deep intermediate form

imh = High intermediate form

whs = Whistle-shake

The index runs from 0 to 1 implying that Body-shakes and Whistle-shakes respectively are exclusively performed.

### Statistics

For the statistical analysis of the frequencies of the different behaviour patterns performed by the test-pairs under the three different experimental conditions we used a repeated measurement MANOVA (one factor representing the frequency of the different shaking patterns of each bird as a repeated measurement; the other representing the different tests as a repeated measurement) in order to look for significant overall effects. In case of statistical significance these treatments were followed by post-hoc paired t-tests to locate significant differences.

### Results

#### Shaking behaviour of the stimulus-males

As was the aim both stimulus males did not differ in the total frequency of shakes when sprayed with water but did differ with regard to the different forms they performed: The castrated male performed Body-shakes exclusively (completeness-index = 0), whereas in the testosterone-treated bird only intermediate forms and Whistle-shakes were elicited (completeness-index = 0.68). Interestingly a significant negative correlation was found

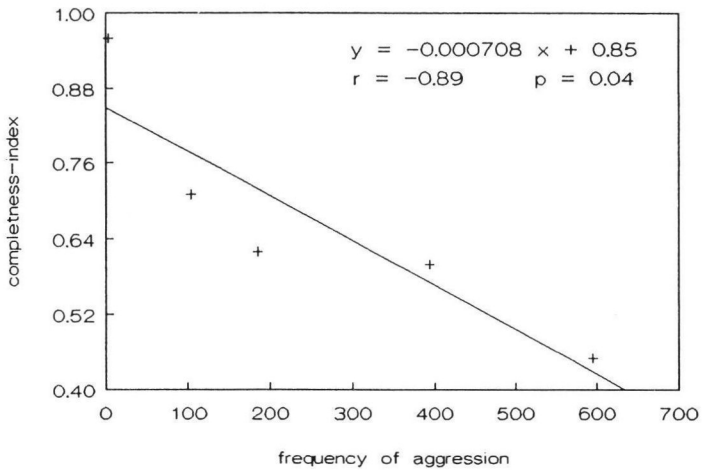


Fig. 5. Correlation between the frequency of aggression produced by 5 different territorial pairs of shelducks in spring against a testosterone-implanted, castrated male and the completeness of the shaking patterns released in the latter by artificial rain stimuli. Birds were separated by wire. For further details see text.

between the completeness of the shakes in the latter and the frequency of attacks directed to him by each pair (Spearman rank correlation:  $N = 5$ ,  $r = -0.89$ ,  $p = 0.04$ ): The higher the frequency of attacks the lower the completeness-index of the shaking responses released by rain (Fig. 5).

#### Behaviour of the test-pairs

In spring the Whistle-shake is the mainly occurring shaking pattern in the test-males (Fig. 6a). Its frequency of occurrence was relatively low in the control situation (empty neighbouring cage), intermediate in the body-shake condition and relatively high in the whistle-shake situation (Fig. 6a; MANOVA:  $F = 5.86$ ,  $df = 2$ ,  $p = 0.027$ ). The difference between the first and the last condition was significant (Paired  $t$ -test:  $p = 0.036$ ). The same results were found with regard to the total frequency of shakes (Fig. 6a; MANOVA:  $F = 5.30$ ,  $df = 2$ ,  $p = 0.034$ ; Paired  $t$ -test:  $p = 0.017$ ). In contrast, the test-females, which mainly produce Body-shakes, did not show any changes in form and frequency of the different shaking patterns, when confronted with either a body-shaking or a whistle-shaking male or

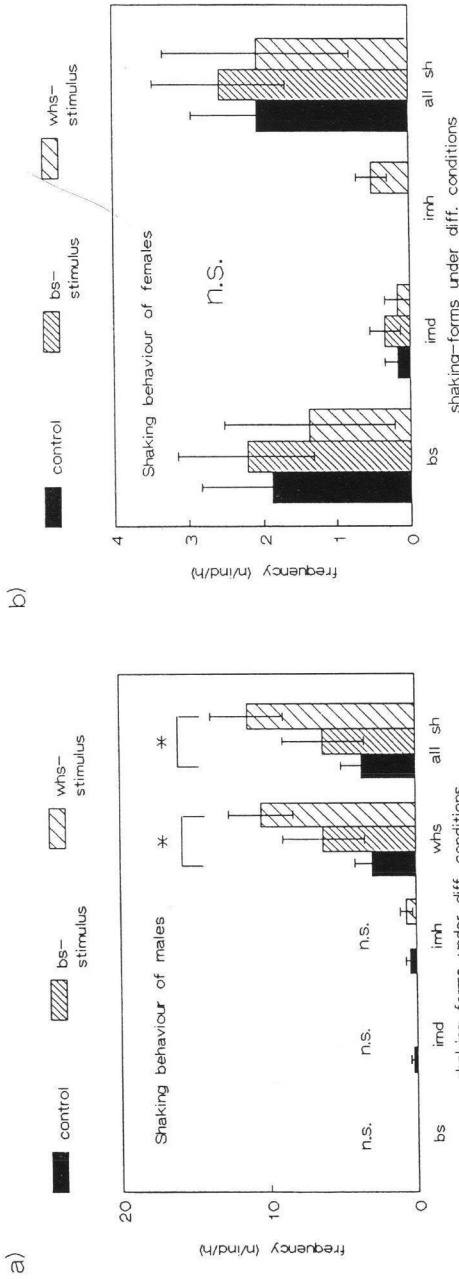


Fig. 6. Frequencies (mean and SD) per hour of different shaking forms (whs, imh, imd, bs) and total shakes of territorial shelduck pairs, which were confronted with either a whistle-shaking male (whs-stimulus), a body-shaking male (bs-stimulus) or an empty neighbouring cage (control); a) males, b) females. For further details see text; whs = Whistle-shake, imh = High intermediate form, imd = Deep intermediate form, bs = Body-shake.



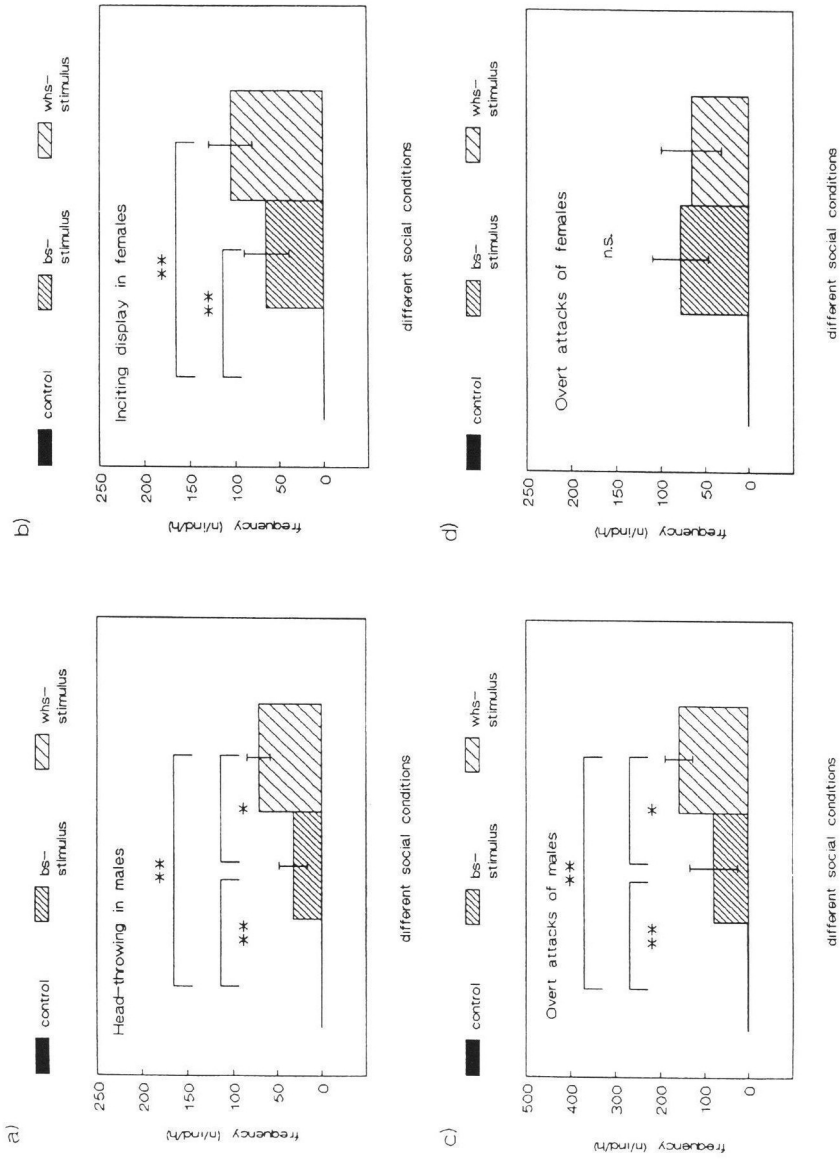


Fig. 7. Frequencies (mean and SD) per hour of different social displays and overt attacks of territorial shelducks pairs, which were confronted with either a whistle-shaking male (whs-stimulus), a body-shaking male (bs-stimulus) or an empty neighbouring cage (control); a) Head-throwing of males, b) Inciting display of females, c) Overt attacks by males, d) Overt attacks by females. For further details see text.

an empty neighbouring cage (Fig. 6b; MANOVA for the total frequency of shakes:  $F = 0.12$ ,  $df = 2$ ,  $p = 0.91$ ).

Apart from influencing the shaking behaviour of the test-males the presence of the stimulus birds also induces other behavioural effects in the test-males and their females (Fig. 7). In Head-throwing, for instance, another epigamic display of male shelducks, which is characterized by a pumping movement of head and neck accompanied by a conspicuous call, a significant difference in the frequency of occurrence was found between the 3 different social conditions tested (Fig. 7a, MANOVA:  $F = 13.60$ ,  $df = 2$ ,  $p = 0.003$ ). The frequency of Head-throwing is relatively high during the confrontation with the whistle-shaking male, intermediate in the body-shake condition and zero when confronted with an empty neighbouring cage. The differences between the three conditions were statistically significant (Paired  $t$ -tests: whistle-shake condition vs body-shake condition:  $p = 0.025$ ; whistle-shake condition vs control test:  $p = 0.006$ ). Similar effects were found for aggression in males (MANOVA:  $F = 10.58$ ,  $df = 2$ ,  $p = 0.006$ ) and the female Inciting display (epigamic display, in which the neck is extended horizontally and head and neck are moved in such a way that they are alternately directed to an intruder and the partner) (MANOVA:  $F = 6.86$ ,  $df = 2$ ,  $p = 0.01$ ), except that the increase of the latter in the body-shake condition was not significant (Fig. 7b, c). In contrast to the males the test-females respond aggressively to both stimulus-males to the same extent (Fig. 7d).

### *Conclusion*

The Whistle-shake is a stronger releaser for aggression and social displays in male shelducks than the Body-shake. It is also more effective in eliciting the Inciting display in the females. Furthermore, the shaking behaviour of test-males and test-females indicates that the Whistle-shake is more sensitive to social stimuli than the Body-shake. The Body-shake releases more social behaviour than the empty cage. This, however, might be due to the mere presence of another bird than to the Body-shake itself.

## General discussion

### *The evolutionary origin of the Whistle-shake display*

The form analysis revealed that the Whistle-shake display and the comfort movement of Body-shake of male shelducks are very similar: Both movements share the same motor elements, do not differ in duration, and contain almost the same number of shaking movements. This suggests that the Whistle-shake display in the shelduck has been derived from the Body-shake in the course of evolution. The relation between both motor patterns is supported by the fact that the display gradually emerges from the Body-shake in the course of ontogeny (Düttmann *et al.*, in prep.) and in the course of the year (Ratermann *et al.*, 1990; Ratermann, 1991).

Both shaking patterns differ in that the Whistle-shake, but not the Body-shake, contains elements of another display, namely Bill-tipping with trill. It has been suggested in the literature that Bill-tipping is associated with alertness and escape, and that the elements of which the trill is composed are associated with both alertness and escape (setju component) and aggression (aggressive trill component) (see conclusion section form analysis). This would fit the classical idea that displays might develop in the course of evolution from intention movements to attack and to flee, and from displacement activities such as comfort movements that occur during social interactions (Lorenz, 1941; Tinbergen, 1952). However, in the past form elements of displays have been too easily related to aggression and fear and the context analyses of Bill-tipping and the call elements of the trill need further study.

### *Proximate causal organisation of the Whistle-shake display and the Body-shake*

#### a) Comfort stimuli

The artificial rain experiments indicate that the Whistle-shake shares the same causal factor as the Body-shake. Therefore this display is not emancipated from the original causal factor controlling its presumed phylogenetical precursor form. This is supported by the finding that even isolated adult males, in the absence of social stimuli, respond exclusively with Whistle-shakes when sprayed with water in spring (Sebbel *et al.*, *subm.*).

## b) Social stimuli

b-1. Whistle-shake. Although the Whistle-shake can be elicited without any social stimuli, the latter do influence its occurrence: First, the finding that a whistle-shaking bird releases more Whistle-shakes in the test-males than a body-shaking male suggests that the Whistle-shake is also under the control of social stimuli. Second, during the confrontation with territorial pairs the completeness of the Whistle-shake in the testosterone-implanted stimulus-male decreased when the frequency of attacks directed to him increased. Third, differences in shaking behaviour between isolated males and males housed in groups, both treated with testosteronepropionate in summer, revealed different results. Whereas the isolated birds due to the hormonal treatment just change from Body-shake to the Whistle-shake, socially housed birds additionally increase the frequency of (Whistle-)shakes (Düttmann *et al.*, in prep.).

b-2. Body-shake. At least in females the Body-shake is not sensitive to social stimuli. Females responded in all three conditions with the same amount of Body-shakes. However, the situation in the male sex might be different. In the artificial rain experiments in spring the total frequency of shaking in subdominant birds was lower than in dominant birds. Consequently those subdominants did not compensate the decrease in Whistle-shake with the performance of Body-shakes. This suggests that the Body-shake can also be inhibited by social factors and this is currently under study.

## c) Aggression and fear

Dominant males produce Whistle-shakes in association with aggression whereas subdominant birds show the same display in association with escape. Furthermore, during interactions between partners of well-established pairs we never observed overt aggression or escape behaviour of the males but the same males frequently performed Whistle-shakes during interactions with their partner. Moreover, we found that the Whistle-shake can occur in a situation (social isolation) in which social stimuli and therefore probably the activation of aggression and fear are lacking (see above). Therefore we are of the opinion that the causation of the Whistle-shake display cannot be satisfactorily explained by assuming that it is under the

control of the simultaneously activated systems for aggression and fear. A similar conclusion was reached by Groothuis & Ros (in press) for gull display. Therefore, if one assumes that the Bill-tipping with trill component of the Whistle-shake display is under the control of aggression and fear (see above) then the causation of the Whistle-shake has emancipated from these causal factors.

### *Functional aspects of the Whistle-shake display*

The Whistle-shake can be released by rain and thereby serves a comfort function. At the same time it serves a social function as well. The latter was demonstrated by differences in the shaking responses of territorial males, which were confronted with either a whistle-shaking or a body-shaking male. As a consequence every Whistle-shake released by comfort stimuli would also signal the social status of the bird. Whether the Body-shake possesses signal value as well has not been clarified conclusively. The behavioural changes of territorial pairs, observed during confrontation with a body-shaking male, might be caused by the presence of a bird and not by the Body-shakes. This is supported by findings that in many territorial bird species even stuffed models or dummies release display behaviour and overt aggression in territorial holders (Tinbergen, 1956; Piersma & Veen, 1988; Groothuis, 1989).

In conclusion the Whistle-shake display of the shelduck presents a case in which the display is not emancipated from one of its assumed original causal factors, rain influencing the condition of the plumage. Consequently the display serves two different functions, a social and a non-social one.

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