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A NEW LOOK AT THE FEATURES OF MALLARD COURTSHIP DISPLAYS

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Abstract. The courtship displays of ducks are prime examples of fixed action patterns. Early attempts to link the apparent stereotypy to an exceptionally low variability in particular features, such as duration, failed, and cast doubts on the concept of stereotyped behaviour. Our single frame analysis of the courtship displays of the mallard (*Anas plathyrhynchos* L.) confirms the variability of duration, but shows that other features combine to sharply delineate tracks in a conceptional feature space. The features 'height of bill-tip above water level' and 'height of tail-tip above water level' are sufficient to define the most common displays of the drake (head-flick, head-shake, grunt-whistle, down–up, head-up–tail-up, bill-dip, nod-swimming) as space curves in a two-dimensional feature space. This result supports the original claim that stereotypy is a valid feature of certain types of complex behaviour.

The courtship displays of ducks, especially of the mallard (*Anas plathyrhynchos* L.), are prime examples of complex but stereotyped behaviour (Heinroth 1911; Lorenz 1941, 1971; von de Wall 1963). They have become the prototype for Lorenz' concept of the 'fixed action pattern', and were studied in some detail by single frame cinematography (e.g. Lorenz 1958; Dane et al. 1959; Weidmann & Darley 1971; Simmons & Weidmann 1973). In a recent paper on the conceptual issues of describing behaviour patterns, Schleidt & Crawley (1980) suggested that the different displays of the mallard drake can be sorted out, and distinguished from each other, by measurements of only two features, namely the height of the eye above water versus the height of the tip of the tail above water. Each particular display is represented in a two-dimensional feature space as a unique location. With this idea in mind, we have analysed several sequences in Lorenz' mallard courtship film (C 626/1952).

In this study we attempt to carry on the tradition of fine-grain description of behaviour patterns, pioneered by Heinroth (1911) and Lorenz (1941), by complementing the keen eye of the skilled observer with sensitive methods of quantitative analysis. The earliest efforts to document the stereotypy of displays with statistical means did not yield the expected results. Whatever features were chosen for analysis, their variability was always greater than intuition had predicted (e.g. Dane et al. 1959). Some investigators became disenchanted and followed Barlow's (1968) suggestion to replace the concept of 'fixed action pattern' with a weaker 'modal action pattern', not realizing that the subjective impression of stereotypy may be the result of a combined effect of several features of moderate variability (Schleidt 1974, 1976). More recent studies support the hypothesis that a relatively few features of low variability contribute substantially to the apparent stereotypy of a display (Schleidt & Crawley 1980; Schleidt 1982). Our study of the mallard courtship displays progressed through the same stages. First, we analysed the duration of displays. However, since in this case duration is not a feature that allows us to distinguish between different displays, we subsequently searched for more suitable alternatives, and for criteria to select those feature variables that contribute most to the subjective impression of stereotypy.

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Materials and Methods

The IWF film C626 on the courtship of the mallard (Lorenz 1952) was analysed frame by frame, using a Bell & Howell 16 mm Time and Motion Study Projector Model No. 173. Based on the English nomenclature of the displays used in the most recent publications of Lorenz (1958, 1971), we prepared an index of the film that lists the scenes and displays in their sequential order together with the respective frame numbers. This index, which is published elsewhere (Lorenz 1982), served as a reference for frame numbers ('fn') throughout this study.

Several display types that are represented in the film by several complete cases (complete in the sense that a clearly marked beginning and ending frame was detectable) were timed for their total duration, and analysed statistically

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(8 grunt-whistles, 16 tail-shakes, 20 bill-dips, 9 head-flicks, 33 head-shakes, and 9 down–ups), while those displays that are rare in the film were excluded (4 preens, 2 nod-swimming, 2 pumping, 1 head-up–tail-up, 1 wing-up). We must point out at this occasion that some confusion in nomenclature exists in the literature. It is in part because of the different translations of the originally German terms, and in part because of the refinements in the analysis. Our 'head-flick' and 'head-shake' were originally lumped as one display 'Einleitendes Schütteln'. Lorenz (1958) distinguished two types, bill-shake (a lateral or vertical movement of the head without involvement of the rump) and head-flick (a lateral movement of the head with a raising of the rump). Because the duck cannot shake its bill without shaking its head, we changed the term bill-shake to head-shake. For additional information on this matter see Lorenz (1982).

We chose from these displays those that appear in a predominantly lateral view (5 head-flicks, 5 head-shakes, 3 down–ups, and one each of grunt-whistle, bill-dip, preen, nod-swimming and head-up–tail-up). These were analysed in the following way: starting at least five frames before the display's onset and ending after at least five frames of resting or neutral behaviour, each frame was projected on a sheet of paper (280 × 350 mm), a line was drawn that approximates the intersection between the bird's median plane and the water surface (the 'body line'), and the location of four points was marked: tip of bill, centre of eye, centre of neck ring, tip of tail (Fig. 1). In the next step, a vertical line was drawn from each point down to the body line, and the distance of each point from the body line ('height') was measured with a caliper to the nearest 0.1 mm. The frame number and the heights of the four points were entered in a data file on the computer (Univac 1108, Computer Science Center, University of Maryland). Each display's data file was normalized to the same mean tail and bill height in resting position, and displayed graphically either on the line printer, or, by use of the Plot 10 package, on a Tektronix No. 4012 CRT terminal and No. 4662 x, y plotter.

Results

The mean duration of the six courtship displays investigated falls within the range of 0.69 and 2.25 s, and the standard deviation is considerable (Fig. 2). The coefficient of variation is low only in the grunt-whistle (0.093), while in the other displays it ranges from 0.140 (down–up) to 0.552 (tail-shake). Therefore, duration is apparently not a feature that is powerful for discrimination among different displays.

The variability of duration of the head-shake may be due to the existence of both a horizontal and vertical shake. However, Student's t-test indicated that the mean duration both of the horizontal shake and the vertical shake did not differ significantly ($P > 0.05$). The histogram therefore presents both types combined. Similarly, one may question whether head-flicks should be included with the head-shakes. The mean durations were significantly different,

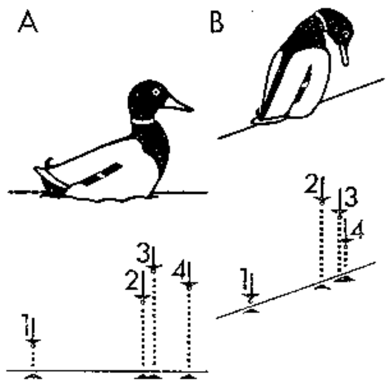

Fig. 1. Two examples of the way in which the height above water level was measured in this study. The upper half shows tracings of a momentary state during a head-flick (A, fn 1483) and a grunt-whistle (B, fn 2967), with the estimated 'body line' drawn in. The lower half shows the location of the points (1 = tip of tail, 2 = ring, 3 = eye, 4 = tip of bill), and the distances measured.

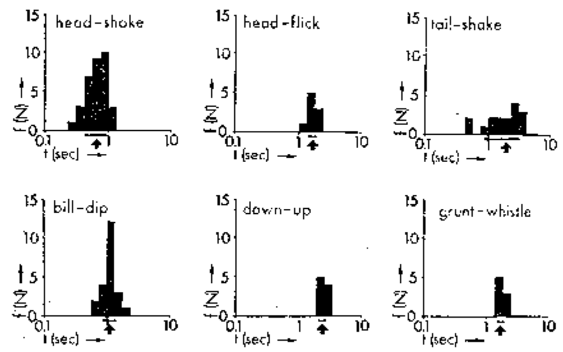

Fig. 2. Frequency distributions of the duration of displays. The arrow under the abscissa indicates the mean, the horizontal line the range of ± one standard deviation of each distribution.

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however (Student's t-test, $P < 0.0001$), justifying two separate classes.

When the height features were corrected to a standard duck size (to compensate for the differences in distance from which the pictures were taken) and plotted versus time, a strong correlation was noted among the features height of eye, height of bill tip and height of ring (Fig. 3). Since the eye was not discernible in about half of the pictures (dark eye on dark feather back-

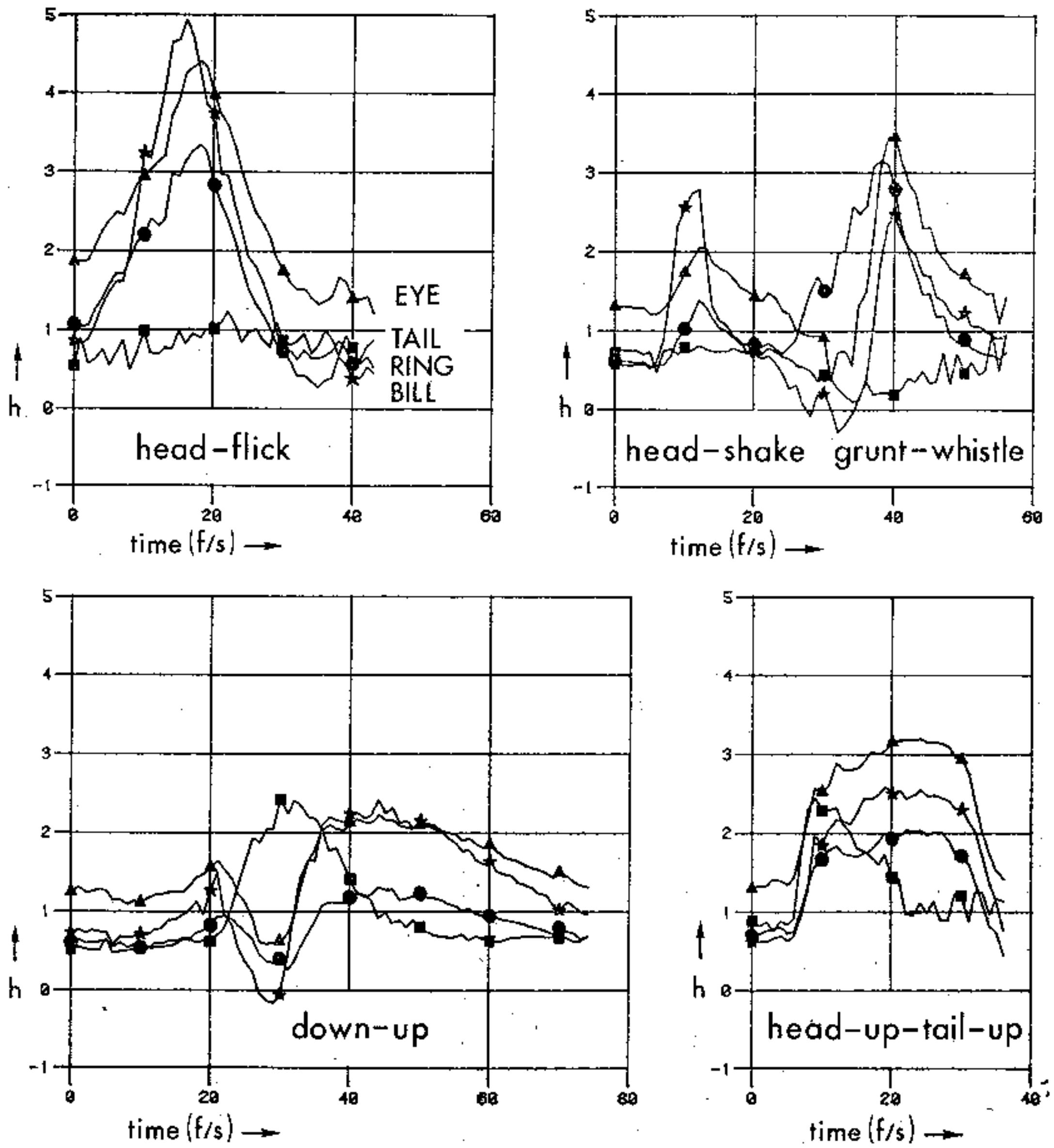

Fig. 3. Selected samples of displays in graphic representation of the four feature variables 'height of bill tip above water' (star), 'height of eye' (triangle), 'height of ring' (circle), and 'height of tail tip' (square) versus time (frame number, 20 f/s). Head-flick (fn 1460–1503), head-shake (fn 2930–2957), grunt-whistle (fn 2958–2986), down-up (fn 3692–3766), head-up-tail-up (fn 5157–5193).

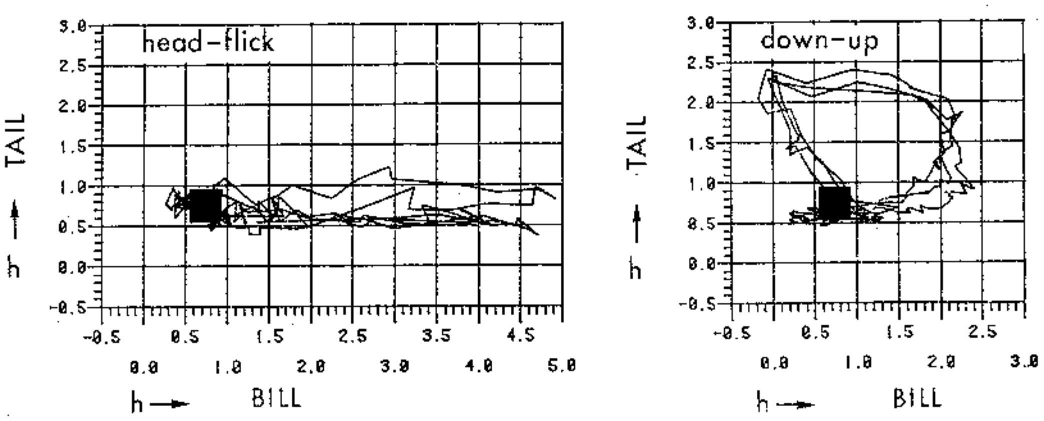

Fig. 4. Three selected samples of each down-up (fn 3692–3766; 4946–5008, two males in synchrony) and head-flick (fn 1287–1320, 1460–1503, 2013–2073) represented in the feature space 'height of bill tip' versus 'height of tail tip'. The black square marks the resting position from which the displays originate.

ground) and therefore must be considered an unreliable feature in the mallard, eye height was excluded from further analysis. Similarly, the bill tip was sometimes hidden by the neck, but since we had selected for this analysis only those sequences in which the duck started in a position perpendicular to the camera's view, no data points were lost. Since the bill tip height showed by far the most dramatic changes in most displays, and resulted in a better signal/noise ratio in our analysis than ring height, we used this feature to represent the movement of the anterior end of the drake.

Within the feature space 'height of tail tip' versus 'height of bill tip,' a given display type of (presumably) different drakes appears as strikingly similar space curves (Fig. 4), while different display types appear as strikingly different 'signatures' in distinct areas of the feature space (Fig. 5).

Discussion

Previous film analyses of duck courtship displays have been concerned principally with measurements of durations, frequency of displays over time, or direction in reference to females (Dane et al. 1959; Weidmann & Darley 1971; Simmons & Weidmann 1973). Our duration measurements (Fig. 2) support previous conclusions, namely that their validity is limited when used as the sole measurement without a coordinated analysis of several features, that represent the form of the display. The wide range of overlap among the different displays makes duration a feature of limited value in the discrimination of displays and suggests instead that a time span of about 1 s is especially suitable for attracting the attention and conveying a certain amount of information. We interpret the similarity in the durations of the different displays as an indication that it is caused by a common selection pressure.

Distinctive patterns emerge, however, when any of the height features are plotted versus time (Fig. 3). The curve of one feature (e.g. ring height in head-flick and grunt-whistle, or tail height in head-up–tail-up and down–up) may show a high degree of similarity in different displays, however, and only when two or more features are combined do we find unique signatures (Fig. 5). Since the space curves of each display type run through unique areas of the feature space (Fig. 6), they are so highly distinct that the numerical calculation of the probability of a significant difference would be statistical overkill. Such numerical expressions of differences (or similarities) could be most valuable, however, in comparisons of small inter-individual and intra-individual differences in one display of a species, or in comparisons of the homologous display in different species; in the case of our animals, the identity of the drakes was not known and consequently, a distinction between inter- versus intra-individual variability cannot be made. Since the film C626 contains behaviours of ducks in Buldern (Westphalia, Germany) and Slimbridge (England), and was filmed with a spring-wound movie camera (Bolex 16; Lorenz, personal communication), some of the variability within the same display type may be due to either intra-individual, inter-individual, or geographic variation, or due to the limited precision of the recording. In this context we also must mention that the limited window of the film made it, in most instances, impossible to judge where an addressed female was located, and therefore orientation and lateral components of the drake's head movement (Weidmann & Darley 1971; Simmons & Weidmann 1973) were not analysed.

Darwin (1872) in his 'principle of antithesis' proposed that 'when a directly opposite state of mind is induced, there is a strong and involuntary

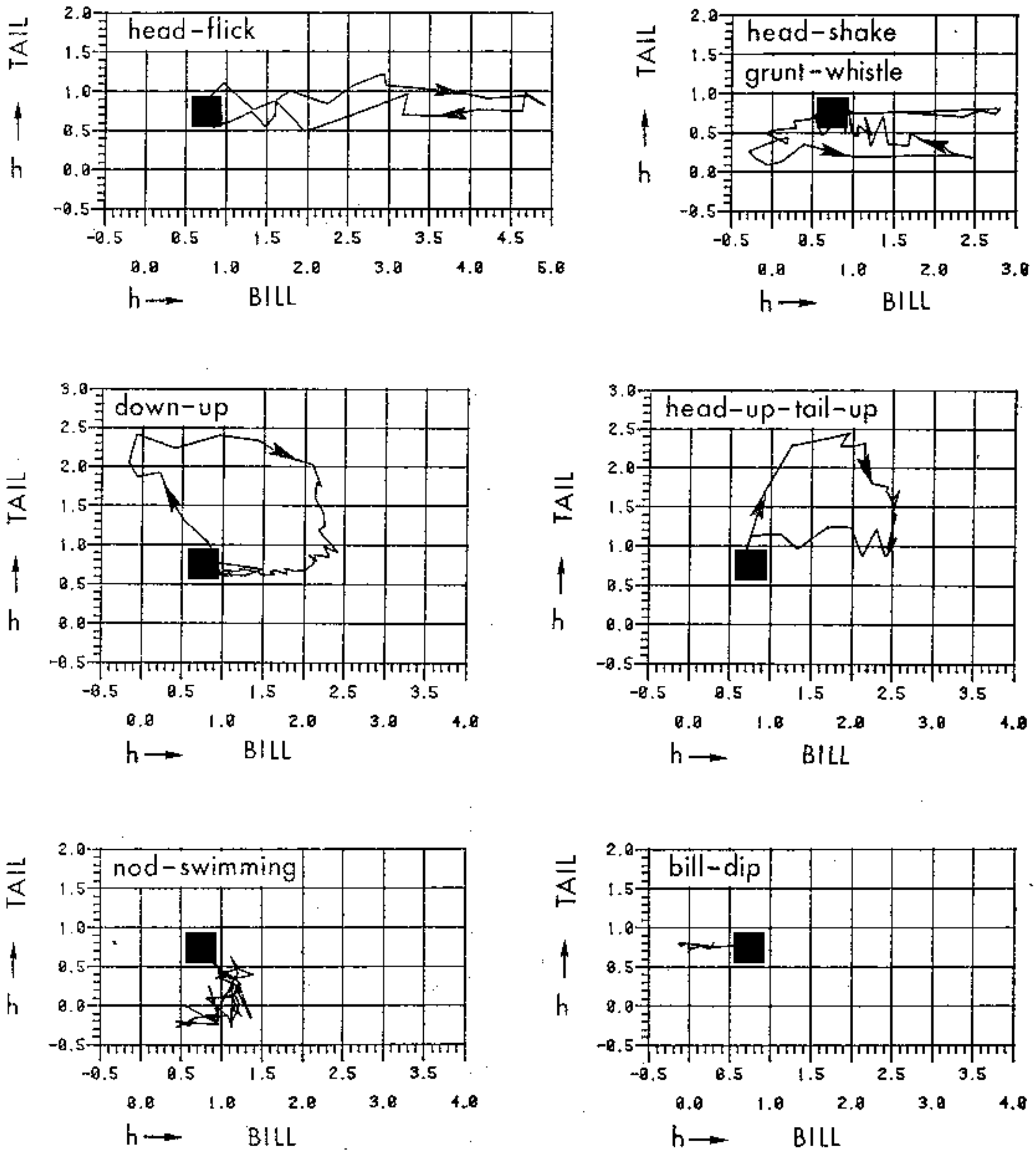

Fig. 5. The same displays as shown in Fig. 3 and one sample each of nod-swimming (fn 5205–5260) and bill-dip (5453–5474) are represented here in the feature space 'height of bill tip' versus 'height of tail tip'.

tendency to performance of movements of directly opposite nature, though these are of no use; and such movements are in some cases highly expressive' (page 28). More recently, this idea was reinterpreted, without the reference to mind and voluntary intent of the animal, to indicate that expression movements of opposite motivation assume in their constituting features the opposite ends of a continuum. But, even if the exact nature of the underlying motivation is uncertain

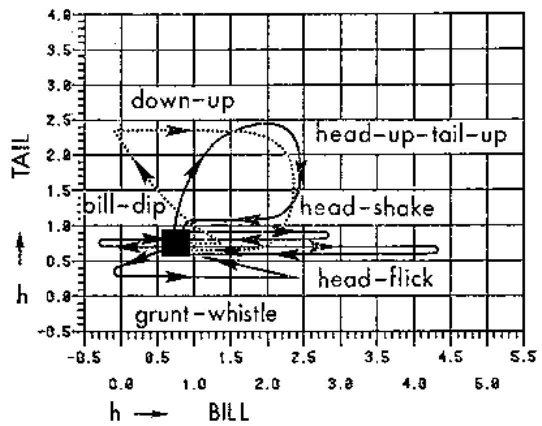

Fig. 6. Composite of the major courtship displays of the mallard in the feature space 'height of bill tip' versus 'height of tail tip'.

for any particular display, we can expect that displays of different motivation (or different meaning) will be different. Thus, we propose that the principle of antithesis can be transferred into the *n*-dimensional feature space within which the particular displays occupy particular regions, and take the Euclidian distance between such regions as a measure for the degree of difference between any two displays.

When we want to represent displays, or behaviour patterns in general, in a feature space with more than two dimensions, we find it difficult to conceptualize such spaces and to represent them graphically. We have, nevertheless, explored the potential of additional features for an even better separation of the mallard's courtship display. Time as the third dimension is an obvious choice, especially when we consider that behaviour is inherently 'change of structure over time' (Schleidt & Crawley 1980). As an example we show here a three-dimensional graph of the down-up data of Fig. 4, generated on Knott's (1979) MLAB system (Fig. 7). As a fourth dimension, the sideway movements of the bill would be an important feature, especially if the direction of the courted female were to be investigated.

The tail-shake is the only display that does not separate from the resting position or from the other displays in our simple 'bill tip height'

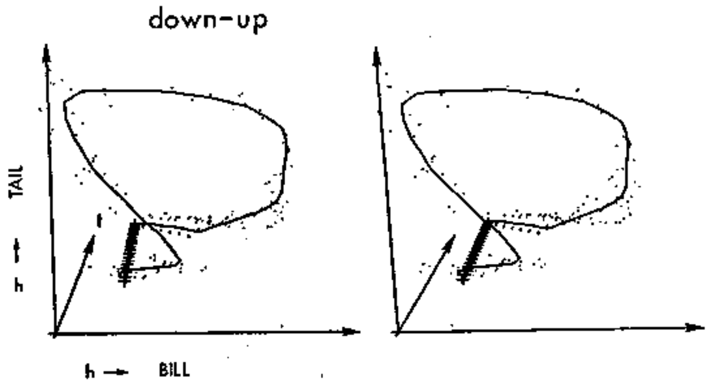

Fig. 7. Down-up in a three dimensional feature space 'height of bill tip' versus 'height of tail tip' versus time, displayed as stereo pair. The same data set as in Fig. 4 is shown as individual points, and as a smoothed mean curve. The backbone like structure in the left bottom corner is the estimated centre of the resting position, from which the down-up deviates. For those readers who are not familiar with viewing stereo-pairs: relax your eye muscles by looking at a distant object while you hold the figure at a distance of about 40 cm; now, lower your gaze at the figure as if you would look *through* the page, so that a double image of the figure appears, as your right eye catches the right part of the figure, and the left eye the left part. With some skill you can fuse the images to a stereoscopic view. If this method fails, use a stereo viewer with prismatic magnifying lenses.

versus 'tail tip height' feature space, but is best characterized by its own unique feature 'rhythmical lateral tail movement'. Similarly, head-shake, head-flick and grunt-whistle are enhanced by lateral bill movements with an orientation component. This tendency is further underscored by the 'turn-head-to-female' (following head-up–tail-up), the 'turn-back-of-head-to-female' (following nod-swimming), and by the measured head movement in 'mock-preening'. All these movements are rendered more conspicuous by striking morphological features: the white tail is framed by black, the dark green iridescent head is set off by the white ring and contrasts with the yellow bill, and the blue speculum is flashed during head-up–tail-up and mock-preen. The 'bill tip height' versus 'tail tip height' feature space thus provides a general frame of reference within which these additional features of physical structure and movement enhance the striking character of each display.

In conclusion we want to express our belief that the representation of display types as locations in an abstract feature space provides an analytical tool that can match the intuition and Gestalt perception of the most experienced observer, and that confirms the claims of Heinroth and Lorenz that the displays of mallard courtship are highly stereotyped. To call them 'fixed action patterns' is no exaggeration, when viewed in multi-dimensional feature space.

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