Media Konservasi Vol. II (3), Mei 1989 : 1 - 10

REVIEW OF THE ORIGIN AND EVOLUTION OF SOCIAL SIGNALS IN DUCKS; IN PARTICULAR THE FUNCTION OF COURTSHIP DISPLAYS

(Suatu Tinjauan tentang Asal-usul dan Evolusi Isyarat-isyarat Sosial pada Itik-itikan, khususnya dalam Perilaku Bercumbu)

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ABSTRAK

Perilaku bercumbu ialah pola perilaku sosial yang berkaitan dengan kawin. Dalam tulisan ini teori evolusi dan asal-usul perilaku dibahas dengan mengemukakan contoh yang terdapat pada suku Itik-itikan (Anatidae) terutama pada marga *Anas*. Dari hasil pengamatan para pakar etologi dapat diduga bahwa perilaku bercumbu berasal dari gerakan yang sudah mengalami evolusi melalui proses 'ritualisasi', sehingga mempunyai aspek komunikatif yang mengandung isyarat. Fungsi perilaku bercumbu dalam pembentukan pasangan dan memperkuat ikatan antar pasangan dan isolasi jenis diterangkan pula dalam makalah ini.

INTRODUCTION

Recently, there has been an increase in the use of behavioural characteristics, especially courtship behaviour, in evolutionary studies. This is because such behaviour is thought to be of fixed pattern and species specific.

In waterfowl, the study of the courtship behaviour was pioneered by Heinroth *(1911)*. His study has been elaborated by Lorenz *(1941)*. Following this, Johnsgard *(1962)* and McKinney *(1975)* also have contributed much in this field of study.

In the beginning, Heinroth and Lorenz used the evolution of courtship displays in waterfowl as indicators of taxonomic relationships. Then, Johnsgard investigated the distribution of homologous display repertoires of Anatidae and found out the relationships of all species. Since then, the study has been directed towards the search for factors which have been responsible for the evolution of specific differences, such as the difference in frequency, in the order of displays linked in sequences and in the degree of elaboration of plumage features reinforcing signal movements. As examples, Johnsgard (1960a) studied the courtship displays in North American black duck (*Anas rubripes*) and mallard (*Anas platyrhynchos*), McKinney *(1970)* observed four species of blue-winged ducks (*Anas cyanoptera, A. discors, A. clypeata* and *A. smithi)* and Prawiradilaga *(1985)* investigated the grey teal (*Anas gibberifrons*) and chestnut teal (*Anas castanea*). So far, not all of these specific factors have been brought up.

It is the aim of this review to examine and discuss aspects of evolution of courtship displays which have been presented; in particular the origin and evolution of social signals in ducks, especially those referred to specifically as courtship displays.

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SOCIAL BEHAVIOUR

Communicative aspect of behaviour

It is known that behaviour is characterized by acts; whereas a communication process occurs as the result of interaction between two or more individuals. In general, Mayr (1976) classified behaviour into three types: depending on the potential responses of its recipient : intraspecific, interspecific and non-communicative. Furthermore, intraspecific behaviour can be said as a communication between individuals in the same species, and interspecific behaviour affects members of another species. On the other hand, non-communicative behaviour does not contain signals which can be interpreted by others. Therefore, intraspecific and interspecific behaviour have communicative functions since they are composed of signals.

Understanding of displays

'Displays' can be categorized as intraspecific behaviour and elicited when an animal such as a bird is in conflict tendencies, for instance the tendency to attack, to flee from or behave sexually towards its mate. There are several opinions about the displays which can be classified in terms of the view point from which they were examined. Wallace (1979) emphasized displays from the communication angle, interpreting displays as behaviour designed clearly to attract attention and show something off. Deag (1980) also considered displays as combintions of signals which have a communicative function. In the same way, Johnsgard (1968) applied the term 'displays' to all means of communication (signals) which have been evolved by species to convey information between individual members. Huxley (1914), on the other hand, restricted it to visual displays as a term of communication. However, Huxley's theory has been rejected by other ethologists. So far, it has been realized that displays can be visible, audible, tactile or chemical releases as suggested by Smith (1977). In addition, visible and audible displays are well-known to be used by birds more than others.

With a background of experience in the observation of behaviour of birds, especially waterfowl, Johnsgard (1968) viewed displays from the point of view of the event that took place. According to Johnsgard's opinion, displays can be grouped as social-integration displays, agonistic displays (those associated with attack and escape) and primarily sexual displays. Furthmore, Johnsgard classified sexual displays in waterfowl into courtship or pair-forming displays, pair-bonding displays and the displays which are soon followed by copulation (Fig. 1).

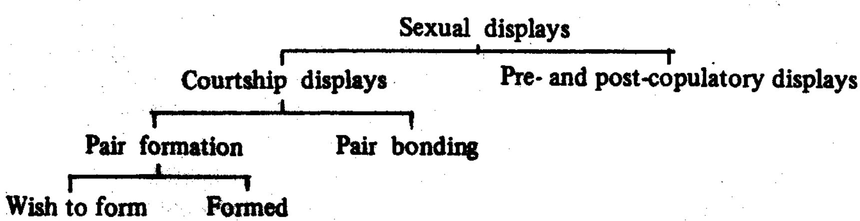

Figure 1. Classification of sexual displays.

Courtship displays

Manning (1979) considered courtship as a specific behaviour pattern that occurs at the beginning of mating. In addition, it can be explained broadly that courtship is a kind of animal communication which consists of a signal system, defined by Meyerrick (1962) for transferring information between actual or potential mates. These opinions are quite acceptable, but Broom (1981) explained the term courtship in a slightly different way, in which he stated that a behaviour that indicates willingness to pair is also considered as courtship which is then followed subsequently by mating. Courtship behaviour is sufficiently different from other behaviour to allow a potential mate to recognize it. The importance of mate recognition to form a bond or a liaison such as between drakes and ducks in social courtship was discussed by Bastock (1967).

THE ORIGIN OF THE COURTSHIP DISPLAYS

Classification of the origin of the courtship displays

Many confusing classification of the origin of the courtship displays have been suggested in the past. The theory of display origins was first discussed by Darwin in the last century (Darwin, 1890). Darwin considered three principles governing the origin of communication signals, in this case visual signals, and his ideas have had an important role in discussing the problems of the origin of displays. The three principles are : the principle of associated habits, the principle of antithesis and the principle of direct action reflecting the constitution of the nervous system. The principle of associated habits is meant by Darwin to refer to intention movements (Marler, 1959) as suggested by Heinroth and Daanje (Brown, 1975). Darwin's second principle of antithesis concerns the displays which are opposite in function and appearance (Brown, 1975); whereas the third principle of Darwin can probably be considered as responses of the autonomic nervous system.

The ethologists who presented the display origins in waterfowl such as Johnsgard (1960b; 1968); Lorenz (1941; 1971); McKinney (1975; 1978) and Tinbergen (1954) believed that intention movements and displacement activities are the main sources of the courtship displays. Moreover, Lorenz stated that the movements which are supposed to be derived from intention movements are often recognizably formalized or 'ritualized'. He also pointed out that most of the motor patterns of dabbling drakes can be envisaged as symbolic motor pattern or displacement activities.

Intention movements

Intention movements are recognized as instinctive patterns which appear also as the first source of courtship displays. These movements are the very beginning of an activity (Heinroth, 1911 and Daanje, 1951) and also called as the preparatory movements. This is because from these movements it can be seen what an animal is intending to do. Thus, the direction of the movements can be judged and also the resultant behaviour patterns which may be expected from them. These movements usually emerge with a full and sudden intensity in response to strong external stimulation but seem to be shown in an incomplete form.

In the courtship displays it appears that intention movements are usually elicited with a specific signal functions in what they strive to magnify as a visual effect. They exhibit exaggerated performance, like the nodding movements of the guiding mallard duck, an example which was suggested by Lorenz (1971).

Displacement activities

Displacement activities are a part of comfort movements which can be shown to be 'irrelevant' and occur as an excess of a drive and then have become adapted signals in courtship displays. Many examples of displacement activities can be found in the courtship displays of waterfowl; but most of them have originated from the behaviour of preening and body shaking.

Autonomic responses

Morris studied the display origins from the causal problems of the nature of the response (Morris, 1956 quoted in Morris, 1970) which also has been touched on by Hinde (1970). Morris separated the responses into somatic and autonomic responses. Somatic responses are basically concerned with adjustment of the bird to the external environment. Autonomic responses, on the other hand, are concerned with adjustment of the internal environment of the bird to the requirements of the somatic responses that it has to perform. Furthermore, Morris categorized autonomic responses into : alimentary, circulatory, respiratory and thermoregulatory effects.

It seems that thermoregulatory effects are related to the subject of this discussion. Feathers are parts of a bird body which have a primary function as a thermoregulator. The feather postures can be changed depending on the external temperature. This phenomenon, then has been modified by the process of 'ritualization' to have secondary functions, that is social signals. Morris (1970) suggested thermoregulation as the source of display in Aves and pointed out that the use of feather postures as such signals are unavoidable. It appears that the feather postures can be used as indicators of the mood of the birds that perform it at that time.

The courtship-display origins in waterfowl

The terminology which describes every movement in the courtship displays was introduced and named by Konrad Lorenz (1941). It seems that there are still no fixed opinions on the courtship-display origins, since most opinions are still vague. In the following, the possible origins of several displays elements mostly in *Anas* species, that have been discovered, are presented.

Burping is known as a drake call which can be described as 'tliu' sound. According to Lorenz (1971) the burping seems probably to be descended from the ordinary alert head raising that coexists with summoning and warning in all Anatidae.

Bridling is a lifting up of the forepart of the drake body and pulling the head backward at the same time. Daanje (1951) thought that bridling was derived from an intention movement indicating rapid swimming which as a matter of fact usually follows it. However, Lorenz (1941) considered that bridling has probably originated from the introductory intention of nod-swimming which is another term of the display element.

Chin-lifting is a movement when a drake or a duck raises its chin as well as the head. It was possibly derived from a low intensity of the down-up movement which also indicates an indirect origin from a display drinking movement (Lorenz, 1971).

Down-up is a movement when a drake rapidly dips his bill into the water followed by raising the head up while the breast is in the water, simultaneous with erected wings and tail. As Lorenz (1971) stated, the down-up movement seems to exhibit a ritualization of display drinking.

Grunt-whistle is a drake movement almost like a body shaking movement, but in this movement the drake throws up a shower of water droplets in a wide arc. It is suggested by Lorenz (1971) to have been evolved through gestural exaggeration of incipient body shaking originally occurring as a displacement activity.

Head-up-tail-up is a very complex movement in which the drake performs jerking of the head backward and upward accompanied by a whistle, simultaneous with bending the rump upwards showing the peculiar plumage of the rump. Daanje (1951) believed that this movement has been derived from the bow.

Inciting is a duck movement showing her rejection to the other drakes. Lorenz (1941) suggested that inciting movement was derived from dual origin, that is the intention movement of pecking at another bird and followed by chin lifting.

Turn the head-towards-the female is a movement following head-up-tail-up movement in which the drake turns his head towards the courted duck. Johnsgard (1962) thought that this movement was derived from an apparently submissive gesture.

There are still some display elements whose origins are obscure. It appears that an attempt to study these display origins in more details is needed.

THE EVOLUTION OF THE COURTSHIP DISPLAYS

Although there are quite a few suggestions on the evolution of behaviour, particularly courthsip displays, much of this area remains uncertain. This is because, it is impossible to obtain fossil evidence of ancestral behaviour (Wallace, 1979).

It seems that an indirect approach is needed to solve the evolutionary problems of behaviour. Several ethologists such as Tinbergen (1951), Hinde and Tinbergen (1958), Johnsgard (1962), Kear (1970) and Mayr (1976) suggested the comparative study of the behaviour of related living species as the solution to the problem. This comparative study can be done by comparing the behaviour traits of species whose phylogenetic relationships have been established. Then, it is possible to make a hypothesis about the course of its evolution.

As Darwin (1890) suggested, if it can be assumed that the behaviour patterns which concern courtship displays are innate or fixed patterns, then it is reasonable to assume that the ancestors of animals in this case waterfowl which are examined, perhaps behaved in a similar way.

It is believed that there are changes of behaviour patterns in the process of evolution such as courtship displays. The process of evolution of courtship displays which is called "ritualization" was investigated by Huxley (1914).

Ritualization

Ritualization may be defined as the evolutionary process by which behaviour patterns have been to serve a communication function. This process can make the movements become simple, unique and conspicuous or in some other way more suitable for a signal function. According to Lorenz's investigation, waterfowl provides several classic examples of the derivation of signals from non-signal functions through the evolutionary process of ritualization.

The evolution of courtship displays in waterfowl

Presumably, there are two ways in which ethologists viewed the evolution of courtship displays in waterfowl, that is from the point of view related to a phylogenetic arrangement of species, genus or family and from the signal content in the displays. However, both of these ways were based on the comparative studies of the living species in order to reconstruct ancestral courtship-display repertoires.

In the evolutionary trend related to phylogenetic, the homology of courtship displays was found, in which several species share a certain number of display elements (for a review see Johnsgard, 1962). These similarities in the display patterns indicate that there is a very closely related evolutionary group which can be considered in a broad genetic concept. It appears that there is an undirectional trend from generalized to specific conditions. In addition, Johnsgard discussed the presence of a remarkable species differentiation of displays and plumage characters.

McKinney (1975) tried to explain the evolutionary problems of the courtship displays from the point of view of the signalling devices. From this study, McKinney proved that signals have evolved to serve the needs of drakes and ducks, or individuals in general, to communicate many sorts of important information in resolving their individual relationships. These signals evolved through individual selection to increase the advantages of their social relationships from performance of the behaviour patterns. Furthermore, McKinney stated that signals are needed for many purposes, for example: pairing, pair-bonding maintenance or intention to copulate. It seems that the characteristics of signal which are required vary with the situation. In addition, signalling needs are likely to be somewhat different in each species depending on the relation of differences in the social system (McKinney, 1978).

THE FUNCTIONS OF THE COURTSHIP DISPLAYS

The functions of the courtship displays was first studied by Huxley in 1914, who interpreted the courtship of the great-crested grebe (*Podiceps cristatus*). From this study, however, only one aspect was discussed that is the strengthening of pair bonding. Since then, several views of the functions of courtship displays other than pair bonding have been explored by ethologists.

The functions of courtship displays in waterfowl may be to release, to initiate, to arouse and to synchronize physiological willingness to mate between the sexes (Tinbergen, 1954; McKinney, 1961; Morris, 1970; Broom, 1981); and also for orientation and supression of non-sexual responses (Tinbergen, 1954; Hinde and Tinbergen, 1958). The occurrence and the form of courtship displays have functions in pair formation, pair maintenance or pair bonding and species isolation (Tinbergen, 1952; 1954; Mayr, 1976; Wallace, 1979).

Pair formation

Pair formation can be considered as a selection process to find out an appropriate mating partner. This selection process is based on the performance of displays. It seems that in waterfowl, ducks of most species have to select their mates actively through elaborate displays (McKinney, 1975). In the courting parties when several drakes are involved, it appears that each drake will try to perform the displays in the most elaborate and persistent way. If pair formation takes place in these courting parties, a drake will direct his display to the courted duck which also responds by performing a display which shows her preference (McKinney, 1975). Thus, there is a mutual attraction in pair formation.

Pair bonding

Pair bonding can be determined as a link which exists between sexes in this case a drake and a duck as a mating partner. It seems that in waterfowl there are also special signals which serve this function other than courtship displays. If a pair is already formed, the birds usually try to keep very close to each other or behave in the same way together. When they are apart, they usually call to contact each other.

Possibly, water plays a role in the signalling methods of *Anas* sp. in maintaining pair bonding. It is because, water is vital for their life. Most of their activities such as preening, bathing, drinking, feeding, shaking or oiling their plumage are carried out in the water. These activities often occur as interactions between a pair as well. However, some activities have now become incorporated as signals for pair maintenance, e.g. preening behind the wing.

Species isolation

There are several suggestions of the functions of the courtship displays concerning prevention of hybridization within species. Since the similarities of the courtship displays of closely related species were found, this isolation function was doubtfully related to the characteristics of plumage. This hypothesis was supported by a phenomenon that in closely related species of *Anas* which share the same courtship-display elements and the breeding range, the drakes usually have different plumage colour, but ducks can be similar (Johnsgard, 1962; 1968). The difference in drake visual characters is important. Therefore, species isolation between these species may operate through recognition of colour patterns of plumage which is inherited and plays a role in the prevention of hybridization between the species themselves. In addition, vocalization that accompanies courtship displays, namely courtship calls, may also serve a function in species isolation (Bastock, 1967). However, this possibility has not been investigated in any other waterfowl to any great extent.

CONCLUSIONS

Courtship displays can be said as a kind of social behaviour which has evolved by the process of ritualization. They are thought to be derived from intention movements, displacement activities and autonomic responses (i.e. thermoregulatory effects).

Courtship displays serve several functions. However, this review has emphasized on pair formation and maintaining pair-bonding as the most important functions of courtship displays.

ACKNOWLEDGEMENTS

I would like to thank Dr. P.J. Fullagar and A/Prof. Manika Wodzicka-Tomaszewska for their valuable criticism of an earlier draft.

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