

AN INTRODUCTION TO THE BEHAVIOUR OF THE
GOLDENEYES : BUCEPHALA ISLANDICA AND
B.CLANGULA (CLASS AVES, FAMILY ANATIDAE)

by

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ABSTRACT

In the summers of 1955 and 1956 a field study was undertaken on the behaviour (locomotory, comfort, agonistic, courting, coition and brood) of the Barrow's Goldeneye (Bucephala islandica) in the Cariboo District of British Columbia. This is the first stage of a five year study of the behaviour of Sea Ducks of the Tribe Mergini.

An attempt has been made to summarise the behaviour of B.islandica and also of the closely-related species B.clangula, that is described in the literature. Generic similarities, and specific differences, in the courtship displays of these two species have been described. An attempt has been made to discover the likely sources of these displays from among the locomotory, comfort or agonistic behaviour patterns.

Illustrations of the postures and movements described in the text have been made from films by the author, and two other sources.

An attempt has been made to link items of behaviour to the ecological, biological and systematic aspects of duck biology. Thus both the behaviour itself comes to have a biological setting and raison d'etre, and behavioural aspects of breeding and population biology, and population management and manipulation, may be better understood.

Among Comfort Movements Drinking appears to have given rise to a courtship display found chiefly in the pre-coition sequence. Wing- and Leg-Stretching is also a comfort movement found in display (only in the pre-coition behaviour). Preening generally (especially Splash-Bathing) occurs frequently under conditions of stress e.g. after a territorial encounter and after coition. The Upwards-Stretch, Wing-Flap, Tail Wag complex of

movements is also frequent under conditions of stress, and occurs especially as a "signing-off" (? appeasement) display at the end of an encounter.

Agonistic behaviour is interesting, in that the diving ducks tend (goldeneye particularly) to use underwater diving as their major aggressive tactic. Threat may derive from intention diving. The "alarmed" position is hard to derive from other postures. Inter-specific aggression is frequent and indicates that the Aythya are more of an irritant to goldeneye than are the Anatini. Case-histories of inter-specific aggression helped to throw light on the nature of territory in goldeneye, and on fatigue and refractory periods in the attack motivation.

Goldeneye have a wide variety of courtship displays. The Head-Up and Head-Raised positions (with the Neck-Withdrawing movement) are rather alike in the two species. The Head-Throw of B. clangula is much more extreme in form than the equivalent movement in B. islandica. In B. islandica the Pseudo-Kick and Kick are much less differentiated, than the Head-Throw and Head-Throw-Kick of B. clangula. An analysis is made of the two forms of pumping motions, to show their basic similarity, but species differentiation.

The Coition Sequence is very similar in the two species. There is a marked Post-Coition display.

The downies leave the nest by scrambling up the inside of the nest cavity, and tumbling from the nest-hole all together. The female has a special call which is used to force all the downies off at one time. On the lake the same call gathers the young together around the female. The

importance of this means of ensuring that the young fledge together is discussed. The actions of the female at fledging are described.

Females are poor guardians of broods, but they show considerable hostility towards each other during the brood period.

Downies greet each other and the female by a movement which at first resembles the Rotary Pumping of the adult drake, and the female. Rotary Pumping thus is a "greeting" movement.

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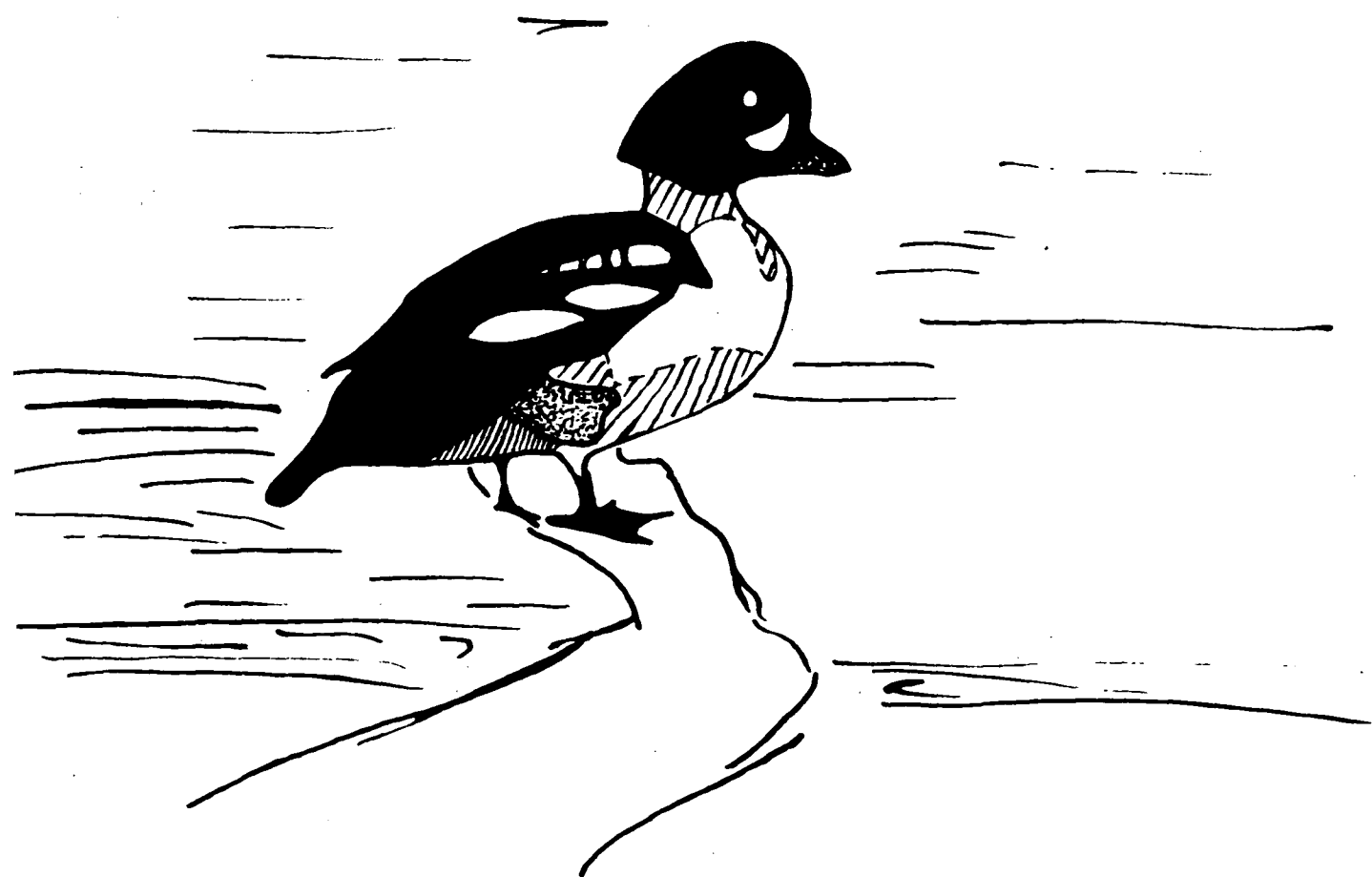
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INTRODUCTION

INTRODUCTION

Ethological Studies and Phylogenetic Relationships

Delacour and Mayr (1945) pointed out, in their much needed revision of the classification of the Family Anatidae, that the use of behavioural characteristics as taxonomic indicators is a respectable activity, because many innate behaviour patterns are as ancient, or more ancient, than the morphological characters which they emphasize. Four years earlier, in a paper that Delacour and Mayr had not seen when they wrote their own, Lorenz (1941) had produced the most elaborate analysis, so far, of the courtship displays of ducks. He described 14 or more elements in the behaviour of 15 species of the surface-feeding ducks (Tribe Anatini). Thereby he established a precedent for the serious ethological comparison of different groups.

Lorenz' paper (I have referred only to the recent translation in The Avicultural Magazine, 1951-52) was almost entirely descriptive, though in it he made a number of statements as to the possible origin of certain displays. These may well have to be revised as further work on motivation of activity, and the ontogeny of movements and postures, is done. Primarily Lorenz was interested to use the presence or absence of the various displays, alone or in combination with each other, as a means of determining phylogenetic relationships, and he illustrated this by drawing up a symbolic "shaving brush" of the species with cross-connections from one "hair" (or species) to another to demonstrate common possession of a certain behavioural element. The number of discrete movements a species

shares with another species is an indication of how closely related they are.

It was on these lines that the present 5-year survey of the Sea Ducks, the Tribe Mergini, was initiated, of which this report on the goldeneyes (Bucephala islandica and B. clangula) is the first result. It was considered that if innate behaviour patterns were "persona" grata with the systematists, and could be treated equally with morphological characters, the time was ripe to try and review the Mergini, which are in a number of ways a very unusual group. Recently ethologists have ceased the use of the word "innate" for patterns which have not been shown (by isolation experiments with young birds from before hatching) to be truly determined by genetic inheritance alone, with no learning involved. There are, however, display patterns which we can be sure will prove eventually not to have been learned, and so, although the word "innate" has been omitted from all discussion hereafter, the stereotyped nature of the displays to be described will be regarded, in the absence of better evidence, as being sufficient indication of their inborn character.

The Mergini merit study, both to elucidate their evolutionary position among the ducks as a whole, and because of some unusual features they possess. The group consists of seven genera, one of which (a single species) is recently extinct, while three others of the remaining six are also monotypic (Scott, 1951). Unless the Mergini are very ancient, and these are relict species from a much larger speciation history, there is good reason to look again at these genera to learn more of their relationships. At the same time it is necessary to study the fossil and zoogeographic histories

of the genera in the group.

Delacour and Mayr (op.cit.) were very clear about what the relationships of the various genera were to each other. Yet the evidence is not, in my view, entirely complete or beyond re-evaluation. They wrote:

Delacour (1936:376), as well as Heinroth and other authors, has pointed out the obvious relationship of the merganser (Mergus) with the golden-eyes (Bucephala); and in spite of the wide difference between the extreme forms of the tribe (Mergus and Somateria), the sea ducks form one of the most closely knit subdivisions of the anatine subfamily. The seven genera are connected with one another by intermediate species. The Hooded Merganser (Mergus cucullatus), for example, connects the larger mergansers, through the Smew ("Mergellus albellus") and the Buffle-head (Bucephala albeola) to the golden-eyes. The Harlequin (Histrionicus) is a link between the Old-squaw (Clangula) and the scoters (Melanitta), as is the Labrador Duck (Camptorhynchus) between the Old-squaw and the eiders (Somateria).

On the other hand, the golden-eyes, the Old-squaw, and the Harlequin are undoubtedly related, as is proved by the same bold pattern of dark gray and white of all their downy young.

However, except for the mergansers (Mergus), of which there are seven, no genus contains more than four species. Each genus is rather uniform in its species, but rather different from every other genus, though both eiders (Somateria sp.) and scoters (Melanitta sp.) are very heavily-built for ducks. Certainly the Mergini as a group must be deemed less uniform in type than either the Anatini or the Aythiini. Delacour (1956) has recently separated the eiders as a distinct tribe, the Somateriini, and he tells me (in litt. March 29, 1957) that he has done so on the basis of the plumage patterns of the females and the downies, and also on behavioural characters "as pointed out by Humphrey". We await further details. It is of interest that (as in the above quotation) the characteristics of the downy young are considered to indicate the common ancestry of modern genera. However in the matter of displays Delacour and Mayr (op.cit.) describe the "Head-Throw"

display in both mergansers, and, quoting Hochbaum (1944), in the Canvasback (Aythya valisneria). They do not apparently realise that this display is almost certainly homologous in the two tribes, and from descriptions of eider display (Somateria mollissima) quoted from Hoogerheide (1950) by McKinney (unpubl.M.S.) I believe it will be shown that the eiders show close relationship both to the scoters and to the scaups (Aythya sp.). Delacour and Mayr (op.cit.) and Delacour (in litt. March 29, 1957) are convinced however that the Mergini are most closely related to the Perching Ducks (Cairinini).

This thesis is confined to an account of the behaviour of the two true goldeneyes (I use this term here instead of Bucephala because the displays of B.albeola are completely unlike those of B.islandica and B.clangula, and B.albeola appears to be quite unrelated to them). The intention, eventually, is to describe the postures and movements employed in courtship throughout the Mergini in the manner employed by Lorenz (1941). B.islandica and B.clangula have a rather large number of displays having sexual motivation, and in this respect are a useful basis upon which to draw comparisons from other, less effusive, species. They fill the same important position as the Mallard (Anas platyrhynchos) in the paper by Lorenz.

The derivation of sexual displays.

Lorenz (op.cit.) did not go at all deeply into the form and variety of the various non-sexual movements, such as those involved in preening, bathing or stretching. These are now classed together as "comfort move-

ments". They are concerned with the maintenance of healthy body plumage and with satisfactory muscle-tonus. Nor did Lorenz consider in detail the maintenance activities of feeding and drinking. Fortunately McKinney has now performed such an analysis for the Anatini (unpubl. Ph.D thesis University of Bristol 1953). He has demonstrated the absolute necessity of studying all the motor patterns, of a visible nature, that occur in the repertoire of a duck, if a true understanding, or an exact analysis, of the behaviour of the whole animal is to be made. The second major function, therefore, of an ethological study, is the establishment of the source, or origin, of courtship displays from the motor patterns having non-sexual internal motivation.

In many recent studies, notably in highly territorial vertebrates such as birds or fish (Tinbergen, 1951;1953, et al.), it has been found that sexual displays can generally be explained as biproducts of (or as accidentally derivations from) such conflict situations as arise from opposing motivations e.g. the tendency to aggression being equally strong as the tendency to escape. Furthermore the displays often resemble attitudes assumed during aggression or flight. Daanje (1950) has discussed the origin of displays from the intention movements of locomotory activities, such as swimming, diving, and flying.

It has become customary, therefore, to suggest that sexual displays generally derive from such aggressive or fleeing attitudes in birds and fish. This judgement is unlikely to be substantiated, as a general law, when rather more species have been studied. For a number of cases are now known where

sexual displays are derived by ritualisation, not of aggressive or fleeing attitudes, but of other activities such as comfort movements. This appears to be the case in goldeneyes.

It needs to be questioned, furthermore, whether the conflict situation which gives rise to displacement activities, and hence ritualisation of aggressive, fleeing, or irrelevant preening etc., into displays, must always be one involving aggressive motivation and fleeing motivation. May there not be a direct tension between the sexual drive per se and the escape drive? Since fleeing by the drake is not an activity which a sexually-motivated female can do much to correct, any irrelevant performance by the drake might rapidly and easily reduce the tendency of the male to flee from the female. It might do this either by becoming symbolic to the female of a tension within the sexual activity of the male, or by means of a feed-back mechanism which would tend further to arouse the sexual motivation of the males so that fleeing does not take place. This latter is possibly the case in goldeneyes, for the female may remain motionless in the posture inviting coitus for as long as 20 minutes while the male swims slowly around her "Wing-and Leg-Stretching", "Water-Flipping" and performing other sexual displays, for a considerable time, before he is seemingly worked into the mood to mount the female.

Since sexual motivation towards copulation must be assumed to be as old, historically, as the activities of mutual shedding of sex products, or copulation itself, there is every reason to look for the origin of sexual displays as much in conflicts between the sexual drive with the tendency to escape, as in conflicts of aggressive tendencies with those of

escape. Especially is this so since "individual distance" towards the mate is very small indeed, or non-existent, in a solidly paired male and female. The stimulating effect of display upon the female such that she "Jives" or invites coitus may therefore help to correct the actions of the two individuals in favour of success in pairing or mating. Feed-back as a mechanism reducing the escape tendency may also be important. It is important here to distinguish the "individual distance" within which another bird is attacked, from that presence of a bird close-by which induces immediate retreat.

Whatever the truth of the matter, the unfulfilled intentions of aggression or escape, as well as displacement activities in other fields, may acquire sexual signal functions of their own. Lorenz (1941) himself suggested some origins of displays from comfort or other activities, though he produced little analytical proof of the correctness of his statements. He pointed out, for example, the close resemblance between the display of the Mandarin Duck (Aix galericulata) --- in which the male dips the beak behind a greatly enlarged, and highly coloured, secondary feather which projects above the back --- and true wing preening from which it undoubtedly derives. And this example also illustrates the important principle that a movement precedes, in such cases, the development of morphological characteristics, which are now associated with the movement and emphasise its visual effects. In the last 15 years a great many examples of the derivation of displays from comfort movements, or from locomotory movements (or rather the intention movements of locomotory activities) have been described.

Movements are regarded as being older than the bright features they display. The colour patterns of the head of the Goosander (Mergus merganser)

are different from those in a goldeneye. Yet each has the Head-Throw. Any correlation between colour patterns of the head and this basic courtship display are therefore secondary. Although other displays may exist (different in the two species) which are emphasised by the differing colour patterns, I am rather inclined to believe, now, that the shape of the patterns is not completely specific to the displays. The effect of a displaying sea duck must always be striking. They are a most highly coloured group. "Threat" in goldeneye is a grotesque spectacle (Fig.7). But it may be rather in the overall effects as a stimulus that colour patterns are important. The actual colour patterns are so distinct from species to species that there can be no difficulty whatever in recognising the male. We are left to assume either that the evolution of colour patterns is not an isolating mechanism on a distinctly specific level, or that Mergini are a relict group in which the intermediate species have been lost, or that sexual selection is operating to produce fantastically plumaged males. No work has been done on this selectivity of females for males of varying plumages. While there may be a slight surplus of males in the population, plumages (except for juvenal birds in their second summer) do not appear to differ greatly in quality.

In the light of the principles enunciated earlier it has become increasingly clear that the "whole animal" has to be included in any study of sexual displays, if any "meaning" is to be found in the various display activities.

In order to discover any phylogenetic significance (or any origins,

for that matter) of sexual displays it is necessary to study more than one species, otherwise there is no means of comparison. McKinney was kind enough to warn me (in litt., 1954) that to avoid the unintentional suggestion of homologies with surface-feeding ducks, it would be necessary to invent quite separate descriptive names for the display movements seen in each species, and only to equate these with each other when one had observed the whole range of movements in each species and had evidence that the displays were homologous. A separate name has therefore been given to each movement in each species, even when they are believed to be the same.

The same principle applies when describing the signal meaning, or function of a display. The "Laying Neck on Water" posture of the goldeneyes without any doubt has a "threat" function, but it is necessary to give it a descriptive name first and only a functional name (or synonym) afterwards. It would be understood that only when discussing goldeneye would this functional name necessarily apply to the "Laying Neck on Water" posture. All the headings in the Table of Contents in this thesis are descriptive names. The meaning or function of a display is sometimes discussed in the text.

It may be argued, by the purist, that Lorenz (or his translator) was wrong to call the "Jiving" movement an Inciting movement, for this is completely anthropomorphic. We do not yet know whether this movement has the effect exclusively of stimulating the male, or whether it also indicates to one male that he is the chosen mate, and to other males nearby that they are not welcome. In the eiders the movement is not a single

whole, but is in two separate parts, with different meanings, if the homologies that have been suggested are correct. Certainly the movement should have a descriptive terminology, for the movement occurs in a number of different contexts (e.g. as between courting parties and territories), and may have different meanings to different birds in the group.

Current Studies and the Literature

The literature of the courtship displays of the Mergini is scant in the extreme. When I had already done my field work on B.islandica for two summers I discovered that Sawyer (1928) had in fact described, and illustrated (from field sketches), all the sexual displays that I had seen, including coition. This was a blessing in disguise for my field observations were made without any knowledge of his paper, and our descriptions prove to be extremely alike. We thus confirm each others work. Barrow's Goldeneye becomes, most probably, the best known of the sea ducks in this respect. For B clangula the written records are less useful. Brüllgemann, as early as 1876, described coition and this description has not been bettered. Brewster (1911) wrote a paper which is the best description of the general courting displays so far. There are a few other literature descriptions of B. clangula from both Europe and America.

It must be remarked that ethological observation requires considerable training of eye and mind, and it is very easy to see and describe a movement or sequence of movements erroneously. Most observations recorded in the literature are written by ornithologists unskilled at describing this kind of event accurately, and usually from single occasions only. Thus they are mere estimates of the essential character of the courtship and

are comparatively little use for a study of this kind. Since most of the descriptions refer to the "Head-Throw" which is the most frequent display in courting parties of B. clangula but is found also throughout the Mergini and also in the Aythya it is clear that but few of the distinguishing displays have been adequately described in any of the genera involved. Coition has been described in almost none of them. It is very important that coition should be described in other species of Mergini in the near future. It may be easiest to do in a waterfowl collection (unnatural surroundings, hence other sexual displays may perhaps be liable to errors of frequency and occurrence).

Pictorial illustrations have so far only been able to illustrate static poses. These may be assumed during more than one type of display e.g. as in the Bowsprit pose of B. clangula and are therefore unsatisfactory. They are not precise and do not finalise any description. It became necessary to illustrate movie-film sequences on a full page plate, by drawing selected frames from the sequence. This technique has been applied in this thesis. I have made drawings of certain displays from my own films of B. islandica. Dr. Frank McKinney, of the Delta Waterfowl Research Station at Delta, Manitoba, has been kind enough to allow me to make drawings of both B. islandica and B. clangula from a short length of film taken in England.

About half the plates included here are ones made up from a film of B. clangula taken in 1956 by Charles Walcott and Benjamin Dane (both now of Cornell University) while they were at Harvard College. The film was taken at Newburyport, Massachusetts. It was a great privilege and pleasure

to be able to work over this film and use illustrative material for the purpose of comparison with B.islandica.

At the present time the only known studies on the behaviour of the Mergini are those being made currently by McKinney at Delta on B.clangula and on the Aythya. Dane at Cornell University is working on B.albeola and mergansers. McKinney, P.S.Humphrey at the University of Michigan, and Gudmundson (Scott, 1953) have unpublished material on the Common Eider (Somateria mollissima).

The Pacific Coast

Probably the most rewarding area in the whole free world for the study of the Mergini in the field, lies along the Pacific Coast of North America from Puget Sound to Point Barrow, Alaska. Eiders, Old-Squaw (Clangula hyemalis), and scoters breed along the shores of the Bering Sea and the arctic coasts of Canada. Two species of Bucephala, the Harlequin (Histrionicus histrionicus), and even one scoter and three mergansers could be studied in the summer in central British Columbia. However much the most rewarding time appears to be in the winter when, with the exception of the eiders (all four of which could however be studied in the Aleutians) and three species of merganser which have relict populations in the southern hemisphere and eastern Asia, all but one (the eurasian Snew, Mergus albellus) of the remaining world species of Mergini can be studied on the South-East coast of Vancouver Island, in the Gulf Islands of the Strait of Georgia, and in the vicinity of Vancouver, B.C. For this reason the University of British Columbia is ideally situated for a study of the behaviour of the Mergini, and there is a great deal to be

to be able to work over this film and use illustrative material for the purpose of comparison with B.islandica.

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said in favour of establishing a waterfowl research station in the Fraser Delta area or in the Gulf Islands. The only other Canadian research station of this type is the Delta Waterfowl Research Station at Delta, Manitoba. There is room for a similar station on the Strait of Georgia or Puget Sound region of the Pacific Coast.

Equipment

Two technical aids proved essential. In the summer of 1955 a 16 mm. Cine-Pathé model movie-camera was used to take about 1000 feet of Kodachrome film of B.islandica. Using an Animated Viewer (Editing Apparatus) it is possible to select individual frames showing the extreme of a movement, and to make camera-lucida-type drawings of selected frames, such as illustrate this thesis. Placing such drawings side by side on a single sheet of paper it is possible to demonstrate in detail the form, extreme positions, and relative speed of a "posture-movement" element--- the whole "going-into and coming-out-of a posture", in a sequence that may last as short a time as 1/10th of a second, or as long as 2 seconds. The Head-Flick that ends many movements e.g. the "Head-Throw", was not seen in the field, and occupied only 2 frames on film being taken at 24 frames/second. For the first time, therefore, it is possible without actually showing a film to an audience, to illustrate in print the form of a movement. Some of the drawings in the literature, because they are not the extremes of a movement, give but a grotesque idea of the movement that actually occurs.

The second technical aid (used for the first time in 1956) was a

"Midgetape" tape-recorder (made by Mohawk Business Machines, Inc.). This light instrument uses hour-long tapes, broken into two $\frac{1}{2}$ -hour lengths which are rapidly changed around. It is possible to carry any number of tapes in the field. This invaluable machine allows the observer (while holding field-glasses) to dictate an exact record of all that happens in front of him, as it occurs. This rules out the necessity of a prodigious (and accurate) memory, or a stenographer as field-companion. Ducks move rapidly and it is not possible without a tape-recorder to record accurately the order of movements in a sequence, or to distinguish the individuals performing them. In really fast sequences film is the only completely accurate means of recording a sequence. Film is also the only way of recording the exact "anatomy" of a movement. But film is too expensive to use all the time, while tapes may be used over and over again. Tape-recordings have the power to demonstrate the stereotyped nature of some sequences. For example the goldeneyes have a great many different postures, but very little in the way of an organised use of these in a stereotyped order, or orientation. On the other hand the Bufflehead (B.albeola), which appears to have very few sexual displays, was clearly shown (by tape-recordings) to employ its normal powers of flight and swimming (with the Nodding display) into an elaborate series of orientation sequences -- or "dances". Owing to the speed of movement and its repetitive nature, these can best be illustrated by means of tape-recordings of the human voice describing the orientation of the birds, with some film sequences of the individual "sets".

Organisation

This thesis will be in three sections: —

(1) Distribution and Annual Cycle of Barrow's Goldeneye. It is vital to place the behaviour (its form, time of occurrence, function and derivation) in the context of the annual cycle (pairing, migration, nesting, post-breeding distribution and winter associations). The descriptions of the behavioural elements is thus preceded by this account of the annual cycle and the part played by the sexual activity and its form in zoogeographical distribution, migration etc. One needs to know why pairing occurs as, and when, it does, and what its effects are, in terms of the whole biology of the animal.

(2) Non-Social Behaviour. The Locomotory and Comfort Movements will be described with no particular distinctions drawn between the two species of goldeneye, as it is not known that they differ in any substantial ways in these activities. The descriptions are however necessary so that it may be seen that certain social displays have similarities with and origins from these more primary activities.

(3) Social Behaviour. This includes a number of spheres of activity. In the description of courtship displays in particular the descriptions of displays in the two species will be separated. This is often necessary for the further reason that we cannot be certain of the homologies between them. Under each movement there will be separate headings for Field, Film and Literature Descriptions. This is not an ideal situation, but is necessitated by the nature of my sources, and the necessity at this stage of distinguishing them.

THE GOLDENEYES

(BUCEPHALA ISLANDICA & B. CLANGULA)

THE DISTRIBUTION AND ANNUAL CYCLE OF BARROW'S GOLDENEYE.

THE DISTRIBUTION AND ANNUAL CYCLE OF BARROW'S GOLDENEYE

Geographical Distribution

The Common Goldeneye (B. clangula) breeds in North America and across Siberia to Europe, but is not found in Iceland or Greenland. Barrow's Goldeneye (B. islandica) occupies the remaining suitable areas of the Holarctic. It is found breeding only in Iceland, possibly in Labrador, and westwards of the eastern foothills of the Continental Divide of North America. From these regions B. clangula is absent. There are only four authoritative records of B. clangula breeding west of the Rocky Mountains in British Columbia: — twice at Swan Lake in the Okanagan Valley in 1930 (Munro, 1935), at Vanderhoof (Munro, 1949), near Enderby in 1946 (a female taken from a nest, now in the Collection of the Department of Zoology at the University of British Columbia) and, less reliably, in 1895 at Sumas (Brooks and Swarth, 1925). Murie (1946) records breeding of B. islandica in Mount McKinley National Park. A few B. islandica breed in the Peace River Country, the Yukon and central Alaska, where there is slight overlap with B. clangula (Cowan, 1939; and J.W. Brooks (pers.comm.)).

Main breeding ranges are however quite distinct and the examples cited are the only known exceptions. The histories of the distinct populations of B. islandica in Iceland and British Columbia are of profound systematic importance. However it will only be possible here to discuss the part played by courtship displays in maintaining B. islandica and B. clangula as distinct species, and in distinct breeding ranges where they nowadays approximate each other geographically in western North America.

Moult Migration as an Outbreeding Mechanism within the species.

For ethological purposes the annual cycle may be said to start at the time that the two sexes meet on salt water, in late October or early November. The adult drakes reaching the coast a week or two ahead of the females and young. This meeting is the climax to a very remarkable phenomenon occurring in most diving ducks, namely the almost complete disappearance of the males from the breeding grounds during June and July. Where the drakes of B. islandica retire is as yet unknown. Swarth (1926) records seeing males flying south in flocks in mid-June at Atlin on the Yukon border. In Iceland males of this species gather in large moulting flocks on the breeding lakes themselves or on the sea nearby (Phillips, 1925 quoting Hantzsch). Phillips suggests a northward flight and Hochbaum (1955) gives evidence for this in other species.

Individual drakes during eclipse would not be quickly identified by any but a competent observer. But assuming that they are gathered together in a very few bands, as in the Canvasback (Hochbaum, 1955), it is still surprising that large groups of moulting goldeneye have not yet been reported in British Columbia. It seems most likely that they retreat to a few lakes in the Coast Range, or to one or two of the hundreds of deep fjords of the sea which run up into the coastal mountains of British Columbia and the Alaska Panhandle.

Both biologically and ethologically this late summer period is important. While the drakes move out a large proportion of the females remain on or about the breeding ground. It must therefore be certain that, when the sexes meet again on the coast during the winter, there is but a

slight possibility of a female goldeneye again pairing with a drake with whom she has previously bred. Thus, within the breeding range, there will be almost complete panmixia. As Mayr (1942, p.241) says after describing how a Maine-bred mallard drake may follow a North Dakota female back to that state from the Gulf coast: "The result is almost complete panmixia and much-reduced subspeciation".

Matrilocality (with Coastal Pairing) as an Isolating Mechanism between species

It appears that most female goldeneye return to the neighbourhood of their birthplace during their second summer in order to breed. Many non-breeding yearlings also return to the region of their natal lake. Females thereafter will breed, if physically possible, in the same stump that they chose for a nest, when they first bred, at two years of age. There is thus a strong tendency in the females to matrilocality.

The outbreeding mechanism inherent in the summer and autumn seclusion of the adult males means that when a pair start inland in March or April to the breeding grounds it must literally be true that the male has no "idea" whither he is being led by the female. She is homing, by contrast, to a known lake and even a particular nesting cavity. This means that should a mixed pair occasionally be formed on the coast, the drake of the pair will be led by the female (if he goes with her) right outside the breeding range of his species: if he is B. clangula, short of the Rocky Mountain chain -- if he is B. islandica, over the Rockies into Alberta, the Peace River Country, the Yukon, or into Alaska.

Plumage characters and ethological mechanisms result in accurate

species recognition, and so mixed pairings are very unusual. Since the drakes, if they pair on the coast, follow the female to the breeding grounds, matrilocality allows neither the females nor the males to pass outside the traditional range to breed. It appears therefore that, except for narrow bands of range overlap, competition effectively prevents the two species, B.islandica and B.clangula, from spreading into each other's breeding range. The present dividing line between the two ranges lies just east of the Rocky Mountains, on the edge of the plains. Why this should be so is not certain, but it seems probable that B.islandica was contained in mountain or inter-montane regions to the west of the Continental Divide (and to mountain regions in the eastern United States) during glacial times and spread north, west of the cordillera, into British Columbia as the ice retreated. Only recently have the glaciers of the high chains of the Rocky Mountains become free of ice and accessible to free passage of range-spreading individual goldeneye. It is likely therefore that B.islandica is spreading east of the mountains at the present time, but only slowly since B.islandica has no reason to fly very far east of the Rocky Mountains at any time of year. Competition must be preventing the colonisation westwards of B.clangula for B.clangula traverses the intermontane region twice each year and British Columbia is good "goldeneye breeding range".

Hybrids

Around Fairbanks, Alaska, goldeneye of both species are found together during the summer (J.W.Brooks, pers.comm.). It would presumably be possible therefore to find situations, in central Alaska, where both species

are present on the same lake and where courting parties and territories of the two species are in close proximity, unless as in the Peace River district the two species tend to breed on different lakes (Cowan, 1939). If the two species do sometimes breed on the same lakes, sexual assaults may occasionally occur and mixed matings arise.

Hybrids have not been identified commonly so far. The only published reference to a hybrid B. islandica x B. clangula is Snyder (1953). This is an adult drake taken in New Brunswick and now in the Royal Ontario Museum. Unfortunately we do not know if the small numbers of B. islandica found on the east coast of Canada and New England in winter come from Labrador, Greenland or Iceland. For the west, Miss Mary F. Jackson has taken a mature hybrid drake on Westwick Lake, Cariboo District, British Columbia on May 13, 1954, now in the collection of the Department of Zoology at the University of British Columbia.

It would be interesting to know whether hybrids are more common in central Alaska, or the Peace River Country, than elsewhere, and if they are fertile. Maybe the ethological mechanisms are too strong to permit mixed matings even if the two species do breed on the same lakes, but whether such competition for space occurs we do not really know yet. Certainly males are too intolerant of each other for small sloughs to be occupied by more than one pair of B. islandica (in British Columbia at least -- Icelandic conditions around Myvatn may be different), and territories may be larger than they are on larger lakes where tolerance appears to be rather greater.

Unfortunately the finding of hybrids will not be easy, even in adult

males; nevertheless if they can be found among the breeding drakes in a higher frequency in one overall region, as compared with another, then (assuming a fifty:fifty sex ratio in hybrid downies) there must be a proportion of female hybrids in the region of their origin, and in particular wherever females of both species are homing to the same locality, as from Alaskan coastal waters to the breeding grounds inland.

It is apparent that female goldeneye do recognise the drakes of their own species on the wintering grounds, and generally pair only with them. Plumage and display differences appear to be successful in preventing mixed pairings from occurring during the winter period, when both species are found together on the salt water. To a trained observer, the males are readily distinguished in nuptial plumage, at a distance, by the amount of white on the wings and flanks. Closer to, the shape of the head, shape of the white patch between the eye and the beak, the colour of the head feathers, and the wing "windows" are distinctively different. No normal female will ever mistake a male. The females may be distinguished by the shape of the head and bill, and from October through until late May, by the amount of yellow on the bill. In June when mating for the year is completed, the yellow bill darkens over in the female. This is an indication of its character as a distinguishing mark. Juvenal males may not be distinguished from females until late winter or their first spring. Yearling males are distinguishable either by the presence of white feathers coming into the brown feathers of the head, where the face patch will appear, or if signs of this are still lacking, by the darker sepia tone of the head colouring, by head-shape and size. Juvenal females of B.islandica

cannot be distinguished in the field from those of B. clangula.

In addition to all these plâumage characters, well known to an observer familiar with both species, and presumably also easily recognised by the birds themselves, there are the courtship displays. These too, are very different in form between the two species (though not in general construction or origin). They may be easily distinguished by a human observer, who knows the body-shape they produce, and the speed of performance in each species.

Winter Distribution and Winter Behaviour.

Around the ~~Straits~~ of Georgia, southwest British Columbia, there is a differential distribution of the wintering goldeneye. Around Vancouver (Howe Sound, Point Grey, Stanley Park and Indian Arm, but possibly not the more open coast at Point Roberts), B. islandica is more frequently seen, while along the east coast of Vancouver Island, at least from Comox to Victoria, B. clangula is more generally found. There is a similar differential distribution in other Mergini, especially scoters.

Display may be seen from almost the moment the sexes meet again in the fall. Relative frequencies of the various displays during the winter (when territorial defence is not needed except around the mate, and mating is rare) are rather different from those found on the breeding lakes (where mating-territory exists and must be defended, and where mating is necessary). Nevertheless mating may sometimes be seen on the coast. Charles Walcott and Benjamin Dane have recorded one such coition sequence on film (B. clangula) at Newburyport, Mass., in April 1956.

It is worth mentioning here that sea-ice is not often found south of the Aleutian chain, whereas on the east coast of Canada and New England it is a regular feature of the early months of the year. But this does not reduce display activity. Walcott and Dane's film shows B.clangula courting even among ice-floes in February, at Newburyport.

During the winter goldeneye are seldom found alone, but occur more often in loose association with other individuals. Quite frequently a number of feeding birds, in a loose flock, will come together every few minutes and sexual displays, mixed with and perhaps initiated by, brief bursts of threat and counterthreat, will be seen. As quickly as it began, this activity relapses back into feeding or preening. Preening is very persistent, and often appears to occur as a community activity. It seems certain that it has a function in maintaining the flock as a whole, or in building up sexual motivation.

On the Straits of Georgia, which are a little south of the centre of bird's winter range along the Pacific coast, there is a preponderance of males. This may possibly be due to the greater hunting pressure, on females, which occurs in the interior in the fall (since the adult males are not there during the hunting season). But this preponderance of males is even more marked in B.clangula than in B.islandica. Both in B.clangula and in B.albeola a differential influx of females from the more southern parts of the winter range certainly occurs in the spring.

Courting parties around Vancouver generally consist of at least three males to one female in the fall. Birds, which have the appearance of being paired, may be found at any time during the winter. Towards spring the

ratio of females may increase, and isolated pairs, male and female feeding together, become more frequent. Whether this indicates an influx of females during February and March is unknown. It could do so, but Mary F. Jackson (pers. comm.) finds that coastal banding recoveries of B. islandica show no differential distribution of the sexes. In other diving ducks however it is the rule, as with B. clangula and B. albeola that the drakes predominate in the more northerly parts of the winter range (Phillips, 1925-26). Whether in B. islandica there is an overall preponderance of males or not, there certainly appear to be a sufficiency on the breeding grounds and the evidence is that there is a higher adult mortality in females, due to unknown biological causes.

The uneven sex ratio in courting parties during the winter in great part explains their great activity. Clearly a group of birds, in which the males predominate, and are liable to threaten each other, or are all performing the "Pseudo-Kick" or "Rotary Pumping" displays again and again around just one or two females will be a more volatile group than would one in which there is only one or two males, with a larger number of females.

Such a situation is indeed sometimes seen in the Interior in July; a lone drake with a drove of inactive post-breeding or immature females. Sexual activity is then low, but somehow the male always looks as though he did not "belong" (possibly this is a general phenomenon in animals in which the male is the more active partner in courtship). It would be interesting to have descriptions of the activity of courting parties in the more southern limits of the winter range of diving ducks. The implication would seem to be that in diving ducks generally those females who move furthest

south may only pair late in the winter.

The behaviour of a pair is different from that of the unpaired birds of a courting party. Premium now is on maintaining the pair bond, rather than on forming it. Paired birds are noticeably less active, unless, as often happened, the males become mixed up in a courting party. Possibly the hormonal state of the paired birds differs from that of single birds. If this is so, the winter population may not be an homogenous whole, even among mature individuals. In any case it appears that an unbalanced sex ratio prevents even the farthest-travelling female remaining unpaired by the time she has been on the breeding grounds for a few days. There is no evidence that juvenal or yearling females go farther south in winter than the adult females, though it is known that the juvenals wander over considerable distances in the fall.

Spring Migration

The goldeneye move into the interior of British Columbia during March and April, many B.islandica appearing on Okanagan Lake in March, while a very few winter there (Munro, 1918). Rather more B.clangula winter there than do B.islandica.

We do not know to what extent the migration takes place as pairs, pairs with unmated birds attached, or as groups of unmated males following an unmated female. It is generally assumed that pairing occurs on the coast almost universally. But it may also presumably happen that an unpaired drake follows another pair. Alternatively we may suppose that matrilocal tendencies might also operate, so that in males also (when

unpaired), wanderings into or settling down in the range of the other species would be unlikely. Such birds might tend to return to the place of their birth and pair up with an unpaired female there (this is the converse of the more usual situation in which a male ends up almost anywhere, but at his birthplace). We do not know the truth about this, and will not do so until as intensive a study has been carried out on the drake of the species as has been done, by Mary F. Jackson, on the female.

As the ice melts (often before) the goldeneye move to the lakes and sloughs that they prefer for breeding. The ice may melt any time from mid-March to mid-May depending on latitude, the hardness of the winter, altitude, and the weather conditions at the time of break-up. In 1955 in the Cariboo District the ice melted in the last day or two of April. In 1956 a fine weather period melted the ice during the last ten days of April. In 1957 the break-up has probably taken place earlier.

Territory (Mating and Brood) and Nesting.

Territories are established by the drakes as soon as the ice melts, and are defended even before the ice has departed completely. It is not long before the old females start laying the first eggs in the old nest-sites. Younger birds who have to find and establish a right to a nest-cavity may be slower to begin their clutch. The number of eggs varies from 6 up to 14 and a female may take 10 days or as long as three weeks, from the time she lays her first egg, before she starts to incubate. Smaller clutches are not laid by the younger birds alone; indeed field data show that each bird lays a more or less fixed clutch, large or small, irrespective of age. Even a young bird can presumably lay a large clutch,

and the factor determining clutch-size appears to be genetical and phenological rather than an expression of the age of the bird (Mary F. Jackson, M.S.).

Taking all years together early nesters may be incubating by May 1st in early years, but late individuals may not start to incubate until the second week in June. By the second week in June, also, the drakes have nearly all disappeared. Their departure may be gradual or sudden. In the later season, 1955, the Cariboo suffered from arctic conditions from May 26th to June 1st, but the first week of June, by contrast, was very hot. The males did not leave suddenly during the cold spell as might be expected, but gradually during the middle of June. In the earlier season, 1956, a rainy spell in the first week of June appears to have caused a rapid exodus of males then, but this is less certain -- there were fewer of them on the lakes that season. After the males leave the females do not necessarily frequent the old mating territory, and do not defend anything but the nest until the young reach the water (Mary F. Jackson pers. comm.).

The incubation period lasts 32-35 days, so that one-twelfth of the whole year is spent sitting in a tree cavity incubating eggs, with short breaks to feed, drink and preen (at that time about equally important). In any one season hatching takes place over a four week period. The eggs (except the last one or two in some cases) all hatch within a few hours, and the young may stay in the nest drying off, and preparing to leave the nest, for a further 24-36 hours.

The young are called off the nest by the female, and all tumble out of the nest together in the space of a minute or two (in the present study young were seen to leave the nest hole only under experimental conditions - a nest box removed from its tree, and placed on the ground in an enclosure at the edge of the lake). The young may have to drop as many as 35 to 40 feet, but this does not seem to harm them. They may fall directly into the water if the tree is one killed by flooding, or one standing on the edge of a lake, with the mating territory immediately in front of it. Mary F. Jackson (pers. comm.) found that the brood territory is often some distance from the nest tree and is not necessarily coincident with the mating territory which existed a month or three weeks earlier. On the other hand the downies may have to follow the female through the bush or across the range for even as much as three miles (Mary F. Jackson pers. comm.). A brood was watched by the writer, just after leaving the nest tree at the edge of the bush, crossing the range towards the lake. They were watched during their first hour on the water, and their activity described.

Deficiencies in Brood Guardianship

The seeming efficiency of the reproductive process in goldeneye is reduced by the post-fledging behaviour of the females. Most females succeed in hatching their clutches (predation at this stage is slight), but some of them are poor brood "coaches" or "nursery school attendants". Some forsake their broods within a few days. Downies that survive this lack of protection may remain unattended or join other broods, so that some females may be attended by as many as twenty or thirty downies, of

whom but a fraction, if any, are her own offspring. Fighting may occur between females for possession of downies. Unattended downies are not usually attacked, but are easily adopted, by other females. Female ducks do not feed their young, which fend for themselves, but they do brood them at night in the early days at least, and this provides protection, but more particularly protects them from unsupportable heat loss on chill nights. The desertion of the young by some females, presumably therefore has a detrimental effect on productivity.

Age at first breeding

Another important fact relating to productivity in goldeneyes, is that the females do not breed until their second year. This habit is found throughout the Mergini, and is an ancient character. It may be associated with low nest predation both in the arctic ground nesters and in the tree-nesting species found below the tree line.

Post-breeding Dispersal.

The drakes disappear in June. From June through August, small bands of yearlings and post-breeding females may be seen on most breeding lakes. As far as is known they do not join the males, but stay in the same general district that they spent the whole summer.

The juvenals are still present during the hunting season (opens September 15th, in interior British Columbia). Mary Jackson's analysis of the banding returns for B. islandica shows that: —

- 1). Some juvenal goldeneye are shot on the lakes on which they were banded as flightless downies.

- 2). that there is a marked tendency among flying juvenals to wander in any direction--in some cases for many hundreds of miles in the Intermontane area, and even east into Alberta, during the period prior to the true coastal migration. The significance of this phenomenon has been discussed by Hochbaum (1955), who says that it is found in most ducks and allows the juvenals to acquire a geographical knowledge enabling them to home to the breeding area at a later date.
- 3). that adult females are also still present on the breeding lakes, but that they separate from the young before becoming flightless, and usually by the time the young are 6-7 weeks old (field observations).

Summary

Since the ice-age a population of B.islandica has again come in contact with a population of B.clangula in western North America. On the east coast certain numbers of the former winter with the latter.

Pairing is generally believed to occur on the wintering grounds. Since the males are separated from the females from June to October panmixia is believed to be almost complete. Since the females home to their natal lakes, a male of a pair breeds in a different locality from that in which he was raised. Unmated males may either travel with another pair, or in a small party, or may even home to their natal lakes. What proportion of the males perform the spring migration unmated is not known, nor is it known which of the three possibilities they most usually follow.

Species discrimination is evidently good, and displays are recognisably different in form (though not in origin). Together these two factors prevent mis^cgenation and hybridisation and maintain the pair bond as far as fertilisation. But displays do not particularly promote reproductive success itself, once the eggs are laid. This distinction deserves to be emphasised.

In theory the matrilocality of the female would result in the drake of a mixed pair passing outside the breeding range of his species. Matrilocality of the females, combined with pairing on the wintering grounds, and ecological competition of an exclusive type would prevent either species of goldeneye from enlarging its breeding range at any considerable rate, or from spreading into the area occupied by the other species. These behavioural mechanisms, and the specificity of the plumage characters and displays has prevented hybridisation between B.islandica and B.clangula though they are evidently capable of it (as are many ducks; the infertility of hybrids has hardly been studied), and has evidently contained the two species within the breeding ranges occupied when they recently came together again after the tongue of ice along the Rocky Mountains melted. The line of demarcation between the breeding ranges of the two species is parallel to the Rocky Mountains, except in a few areas, although B.clangula regularly flies across the mountains twice each year. As far as is known the nesting and other requirements of the two species are very similar.

THE GOLDENEYES
NON-SOCIAL BEHAVIOUR

1. Locomotory Movements
2. Comfort Movements

LOCOMOTORY MOVEMENTS

These are a group of muscular activities without which life would be impossible. They are important since they provide the means whereby orientations and hostilities are expressed, and feeding and other vital biological activities performed. Thus the following of the female closely by a male during the migration, rising from the water and its intention movements, the flights preliminary to going to the nest, landing in or leaving the nest tree and landing on the water are points of interest in the Flight of Ducks. The form of diving, especially in downies is also of interest, as is the mode of feeding in shallow water and in deeper water. Swimming and Walking are of only minor interest.

Locomotion movements also have the potential to produce courtship displays, or have produced these from them, by ritualisation of intention movements. Thus the Head-Up position of B.islandica and its counterpart in B.clangula may well be derived from the "alarm" or "anxiety" pose of goldeneye, which in its turn may be derived from the intention movement of flight. Since activities differ considerably between adults and downies they have been described separately.

Flight

I have not described the intention movement. Millais (1913) however describes it. He writes: "If observant of danger and about to rise, the neck is straightened and the head held high, with the crest somewhat raised." Only once has an upward lifting of the wings been seen in B.islandica, though a similar flicking of the wings is a ritualised part

of the Head-Bobbing display of Bucephala albeola at high intensities, and is seen in Anatini on occasions. A party of post-breeding female goldeneye were seen at Boitano Lake in June, 1956 and they were sitting on a raft. On seeing me four of them stood up, and raised their heads so better to watch me. One flew to the water from the raft, the rest remaining standing. One of these suddenly lifted the wings off the back with the carpal joint forwards and raised, the primaries rising no higher than the joint, but the leading primary forming a horizontal line with it. However this individual did not fly immediately. In B.albeola, furthermore, landing on the water has become regular display activity. In Anatini actual flying itself has developed display features (e.g. Anas americana) though in other species these so-called "courtship-flights" do not have sexual, so much as territorial, significance, for the female in them is usually paired (Hochbaum, 1944).

Goldeneyes, like other Mergini go a considerable distance over the water before becoming fully airborne.

Brewster (1900) describes in detail the manner in which females (B.clangula) search for a nest, and attempt to alight at a potential site:--

Four female Whistlers flying together in a peculiar manner over the trees, now rising high in the air, next descending and dashing among the trunks and branches, vibrating their wings rapidly and continuously as in ordinary flight, but describing circles about a remarkably tall stub with a shattered top. Around this they would pass a dozen times or more, gradually drawing nearer until one bird leaving the rest and pitching first downward, then sharply upward would fly directly towards the stub and try to alight on its jagged top. The attempt usually failed, when the bird, continuing its flight, would disappear among the trees, presently returning to begin circling again; but twice it gained a foothold and remained perched for several seconds,

although it had to keep its wings in constant motion to maintain its balance. Sometimes its flight was directed to a point near the top of the tree where there was a round, neat-looking hole, no doubt the entrance to a nest, for we afterward saw two whistlers emerge from it in quick succession. We thought that all four birds tried in turn either to alight on the stub or to enter the hole...no two made the attempt at the same time (however). They were silent for the most part, but occasionally one of them would utter a sound not unlike the quack of a Black Duck but shorter and flatter and repeated very rapidly six or eight times.

I have seen similar flights in the Cariboo District of B.C. by B.islandica in which four, or even more, females may be seen flying around together very fast, along the edge of the bush or over the forest, coming back to the vicinity of the lake over and over again. Brewster's observations sound a little like prospecting, but the date was May 30th, which is rather late. Mary F. Jackson (pers.comm.) believes that such communal flights by females take place even when each one is herself incubating a clutch in a separate tree, and that similar flights may be performed by ganged-up yearlings and adults.

Generally the return to the nest is not a communal affair. The female takes off from the territory and the male follows after her (Hochbaum, 1955, states that the male follows closely behind the female during migration). The pair circle around the lake and then, in ever increasing circles, expand beyond the lake as their altitude increases. If the nest is some considerable distance from the edge of the lake, the circling flight may continue for some minutes before the male returns. On one occasion I watched the pair circle along the edge of the forest, a number of times, before the female suddenly cut in opposite the spot where I knew the nest to be, and the male returned to the water. On another oc-

casion I watched a pair circle round a lake, a number of times, before I saw the female cut in sharply towards the nest tree at the water's edge.

Brewster (1900) saw a female B. clangula return to the nest on June 2.

She first alighted on the water near the tree and for fifteen or twenty minutes swam or drifted idly about preening her feathers. Then she flew out over a space of open water and turned back toward the tree, describing a great loop and rising gradually until she had attained an elevation of about twenty feet when she made directly for the entrance to the nest, which was about thirty feet above the water. On nearing it she pitched up sharply for the remaining ten feet, keeping her wings in rapid motion up to the last moment but checking her speed very considerably before she reached the hole.

and again (Brewster, 1900):--

.....without any preliminary circling dropped into the water within a few yards of the nest tree. After floating motionless for about two minutes with head and neck erect, evidently watching and listening intently, she flew directly to the hole and alighting on its edge, perched there for an instant, flapping her wings a little to maintain her balance. She then popped in, throwing up her spread tail just as her body disappeared.

Other observers (e.g. Harper in Phillips, 1925) have noted how a female plunges, with no pause whatever, directly into the hole and disappears. It does seem likely that the habit of flighting around at very high speed, often at a considerable height, before plummeting into the nest hole has protective value.

When undisturbed the female may spend some time, in the entrance of the nest, looking around before leaving but, if disturbed, she emerges from the hole at high speed and is away through the trees, often before she can be recognised. Brewster wrote of this: "The blow (from a paddle on the tree) was immediately followed by a scratching sound, and the next instant the whistler shot out over our heads."

Bernhardt (1940) describes how the female flies around a great deal in search for a nesting site and makes a "slide" over a tree having a suitable hole. He seldom saw a female settle in the tree and look at a hole. Rather she flies directly into it, unless disturbed, as she flies into the tree, in which case she may perch in the tree. In searching for holes the drake follows the duck, "twice I saw one sitting waiting on the tree, into which the female had flown". During laying and incubation, however, the male waits on the water.

Millais (1913) describes B. clangula crash-diving as scoters and eiders may do, when frightened. A Peregrine Falcon (Falco peregrinus) was following a group in flight: "I should say 80 yards in the air, and closed their wings as they heard or saw the Peregrine coming, and dropped as if shot to the surface of the water. On striking the water there was no pause, they just passed out of sight". It is possible that elaborate "landing" displays exist in goldeneyes as they do in B. albeola.

Diving

Adults

Allan Brooks (1920) wrote an important comparative paper on diving habits in diving ducks with illustrations of B. clangula, Melanitta fusca and M. perspicillata. He says that in B. clangula the "wings are never used under water but are held tight to the sides beneath the flank feathers. The tail is expanded to its full extent and appears under water to be about as broad as the body." Pearse (M.S., 1928) and Brewster (1911) agree with Brooks that the wings are not used under water (contrast scoters). Brewster

(1911) agrees with Brooks that the tail is fully expanded: "to the utmost possible width just as they disappeared". Pearse (M.S., 1928) remarks the power of swimming under water against a strong current, and he saw single dives for even more than 30 feet. Millais (1913) remarks "the powerful strokes of the legs of these ducks, which seem to beat with great rapidity under water and much power. The stroke is more or less parallel to the wings, the head is held out straight in front". Brooks says that under-water actions are exactly similar in B.islandica.

Brewster (1911) says that the downward plunge is begun by the bird "simply immersing its head and then vanishing with surprising if not mysterious quickness". He notes that the dive may sometimes appear more as a jump up and a plunge forwards in the manner of a grebe or merganser, so that the lower contour of the body becomes visible above the water; "also the whole of the legs and feet, just before re-entering the water". Phillips (1925) writes that feeding birds disappear with a push of the feet and "go down at a steep angle or in circles, with the tail spread and the wings closed or nearly closed. Progress is by the feet alone, these being kicked out at a wide angle from the body; almost it would seem at a right angle."

Feeding birds are readily seen to bob to the surface and, often get lifted a good way out of the water by virtue of their uncontrolled buoyancy. Phillips (1925) writes that "In rising to the surface the body and feet seem to be held rigid and the bird bobs up with great speed." Brooks (1920) writes that "Upon emerging, the tail is held flat on the water or slightly under the surface; at rest, the tail is elevated or even cocked

up at an angle when the bird is asleep." Alford (1920) writes "In rising to the surface they seem to depend entirely on their own buoyancy and when ascending remain absolutely motionless."

It is apparent, of course, that the adult has some control (which very young downies may lack) of controlling the way they surface, if they so desire, for an aggressive bird surfaces very smoothly, and in a crouched attitude breaks surface at an angle. Often when watching for an aggressive bird to rise one fails to observe his reappearance.

Downies

Diving in downy ducklings takes two forms True Diving and Flap Paddle Diving.

Downy goldeneye sit very lightly on the water (Figure 1a). Thus diving requires a sudden sharp effort. Flap Paddle Diving is the commonest type of underwater behaviour on the first day that downies are on the lake. The head is lowered below the surface, and the legs splash out to the side and rear of the body (rather as Figure 1c). Great jets of water are thrown out at the back, and the young emerge from the water very soon. In this half-submerged position the body is held at about 45 degrees downwards. The legs are placed lateral to the body (horizontally) and do not project downwards. Using this technique the downy can become completely submerged, but they do not stay under at all long, but bob up to the surface very suddenly, like balloons. The activity is sometimes followed by Upwards-Stretch and Wing-Flap.

This activity enables the young bird to gather food just below the

surface. The pose greatly resembles that assumed by adults either when feeding in water too shallow for diving, or prior to diving in deeper water, the Head-below-Water, or Looking-for-Food posture. This is sometimes observed in adults even in deep water, and acts as an appetitive orientation of feeding. The pose also has an intermediate pose such as one might expect of an intention movement of diving, for the head is not lifted again before a dive takes place.

True Diving is similar to the diving of adults with a forward plunge and smooth breaking of the water (sometimes lifting out of the water first). It replaced Flap Paddle Diving as early as the first day, though the latter may continue for some time. First-day downies could dive during their first hour in the water. Dives lasted 1-5 seconds. They often preceded this type of diving by holding the face half-under water---as described above for adults (Looking-for-Food pose), though diving did not always follow this pose (rear view seen in Figure 1b). On one occasion a downy was seen to run over the water almost treading it before diving.

Swimming

Adults

Phillips (1925) writes the B. clangula swims with head stretched forward as if looking down into the water. When feeding the tail is submerged or floating on the water (Brooks, 1920; Phillips, 1925). This attitude of the tail is also apparently found when the bird is alarmed, but Brooks says that "at rest, the tail is elevated or even cocked up at an angle when the bird is asleep". Other aspects of swimming, in moving

away from danger, in the threat posture, or a fight or in coition will become apparent when these are discussed.

Downies

In swimming the feet appear to be paddling much faster than in adults, though at times the downy merely sits idle, or preening. However being very active little birds they are seldom still, but are darting back and forth after insects or other food on the surface, when not diving or preening. Because of their smaller size they can change their orientation much more rapidly than can adults. Their overall rate of swimming is however low. When a brood is being chased by boat, or the birds are surprised on the shore, the young may skitter, as a group, over the water. In this way they can make good speed and can keep up with their mother. They maintain almost an upright position during skittering and only a small part of them is below the water. I am not sure if they use their wings.

Downies are very curious about objects just above their heads. An object part way up a reed stem would presumably attract their attention, for weed on the netting of an experimental enclosure often attracted attention. To reach it they would either rise up almost vertically towards it, or would even (paddling with their feet) jump up in the air in an attempt to snatch it. As Phillips (1925) writes "they can leap from the ground or water to a height of eight to twelve inches by the power of their legs alone." They are very persistent on such occasions, and failing to get it will subside onto the water and Tail Wag.

WalkingAdults

Adult diving ducks seldom have occasion to walk on dry land. A female may lead her brood overland in which case she has a very waddling gait with the head drawn quite far back and down. In winter, pairs (especially drakes) may haul out on log booms, or on rocks, but groups of birds do this less often. As the ice melts off a lake, drakes haul out on the ice for short periods between periods of defence of the expanding area of water that they have staked as territory. Both leaving the water and re-entering it are slow, leisured movements appearing to require very little effort. These actions are almost invariably followed by the Tail Wag.

Downies

The first act of the downy is to climb up the side of the nest cavity (an action for which it is well fitted as it has sharp claws). They tumble from the nest, as described later, and very often have to walk a considerable distance over dry land to a lake or slough. They are however very strong on their feet when they leave the nest and walk in a rather erect manner, following the female (who is calling).

FIGURE 1

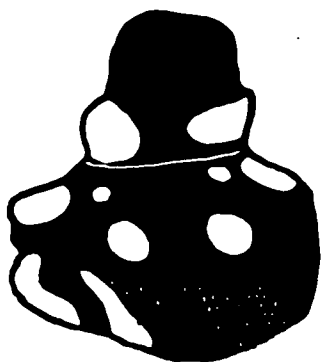
B.islandica (B.C. population)

THREE STUDIES OF DOWNIES

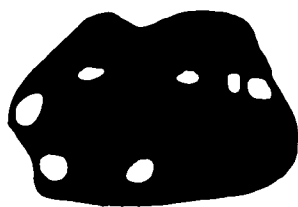
From a film by M.T.Myres

- A. Rear View. Floating. Shows the puffed out shape of the white cheeks, and the two round white "guiding marks" on either side of the rump. Further forward there are two smaller white spots on the wings. These marks are conspicuous and also lined up on each other as seen from behind. They are probably visible even on dark nights.
- B. Rear View about to Dive. Head down (below the water, in the Looking for Food pose) at the beginning of a dive. Back and rump humped up, and "guiding marks" visible.
- C. Side-Scratching. The head is being pushed back and forth along the side of the body. The right leg is braced and above the surface of the water, in a similar position to that in the Flap Paddle, which this view of the legs closely resembles.

A.



B.



C.



M.T.M.

COMFORT MOVEMENTS

It is not intended to give more than a brief outline of those body movements which are concerned with the maintenance of a satisfactory resting state in ducks. Feeding and Drinking are included here, on the grounds that thirst and hunger are to be considered unsatisfactory and uncomfortable states of body condition. True Comfort Movements may be divided into (1) Muscle-relieving (or Stretching and Shaking Movements), and (2) Scratching and Preening Movements.

A number of aspects of comfort movements are worth consideration at this stage. The first is that while certain of them have developed a second, ritualised form, others appear to occur as displacement activities, and yet others are performed most frequently and most actively on occasions when groups of birds (migrating or winter flocks, or courting parties) are as a whole in a highly excited state. Ritualised comfort movements in golden-eye are the Water Flip (Drinking), Head-Flick, Upwards-Stretch + Wing-Flap + Tail Wag at the end of a sequence, and the Wing- and Leg-Stretch. The Water-Flick may be a displacement activity. Splash-Bathing is an activity which is expressive of high social stimulation in courting parties. It is an activity which regularly follows coition, in the female immediately, in the male at the end of Post-coition Steaming. It is also performed (with other types of preening) after a long or a fierce aggressive encounter on territory.

The second aspect of comfort movements is the localisation of preening. The whole body is, of course, a surface continuum, and since almost all

preening is performed by the bill there is but one centre for the activity to originate, or in other words the various regions of the body bear a certain spatial relationship to the head region, and to the accessibility of them to the bill. We may think of the surface of the body as consisting of a series of overlapping fields of stronger preening orientation and of the bird of having a general idea of where it desires to preen. The physical difference between contact of the bill with one part of the body, and with another lies in the differences in tonus in the various muscles that are involved in bending and twisting the head and neck so that the bill comes in contact with one region rather than the other. Thus preening of the lower breast forwards differs from preening of the upper breast and neck only in the curvature of the breast (and amount of leg paddling), the degree of arching of the neck and articulation of the head forwards, and in the amplitude of the movement of the head up or down, or from side to side, on the spinal column. Thus many of the various types of preening to which names have been given are mere abstractions which have been used to indicate which part of the body is receiving attention, and the descriptions are really only of the contortions the bird goes through to reach them. Again ear-scratching and scratching of the neck are distinguished merely by the relative bowing of the head to the side and the amount of lift of the foot.

When a comfort movement acquires epigamic signal value, however, the movement becomes stereotyped both in form and in timing. There is a movement in the display of the scoters which greatly resembles the scooping motion that occurs when the upper part of the breast is being preened. But

nibbling as a preening movement requires very rapid and continuous movement. There would seem to be no way in which it could become recognisably different (as a display) without its losing its functional effectiveness. On the other hand, the Water-Flip of goldeneye is very similar to the Drinking movement, so alike indeed that I have confused them in the field. But the movement is a rigid one, with only slight variations in intensity, and the distinguishing marks are to be found in the more rapid lift of the head, and in the tendency to frequent repetition, which there is no reason to suppose is necessary in true drinking. I noted in the field one time that "The Elaborate Water Flip and the Stretching of the Wing and Leg in courtship have fixed lines of orientation and muscle tonus. They may occur in weak form, but the ratio of muscle tonus in one muscle to that in another should be the same provided the articulations are not themselves altered by the weakness of the movement...movements not yet fully ritualised would show a lack of 'place-to-preen' localisation, or directed orientation of the movement". The Wing-and Leg-Stretch in the Pre-Coition Sequence appears to be a slower and more deliberate movement than in normal relief of wing tension.

Feeding

Diving ducks feed on the bottom of the lake, river or sea on which they are swimming, and thus differ basically from the feeding habits employed by the surface-feeding Anatini. However when goldeneye are swimming in very shallow water as they sometimes do along the tide-line, or around the margins of a slough they may feed merely by dipping their heads below

the water and stretching them down to the bottom (Looking for Food posture). But they do not up-end, and paddle with their feet violently, as the puddlers always do. The method of diving has already been discussed earlier, but Millais (1913) describes feeding on the bottom in B. clangula as follows:--

On reaching the bottom, it at once commenced to turn the stones over with the bill, and from under these, various water insects were found or caught as they attempted to escape. Sometimes it would find a small batch of young freshwater mussels, and these it would devour very quickly one after the other... all food was swallowed where it was found, and small pebbles and fairly large stones were pushed over in the search. Several times I saw the bird just move a flat stone. It would go all round it and try it from every point... In a lake the Golden-Eye will dive in perpendicular position, but in flowing water it dives in a slant against the stream or tideway... In still water the Golden-Eye often dives in circles to get to the bottom... bounce up to the surface like a cork immediately they cease to push-downwards with their feet.

Phillips (1925) believed that "nearly all food is swallowed before rising but no doubt an occasional tough bit is brought to the surface (as it often is with Scaup), readjusted in the bill, and rapidly bolted." A. Chapman (1889) has watched them 'chewing' small fish before swallowing." This refers to B. clangula but Phillips said that in B. islandica "crayfish are brought to the surface to be swallowed, but this is not so with the small shellfish" and Munro (1918) wrote that abrasion of the fore-head against stones while foraging for crayfish wore the feathers badly during the winter. Phillips (1925) described the Looking for Food posture as follows: "swim along with its head immersed looking beneath the surface preparatory to diving, just as we sometimes see grebes, loons and mergansers do."

Downies of B. islandica nearly always bring the food to the surface and generally have a considerable tussle with it before swallowing it. They frequently give the food a violent shaking sideways, resembling the Head-

Flick. The attempt to swallow often involved a continual jabbing at the food, resembling the Jabbing seen in B.clangula (at least) just prior to coition.

Drinking

This is an activity whose importance for a water bird it is not easy to gauge. Figure 2 illustrates Drinking in B.islandica. On this occasion a drake had been sitting out on a log. He was disturbed from this position and swam slowly away in shallow water. As he swam he made two Drinking movements (as illustrated) and then began feeding by lowering the head below the water in the Looking for Food position. The movement consists of a dip to the water with the bill, then raising the head until the beak points vertically upwards, and then lowering the head to the resting position again.

Generally only one or two Drinking movements will take place at any one time, i.e. drinking for a water bird can be spaced out very evenly. Exceptions to this will be during the migration, when a flock comes in to a lake to recuperate, and when the female comes off the nest, during the incubation period. One morning, when the temperature in the shade was nearing 80 degrees F., a female was observed to leave the nest. On her alighting on the water I began recording her activity on tape. The tape began "Water-Flip; Water-Flip (really drinking I think); Drinking" and I recorded six more Drinking movements in the next minute or two. Clearly the temperature inside the nesting box had been very high and the bird had become thirsty. In 1955, an experimental group of downies of B.islandica

were put on the lake, for the first time in their lives, after being held captive over-night: "When first put into the water all first indulged in Drinking. This is a dab to the water followed by a rapid jerk back and up of the head into a position immediately over the base of the neck, but the beak just above the horizontal. In the movement the body is first tipped forward slightly, as the neck is dipped, and then raised so that it bobs as in the adult. At the fuller extension of the head the head may be dropped a fraction."

It will be noticed how great is the resemblance of Drinking to the Water-Flip (illustrated for B. clangula in Figure 31), which is an important element of the pre-coition behaviour. It should be noticed how much slower true Drinking is than the courtship display (44 frames instead of 29) and that in Drinking the neck is not elevated so far.

It is as much in the occurrence of Drinking, as in its form and rapidity of occurrence, that the movement is distinguished from the courtship display that clearly derives from it, and so very much resembles it. Drinking seldom occurs in bursts of more than one or two movements. The courtship display either takes on a very elaborate form, described later, or else is distinguished by the mere fact of rapid repetition.

Tail-Wag

The Tail Wag is a slow turning of the whole tail area from side to side, such as is seen in many Anatidae. It is not clear what tensions it relieves but it occurs in a great many contexts. The Upwards-Stretch (with or without the Wing-Flap) almost invariably ends with a Tail-Wag. It occurs by itself, on some occasions, and gives the impression, to an observer,

that the bird feels content, and is in no way fearful of anything in its present environment. I believe I have seen it performed spontaneously when goldeneye were loafing, neither feeding, preening or engrossed in any other action. It occurs at the end of many preening bouts. It also occurs, in both downies and adults, when both entering or leaving the water.

What the Tail-Wag really signifies is uncertain. It is a cosmopolitan movement which often comes at the end of a movement sequence, associated most commonly with the Upwards-Stretch and Wing-Flap. The tail may be spread during preening, and spread and oscillated sideways during coition, but in the Tail-Wag movement does not take place with the tail spread.

Head-Shake Complex

In the field I distinguished the Head-Shake movement from two others which might be included with it. Here I shall discuss all three together: Head-Shake (a true comfort movement), Water-Flick (partially ritualised?), and Head-Flick (fully ritualised). Whether they are in essence the same movement I am not at present sure.

- (1) The Head-Shake was used to describe the original comfort movement, as it occurs in the Upwards-Stretch movement (with or without the Wing-Flap), and at other times in the resting position on the water.

The comfort movement is a twist of the head from side to side in the air with beak pointing up or horizontal or down. It is discussed in the section on the Upwards-Stretch movement. It appears to start as a rolling shake from the shoulder region, which passes up the neck outwards to the base of the skull, until the skull is being rotated sideways on the neck.

The Head-Shake evidently has the function of shaking off some of the free water from the head, particularly from around the eye and from the nostrils, after diving. When an adult is feeding the occurrence of Head-Shakes between dives is enormously reduced.

- (2) Sometimes the beak is dipped in the water so that water is splashed sideways. This quite frequently occurs as a displacement activity, the Water-Flick, during the Laying Neck on Water (Threat) posture. The Water-Flick implies a flick of water (beak down) sideways rather than an upright or horizontal position of the beak. In the Water-Flick the beak starts almost entirely below water level, and with a violent sideways twist of the head on the neck, water is sprayed sideways in large drops.

Water-Flicks seem to indicate internal tensions as when they occur during the Threat attitude. In the downy the movement is seen most frequently when the little bird brings weed or an insect to the surface (as they frequently do). While worrying the food objects forwards (like Jabbing) the object is often seized and roughly shaken from side to side a few times, between bouts of nibbling.

A brood of six downies were watched in their first hour on the waters of the lake. "As soon as they reached open water the young began flicking their heads from right to left and vice-versa, but after about five minutes this became converted into true water flicking with much water flying sideways."

- (3) The Head-Flick is a single ritualised flick of the head once to each side occurring at the end of certain courtship displays: Head-Throw and

Head-Throw-Kick of B.clangula; Pseudo-Kick and Kick, and at intervals in Rotary Pumping between periods of Laying the Neck on the Water in B.islandica. Otherwise than this ritualised form it does not seem to differ from the other movements, though the beak does not contact the water.

The Water-Flick (sideways) should not be confused with the Water-Flip display (upwards), in which only the tip, of the whole beak, is dipped in the water, but no sideways turning of the head occurs.

Water-Dip Complex

- (1) There is a frequent movement, the Water-Dip, which does not appear to have any display significance, but equally does not seem to have any comfort movement value. The bird merely dips the tip of the beak into the water, holds it there a short while, and lifts it dripping from the water.
- (2) What the relationship of the Water-Dip to the Water-Flick (see under Head-Shake) is not known, unless it be a Water-Flick without the actual flick.
- (3) The Looking for Food posture, likewise, is a dipping of the beak, and usually the whole beak into the water. Is there any relation with the weaker, and more stereotyped Water-Dip.?
- (4) The last movement with similarities to the Water-Dip is the Jabbing which is found in B.clangula in the pre-coition sequence, and which downies employ to get food into a suitable position for swallowing.

Upwards-Stretch

This is the most frequent of all the stretching movements. It is a movement in which the breast and upper parts of the belly are raised clear of the water and the neck elongated upwards and forwards at an angle of around 70 degrees. In Figure 3 it is illustrated in B. clangula that the elongation of the neck is accompanied by a shaking movement which begins at the base of the neck, in the shoulder region (Frames 16-20), and travels, like a wave, distally with increasing amplitude, reaching the base of the crest in Frame 20. Water is seen to fly off the neck during the shaking. As soon as the shaking reaches the head the first, and weakest, turn of the head takes place. The head had been directed horizontally, but the beak tip is now raised and there are (in this sequence) four Head-Shaking movements, each of which only lasts 2 frames (1/12th second). The feet are paddled in order to enable the bird to retain its upright position.

In the early part of the movement there is a resemblance to the initial stages of the Head-Throw or Head-Throw-Kick, but as the beak is held horizontal there is no resemblance to the Masthead posture. While the head is flicked during the Upwards-Shake, there is not a Head-Flick at the end of the movement as there is in the Head-Throw. Maybe, if there is any relationship at all, the Head-Flicks have been reduced and deferred to the end of the whole movement in the Head-Throw.

The Upwards-Stretch may occasionally occur without any Head-Shake but this was not certain.

Wing-Flap

This frequent comfort movement, only takes place when the body is lifted in the Upwards-Stretch position, but does not always accompany the preceding movement. An interesting analysis remains to be done on the dynamics of the movement, particularly its closing portions.

Wing-Flapping in the downy of B.islandica is illustrated in Figure 4. As the chest is raised off the water the wings are lifted back. The first stroke of the wings takes 3 frames (as opposed to 1 frame in later wing strokes). The effect of the first wing stroke and subsequent lift back of the wing is to raise the body even higher, and the lower part of the belly is lifted off the water. During the second wing-stroke the head drops forwards again, rather as it appears to do after the final beat in adults, of other species than goldeneyes. After the third (and final) stroke of the wings the belly collapses onto the water as the wings are lifted back again. The wing is lifted especially high and forwards towards the head before folding.

In downies the head was drawn back (and ? up), wings lifted, and the feet paddling. Possibly the feet stop paddling, when the body is raised, for they appear to start paddling again as the body subsides onto the water. Within a few minutes of entering the water, for the first time, downies were accompanying the Upwards-Stretch by flapping their tiny wings. The movement was not seen until the young had Splash-Bathed or done Flap Paddle Diving, and it followed closely upon their surfacing from these activities. Probably the direct presence of water on the down, or on feathers, is a stimulus to this shaking activity. However, not every dive was followed by

the Upwards-Stretch and Wing-Flap. One individual came up quite entangled in green alga and had a struggle to free himself.

The Upwards-Stretch, Head-Shake and Wing-Flap are one of the commonest forms of comfort movement. To a great extent they occur in situations of his social stimulation, and, with other preening, are found after border encounters. The signal function may be said to be one of appeasement, for the "end of sequence" aspect of their use together is very noticeable. It is most usually the loser of an aggressive encounter in a courting party or on the boundary of a territory that performs the Upwards-Stretch + Head-Shake + Wing-Flap first of all. Almost immediately afterwards the winning bird does them, and the two birds then appear to ignore each other once more. Upwards-Stretch + Wing-Flap occurs at the end of Splash-Bathing.

Bernhardt (1940) discusses the wing flapping which is so common during the early spring and summer: —

especially after diving, as if they were shaking the water out of their feathers, an act which they, as diving ducks, have no need of, and which also they do not usually perform. The drake practices this wing-flapping more often than the duck. Whether he always turns his back, in order to show off his contrasty upper surface, I can not say. I have not interpreted this rising on the water as impressive behaviour, and it is not directly connected with mating, but seems to be more an expression of general excitement and "nervousness", a state experienced by the ducks at this time. Bright colours would have little meaning in the female.

Wing- and Leg-Stretch

This is occasionally seen, but (like false drinking = Water-Flip) only becomes noticeable when in the ritualised display form (Figure 30). The bird lies on its side and stretches the wing out behind it, lifting the leg out of the water at the same time. It is possible that this muscle-relieving

movement may be seen most often in females during intervals on the lake during the incubation period. Downies were seen lying partially sideways in the water stretching their legs out behind them--with the toes expanded (about 13 days old).

Yawning

This is the last of the muscle-relieving comfort movements. I have not recorded it in adults though I believe I may have seen it even in them. In downies it is not infrequent, as they sit out on a log, or idle on the water. I have described it in Stage 2 downies. The head is held into the shoulders, beak at 45 degrees and the beak is opened and closed, as in nibbling. Possibly it has threat signal function in downies, as it appears to have (a similar motion at least, with beak open and head held back at an angle, neck into shoulders) in the "Gesture of Repulsion" of the female Mallard (Anas platyrhynchos).

Ear Scratching

This, as discussed earlier, is a name for any scratching movement by the leg which is aimed at the head region, whether it actually relieves the neck, ear region, or face region. The body is turned slightly over and one leg is raised above water level to scratch the side of the face. The head is slightly turned over towards that side. It is a fairly frequent movement on all occasions, but does not appear to be commoner under conditions of excitement. The early stage downy frequently rolls right over sideways during Ear Scratching -- being too light of body to have complete balance control until it has grown a little more.

Forward Preening

In this form of preening the head is depressed forwards and the beak slides sideways, from one side to the other. As the feathers point downwards and cannot be parted, as they can on the back by manipulation, the beak performs violent nibbling movements, and the contact of the mandibles can be heard as a slight rattling noise on some occasions. The front of the body is often lifted off the water by means of paddling with the feet as in the Upwards-Stretch (tail often raised?). In the downy the movement seemed to take the form of 2-3 runs of the beak vertically downwards through the plumage before the body subsides into the water again.

Sideways Preening

This may develop out of preening or nibbling on the shoulder region or on the flanks lateral to the wing. The bird shifts its weight over and lies on its side, the head bowed forwards and ventrally towards the belly. Often the tail is spread, and bent forwards ventrally. It may be preened. The main preening activity in this sideways position (which also occurs in the moments preceding the Wing-and Leg-Stretch) is that found in Forward Preening, namely jabs along the line of the feathers and nibbling. It is often interspersed with Water-Flicks or Water-Dips. In the downy (see Figure 1C) the leg is braced and flapped above the water, on the side opposite that being preened

Back-Preening and Head-Rolling

These are performed while the bird is in the resting position. It includes preening, or nibbling, on the shoulder regions and preening behind, or under (in front of), the wing when raised to enable this. It is a very

common activity. The theory of "fields" has been discussed in the introduction to this section, and applies to preening on the back, around the wings and on the shoulder regions. Head-Rolling, i.e. a dip to the water (Water-Dip -- the static pose which is often seen and resembles the Water-Flick without the flick), followed by rolling the head on the wings, or rump is probably part of the same motor pattern. This also includes dipping to the oil gland. Head-Rolling is seen in Figure 5. Nothing more will be said about this form of preening until film analyses have been made of the actual movements, as has been partly done for Splash-Bathing. Boase thought Head-Rolling had display value. He wrote:

The Goldeneye also uses what may be a form of preening pretence, where both male and female may rub the sides of the head on the plumage of the back, behaving excitedly--in one instance the male began and the female immediately copied.

Splash-Bathing

This is an important activity, both as a comfort movement, and also as expressing social excitement. I have seen a flock of eighty B.islandica (nearly all drakes) on Lost Lagoon in Stanley Park, Vancouver in early fall perform this activity (with preening) in unison for some minutes, then turn over to feeding, and then all turn back to Splash-Bathing. Splash-Bathing also occurs (often as the first activity) after an aggressive encounter. It occurs invariably following post-coition Steaming in the male, and after coition in the female.

The front of the body and the head are alternately dipped and raised throwing water along the back and causing an undulating movement of the body. A Wing-Flap follows the activity.

A film sequence of Splash-Bathing in B. clangula is seen in Figures 5 and 6. In Figure 5 (see explanations) the movement starts as a Water-Dip, or weak Water-Plunge, at the end of which, while the head is still under water, the head is flicked (Frames 14-16) from side to side. Head-Rolling follows. The head is turned over sideways and then drawn backwards. The crest is then lifted off the back and the beak swung forwards (lateral motion) and then lowered and drawn back again. In Figure 6 the Head-Rolling is not repeated, but the Water-Plunges become increasingly violent. Each still ends with a Head-Flick (Frames 58-60). The tail is raised, and in Frames 67-68 the body is thoroughly arched, as the bird were going to make a deep dive. By Frames 73-79, the third part of this action Wing-Shimmering has begun, and is continued a considerable time before next plunge begins. While Wing-Shimmering the head and tail are held up and only the wings are moving. The whole sequence may be repeated over and over again.

Thigmotaxis

Other than Sleep, only one other Comfort movement remains. This is the tendency for downies to proximate themselves. In adults the only signs of this activity would be in brooding the downies, and in gregariousness in fall flocks.

Just after birth when the downy has dried off there is a nuzzling into the crevices of the human hand, but this is lost some hours (?) after hatching. Certainly for the first few nights after they reach the water the female appears ^{to} brood the downies (Mary F. Jackson, pers. comm.), and this sort of contact would seem to be sought after.

An interesting observation was made on some downies 17 days old. The female and 7 of 9 young left a log on which they had been resting and entered the water. The two left on the log had formerly been separated by one duckling. One of the two remaining got up, reversed and sat down again a little closer to the other but not in contact. Shortly afterwards it again got up, reversed again and sat down in contact with its neighbour and now facing in the same direction.

FIGURE 2.

B.islandica (B.C. population)

DRINKING

From a film by M.T.Myres

Frames 1-16 Dip to the Water
Frames 17-26 Raising of the head to a vertical position--
neck not elongated.
Frames 27-33 Head passed forwards and beak depressed
Frames 34-37 Head drawn back into shoulder
Frame 44 Resting position

24 frames/second. Shutter speed 1/48th second.

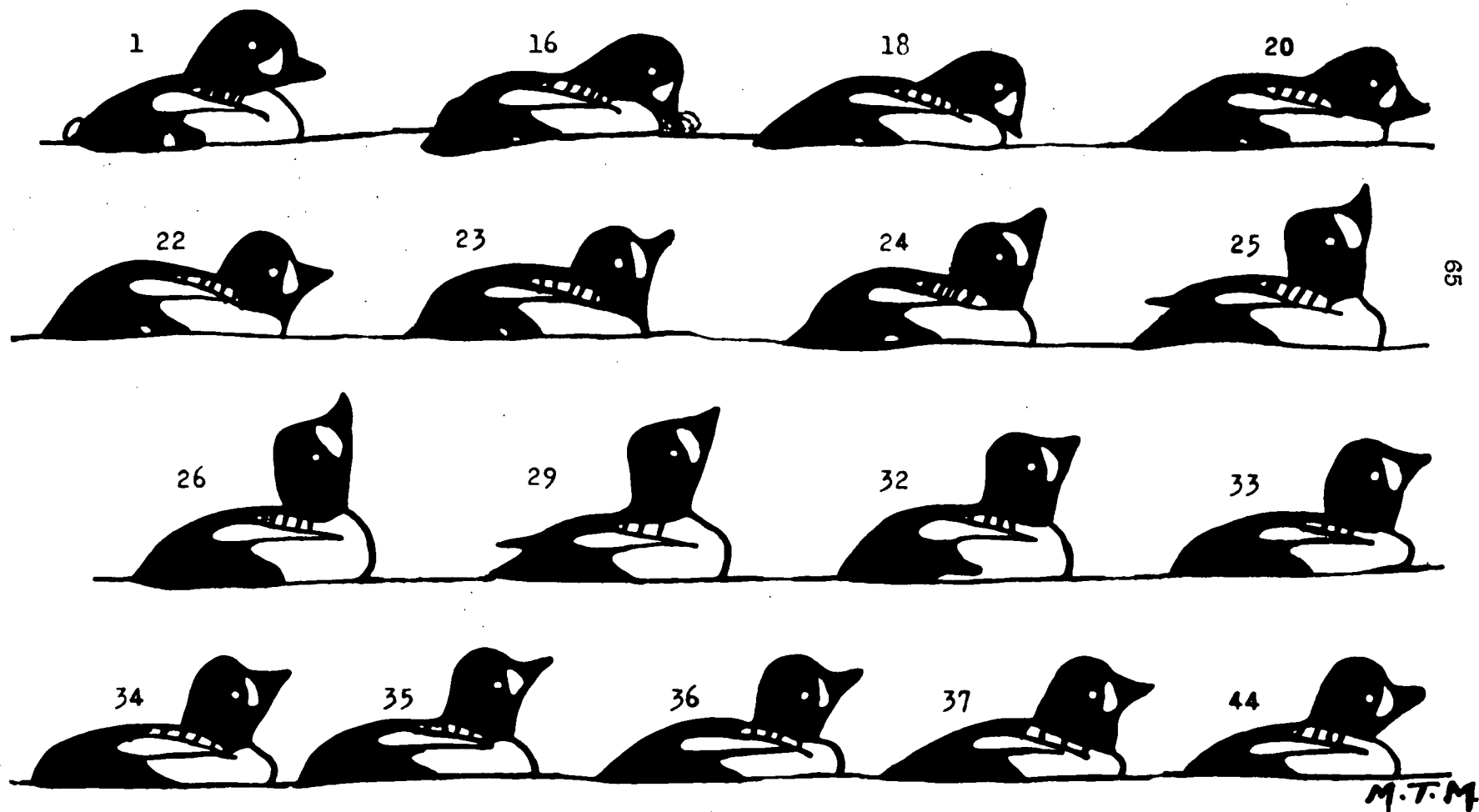


FIGURE 3.

B. clangula (American population)

UPWARDS-STRETCH

From a film by Charles Walcott and Benjamin Dane

It can be seen that the turning of the head begins in the shoulder region (Frames 16-20) and travels distally. It appears as a swelling at the shoulder in Frame 17 which reaches the crest feathers in Frame 20. The first, and weakest, turn of the head begins in Frame 21 (to the left). Its complement to the right is in Frame 22.

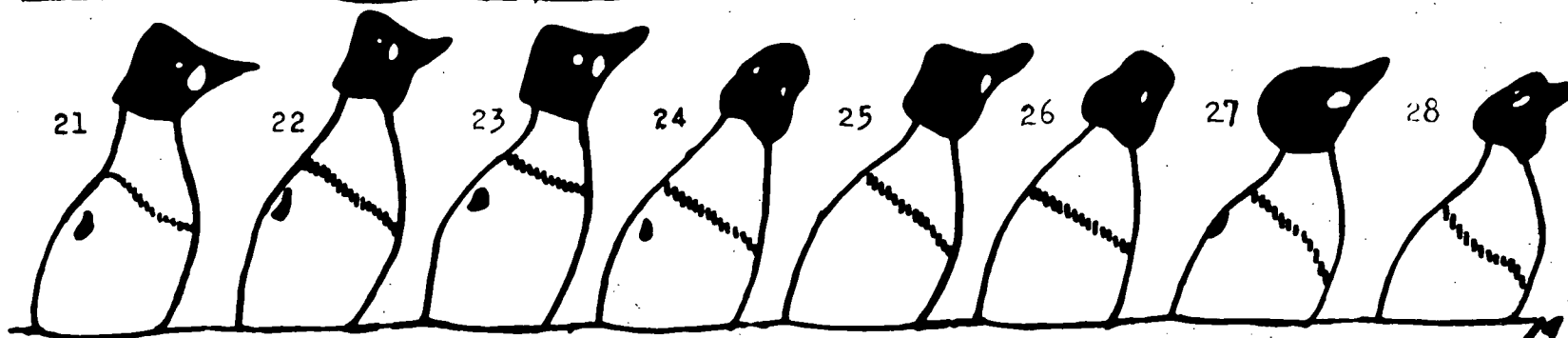
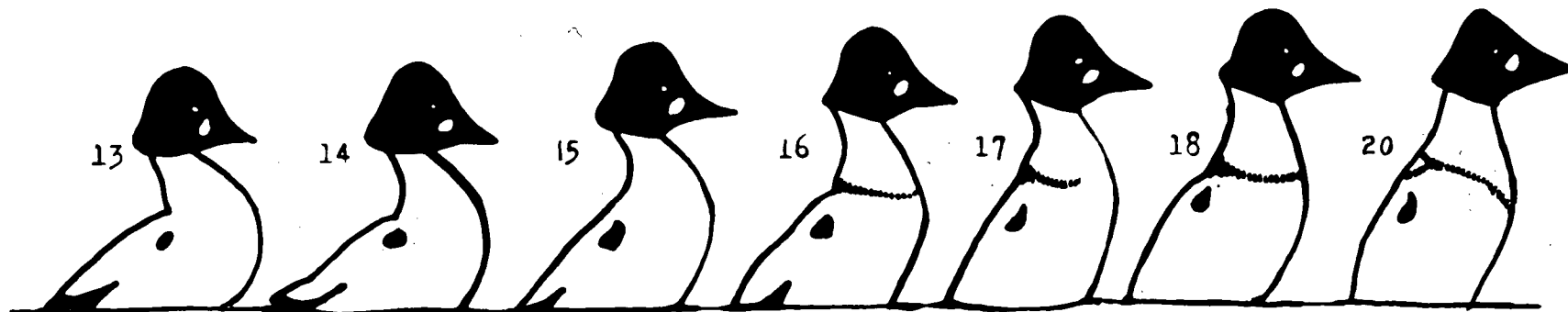
Turn 2	Lt--Frame 23;	Rt--Frame 24
Turn 3	Lt--Frame 25;	Rt--Frame 26
Turn 4	Lt--Frame 27;	Rt--Frame 28

The early part of the movement (Frames 7-15) bears some resemblance to the initial stages of the Head-Throw-Kick, but does not resemble the Masthead as the beak is held horizontal.

There is no Head-Flick at the end of the movement.

The Paddling which occurs with the feet, to support the upright posture, is not visible in the drawings.

24 frames/second. Shutter speed 1/48th second.



M.T.M.

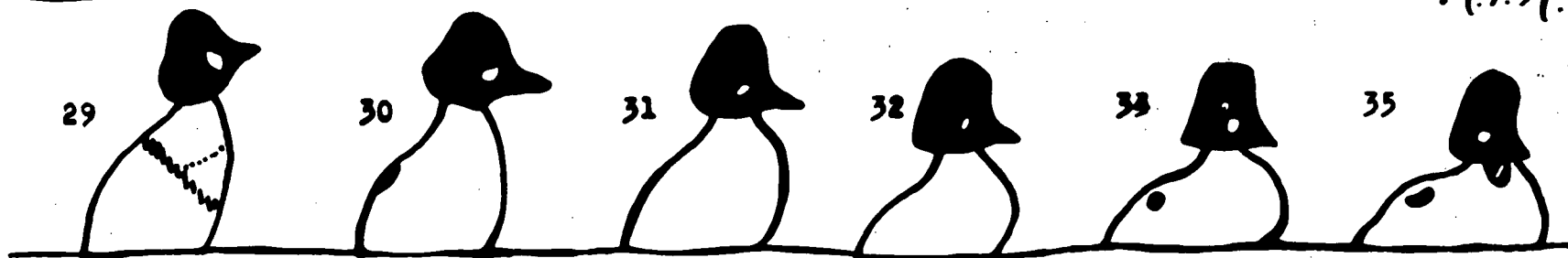


FIGURE 4.

B.islandica (B.C. population)

UPWARDS-STRETCH AND WING-FLAPPING IN THE DOWNY

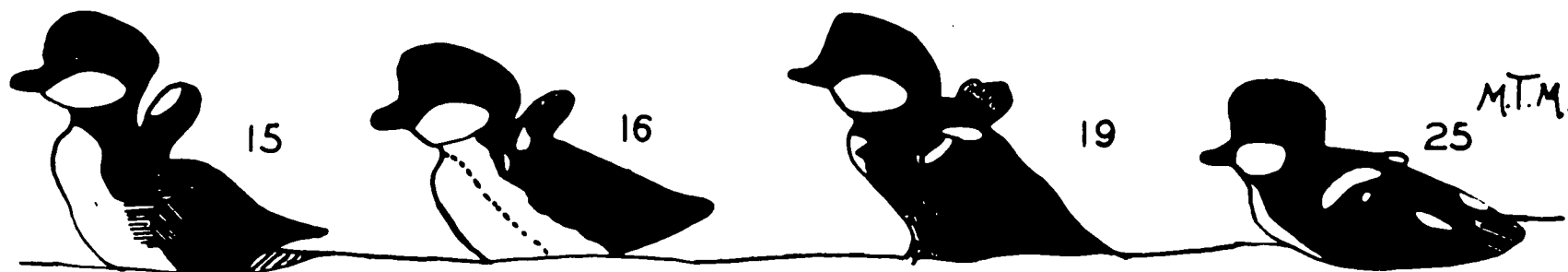
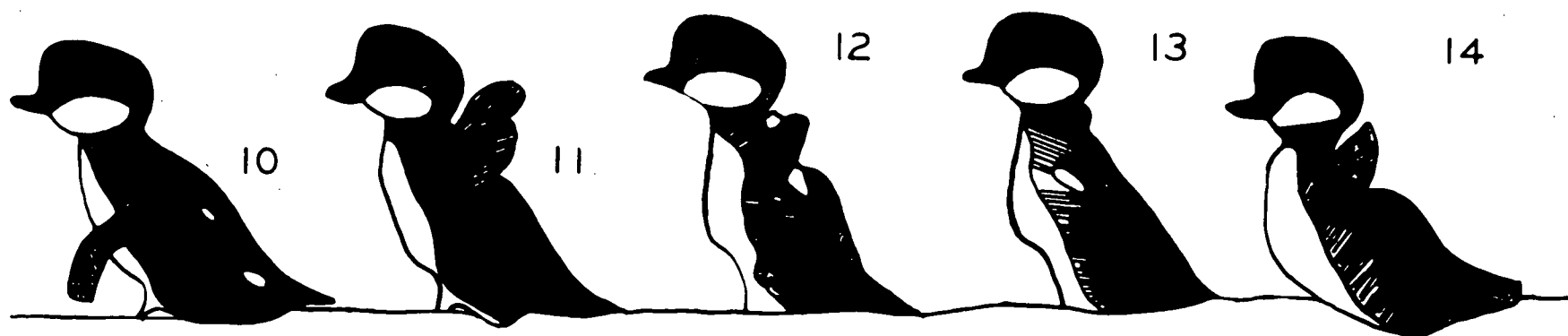
From a film by M.T.Myres

Three beats of the Wings.

- Frames 1-5 As chest is lifted wings are lifted back, and then--
 Frames 6-8 Wing Stroke 1. At the end of the first beat and the lift for the second the lower part of the belly comes away from the water.
- Frame 9 Wings lifted back.
 Frame 10 Wing Stroke 2. A hard down stroke. Head drops forward again a little.
- Frames 11-12 Wings lifted back.
 Frames 11-13 Head goes back again until almost vertically standing.
 Frame 13 Wing Stroke 3.
 Frame 14 As wings are lifted again the bird's belly drops suddenly as it collapses onto the water belly first.
- Frames 14-28 Collapse onto the water. Wings shuffled.

N.B. Note how wing is lifted sharply in Frame 14 as in Bufflehead (B.albeola) courtship, as it has to be for the base of the humerus to be in the folding position.

Shutter speed ?



FIGURES 5 & 6.

B. clangula (American population)

SPLASH-BATHING

From a film by Charles Walcott and Benjamin Dane

This comfort movement often has social signal effect. It may be broken into three stages (of which the last is not illustrated): —

FIGURE 5. Stage 1. Dip to the Water and Head-Rolling on Shoulder.

FIGURE 6. Stage 2. Water-Plunging.

Stage 3. ----- Wing-Shimmering (not illustrated.)

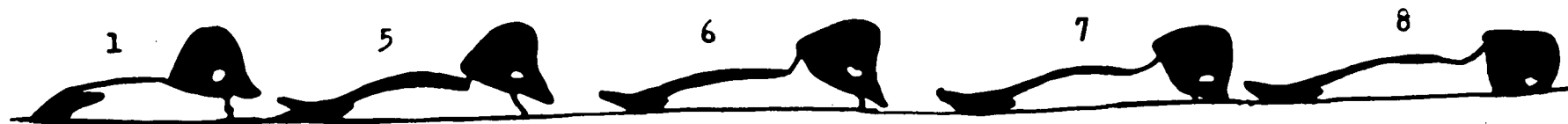
These three stages occur as one, and Stage 3 is followed again by Stage 1, after a brief pause in the Normal resting position. In any one instance of Splash-Bathing the three stages may be repeated as many as two dozen times over.

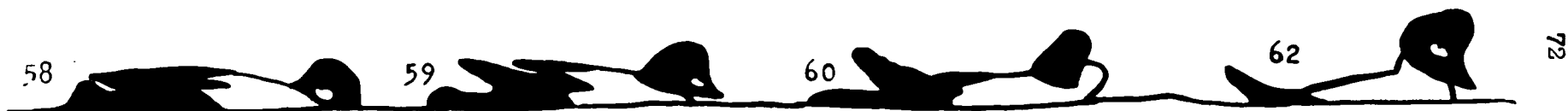
Figure 5. Frames 1-13 The dip of the head to the water
 Frames 14-16 The head is turned sideways while still under water and is then directed forwards again.
 Frames 20-37 Head-Rolling. The head is turned over sideways and then drawn backwards. The crest is then lifted off the back and the beak swung forwards (lateral motion) and then lowered and drawn back again. During the lateral motion forwards it may be laid down flat again (as in Frame 34).

Figure 6. Frames 41-60 First Water-Plunge (with Head-Flick in Frames 58-60).
 Frames 62-77 Second Water-Plunge (possibly with Wing-Shimmering beginning in Frames 72-77).
 Frame 78 + Third Water-Plunge (start of).

Wing-Shimmering thus does not develop until there have been a number of Water-Plunges (without Head-Rolling, which precedes the deeper plunges). Wing-Shimmering occurs in a pause between plunges. The body is sunken, with head and tail raised, and the back and wings lowered (as in Frames 77 and 78). The wings are then shimmered in and out sideways in the water a number of times. Head-Rolling precedes Plunging and is itself preceded by a weak Plunge or Water-Dip (the rear of the body is humped up--Frame 11--as in Plunging). The first plunges have less amplitude than the more rapidly performed later ones).

? 24 frames/second and Shutter Speed of 1/48th second.





M.F.M.

THE GOLDENEYES
SOCIAL BEHAVIOUR

1. Agonistic Behaviour
2. Courting Displays
3. The Coition Sequence
4. The Brood
5. Interspecific Behaviour
6. Summary of Similarities between B.islandica and B.clangula.

AGONISTIC BEHAVIOUR

I have more notes on conflict situations between males, than on courtship. This is because the repertoire of movements is limited in true goldeneyes, making the actual locomotory performance easy to describe. In courtship the opposite is true, the variety of movements is great and the spatial movements circumscribed.

This section is divided into two parts: Intra-specific and Inter-specific agonistic behaviour. The latter is included here, not because the movements and postures are different, but for the light that some of the Inter-specific aggressive activities throw on the nature of territory in goldeneyes.

INTRA-SPECIFIC AGONISTIC BEHAVIOUR BETWEEN MALES

The term "agonistic" is a useful one since it covers postures and movements which derive from both attack and fleeing drives, and all the intergrades between them. It is possible that the currently accepted notion that all actions expressing incompatible social relations are the motor response of one of other of two opposing "drives", may be wrong, and that there are other motivations responsible for some hostile or avoidance behaviour. Certainly, without proper experimental work, it would be rash to label all such behaviour as due to attack and escape tendencies only.

Scott and Fredericson (1951) wrote:

When fighting behavior is analyzed, it is found to be one of several patterns of behavior which may provide some measure of adjustment when two organisms come into conflict. Other common and closely related alternate patterns are escape behavior, defensive behavior, and passivity. It is

difficult to consider any of these without the others, and it is with this general group of behavioral adjustments, which may be given the name "agonistic behavior", that this paper is concerned.

Passivity in particular is not readily labelled. The motivation of a passive animal certainly need be neither aggressive nor the desire to escape. Yet appeasement postures (of which the resting position by itself could be one) do tend to prevent an attack from being made without any loss of position being necessary. Indeed the second party to a hostile encounter may avert the threatening actions of the first party in two hostile ways: assumption of the threat attitude also, or an appeasement action. The assumption of an appeasement posture may quite well be a fixed motor response to the sign stimulus of the threat posture. It would be a rash man who would say that any particular appeasement posture is necessarily motivated by the escape drive, or is a displacement activity from another field which has or has not yet been ritualised in a conflict situation, rather than that it is motivated by aggressive tendencies.

Diving ducks are particularly interesting, for their agonistic behaviour is rather different from that of other animals. This is due to the peculiar nature of their territory, and to their powers of diving. In cases of terrestrial territories an attacker can be observed all the time as he approaches the victim (unless he has some means of hiding his approach by choosing his route to effect invisibility). In the goldeneyes (which have territories covering a water area) attacks, from any distance, are invariably made from below the water surface, although occasionally a bird on the water is attacked from the air. Underwater attacks can only be avoided therefore by observing the behaviour of the attacker, while he is still

some distance from the victim. Furthermore if the victim does not see the attacker at a distance, he is not aware of the attack until the moment of actual body contact. I have seen a Ruddy Duck (Oxyura jamaicensis) almost turned over on her back by an attacking drake of B.islandica. Thus in aggressive actions the diving ducks differ fundamentally from the surface-feeding Anatini.

Aggressive actions on the breeding grounds take a number of tactical forms: —

(1) the male maintains the Threat posture at some distance from the boundary of the territory. Often the male assumes the aggressive posture even when no individual intruders are actually visible,

(2) one male has an initial advantage from a distance e.g. over an intruder who has flown in, or other wise come some way inside a territory-- in which case signs of impending attack, by the territory owner, result in the intruder flying out of the area,

(3) the owner-male again has the initial advantage and the intruder retreats by swimming, or more rarely diving,

(4) there are times when a male in the Threat posture is making dives which look aggressive near a pair of birds on the borders on his territory, but is content not to direct these dives in fact at them (although it looks as though he may be directing an attack at them each time). The male, in these cases, always surfaces about as far away, from them, as he was when he submerged. He is merely circling about them. The pair, surprisingly, often seem to ignore this behaviour, and he does not actually attack them,

(5) both individuals are close to a territorial boundary and both in the Threat posture, and both evidently certain of their claims. Immediate retreat is rare, and a fight generally occurs.

In what follows there will be a discussion of the intention postures of aggression (Crouch and Laying Neck on Water), the mode of attack and fighting, a surreptitious posture of encroachment, and a position indicating a state of increased awareness, or "alarm" (Expectancy Look). The postures indicating aggressive motivation appear to derive from intention movements of diving. They are therefore fundamentally different from the aggressive acts of the Anatini. Apparently the latter more resemble the Anserinae in their mode of combat, but this might be due to convergence and lack of the diving habit. The posture indicating alarm may be derived from the intention posture of flight (the opposite in form to intention diving). It resembles the neck-stretched, head-raised position assumed by all ducks and geese when "alarmed", and trying to get a better view of the environment, so that they may detect danger in time to make an escape by flying. On the other hand I have not analysed the actual take-off into the air from ~~like the~~ ^{the} film to discover the pose of the head at the beginning of flying. It might almost be suggested that since the "alarm" attitude can be maintained for a considerable time (both in goldeneye and in the "sentries" among a flock of geese) that this position is not directly related to the activity of flying, but is rather only the appetitive action of escape motivation, or even that it is merely an "external" comfort movement. Whether the "alarmed" position (expectancy Look) is, in its modern form at least, an intention posture of flying is

at least doubtful, for once body contact of the two contestants takes place escape by flying is unusual in the two goldeneyes (? in B.albeola).

Crouched Posture

The weakest form of aggressive motivation is expressed by the Crouch attitude. In B.islandica this resembles the Normal resting position, but the neck is not drawn into the shoulders so far and the head is lower, beak perhaps a little further forward. It resembles the "threat" posture of Aythya vallisneria (Hochbaum, 1944). From this posture the Laying Neck on Water (or full Threat posture) is often assumed as the bird has its aggressive motivation increased. A position resembling it is assumed between dives during feeding (a resting position between dives), when it is presumably occurring in its natural setting without any aggressive intent.

Brewster (1911) described this posture in B.clangula under the name "Crouching Posture". He also noticed that it was assumed prior to the "Wounded Duck Posture" as he called the Threat posture. He says "the head being thrust forward well above the surface, the neck deeply curved, back somewhat humped". I have noted that in B.islandica the tail is depressed, that there is a sharp angle down at the shoulders and that the head is held forward as though on a stick. This illustrates the distinction between the Crouch and the resting pose between feeding dives.

When an intruder appears, a territory owning male drops into this position or directly into the Laying Neck on Water position. The Crouched posture seems to be assumed quite often, even when no likely victims are within view, and the bird appears restless, turning around, eyeing the environment. The posture may be assumed in the presence of other species

e.g. Coots (Fulica americana) or scaup. If the male goldeneye swims towards them in this posture they tend to drift away from him.

It seems likely that the Crouch is the earliest intention posture of diving, which in A.vallisneria now has threat function, while in the goldeneyes the more extreme intention posture of diving has acquired the specific signal function of indicating the possibility of an underwater attack.

Towards the end of the time that drakes are on territory there is a marked lowering of their aggressive tendencies. This is indicated by an observation made on June 5th, 1955. A male B.islandica did not attack a pair of B.albeola which were feeding there. He only swam after them in a hunched position. He similarly evicted a pair of Eared Grebes (Colymbus nigricollis), simply by following them. Later the Buffleheads returned and tended to keep away from his approach. These birds turned their heads from side to side, and kept swimming ahead of the goldeneye, until he stopped and turned at what was evidently the boundary of his territory.

Laying Neck on Water (Threat Posture)

In this position the neck is thrust out ahead of the body and is lying on the water. The whole body is flattened and rather submerged. Brewster (1911) called this the "Wounded Duck Posture" in B. clangula. Munro (1939) also described it in B. clangula and noted that the bill points slightly upward so that the chin is raised above the surface. This is my experience in B. islandica, but evidently on occasions the lower mandible is lying on the surface (beak open), and the upper still pointing upwards. This is the situation when there is a ticking noise from the Laying Neck on Water forward position during Rotary Pumping in B. islandica. I am not sure whether this aspect of the pose is found exclusively then, or whether it also occurs during true Threat motivation. Brüggemann (1876) gives the earliest, and almost the fullest, account of this position in B. clangula. He refers to "territory", nearly 50 years before Elliot Howard (1920), though Altum (1868) had already discussed territory. Brüggemann wrote "Jeder Enterich dieser Species hat sein besonderes, genau begrenztes Gebiet auf dem Gewässer. Kein fremdes Männchen wird innerhalb dieses Bezirkes geduldet sondern bei seinem Erscheinen sofort verfolgt" (my italics). He says (in transl.) "It goes initially towards it menacingly, its neck stretched out horizontally like an angry gander, and dives suddenly under the surface." But he believed that boundaries (Grenze) are never crossed and that the owner turns about while under water, so as to get back into his own area. Meanwhile the invader has swum back into his own area, and may assume the threat posture. He did not think actual conflicts were common. Brooks

(1920) refers to "Chasing" and describes territorial boundary conflicts and attacks in B.islandica.

The posture is illustrated in Figure 7. When the motivation is really high the forepart of the body is placed so low that the beak is touching water, and only black shows along the neck and fore-part of the breast. In the less extreme form the black triangle or V on the shoulder comes down between the white flanks and the white feathering of the neck, either pinching them apart or completely dividing them. In Figure 1 there are also two impressions of the front view as seen by an intended victim. In the upper picture the aggressor is seen from some distance. The feathering of the back is still visible and the white windows form a prominent pattern on each side behind the head, a line of contrast leading away on each side. The first window is very prominent between the face plate and the white of the flanks. In the lower picture, seen also from water level, but very close-to, the angle of vision of the intruder which is taken up by the head of the aggressor male is much greater. The head appears enormous, the flanks and wings less striking, and the contour of the head breaks the contour of the back and rises above it. The beak will be more prominent than a black and white sketch can indicate. The white crescents on the face, lining the rear edge of the upper mandible (which reaches high up on the bridge of the skull between the eyes) are very prominent. The yellow iris, of a comparatively large eye, stares right out of the black sides of the head behind the white crescents, and the whole appearance is very "mask-like", and presumably intimidating. Though it has not been noticed in B.islandica Hochbaum (1944)

records that in Aythya vallisneria the pupil is contracted to a pin-point, during the Head-Throw of that species, so that the iris blazes out a rich vermillion colour. Possibly this same enlargement of colour may occur in the Threat of the goldeneye. The eye will in any case provide contrast, since the feathering of the head (the slope of the face) bears away at an angle of about 45 degrees. Possibly too the feathers behind the eye are raised providing a back-drop to the yellow eye. The eye may even be rotated forwards to increase the angle of binocular vision.

A territory owner may initiate an attack as far as 300 yards away from the victim. He makes a number of dives in the general direction of the intruder. The dives are not always in a straight line towards the intruder, but may shear off at an angle. Possibly differing views of the shore-line, behind the victim, may give the attacking bird an idea of the distance away that the intruder lies. It is noticeable that while in the Threat position, the attacker may swing his body one way and then the other, so that he is seeing the intruder in the monocular field. The final submergence, may be estimated^{at}, as beginning generally from 5-20 feet away, but on occasions from as far away as 30-40 feet. Often two drakes will do much hesitant diving, parallel to each other, without ever getting any closer to each other, or attacking each other.

The Attack

Brüggemann (1876) is quoted by Phillips (1925) as saying that actual battles do not occur. But Brüggemann did not actually write this. Heinrich (1911) remarked on the peculiar form of the attack in B. clangula saying (in transl.) "No other German duck has a similar method of attack. As a result its neighbours usually dash away terrorised, when they see the goldeneye attack them from below". Bernhardt, as late as 1940, believed that other species were not attacked by B. clangula except in captivity, but in light of experience with B. islandica this is very doubtful. Lilford (1895) is also reported as having described under-water attacks in goldeneye. Johnsgard (1955) describes how males attack one another from below both in B. clangula and B. albeola.

Bernhardt (1940) wrote of B. clangula: —

If another drake goldeneye approached, he flew over to the latter while he was still 60 m. away, swam up to him, dived, and attacked under water. Two goldeneye females, without males, that were in the vicinity, were driven away in a similar manner, when they came near the duck.

In my experience with B. islandica most diving attacks would appear to begin between 5 ft. and 20 ft. away from the intended victim. Closer than five feet the attacker will rush at the victim over the surface of the water as in a fight. The submergence for an attack is smooth and without splash. A moment later the attacker may come up head first under its victim, which will flap over the water, or may turn and dive, or aim head-first at the attacker. I once saw a Ruddy Duck (Oxyura jamaicensis) almost turned right over, on its back, by an attack. There are occasions when the victim changes his position (by swimming), between the time when

the aggressor dives and re-surfaces, but this does not necessarily prevent the aggressor from coming up right at the belly of the victim.

If the victim is outside his territory, and has not already flown or swum fastly away when the attacker surfaces he may, when contacted, flap over the water. Sometimes this takes him back onto his own territory, but at other times he traverses a smaller or larger arc, so that the two birds often arrive back on the spot where they started from. If the victim does not actually escape, or if he does and gets back onto territory he usually defends, a sudden reversal of roles may be seen, as the fleeing bird in a Flapping Chase (neck forwards at 45 degrees, and beating the wings against the water, as in the display of Oxyura jamaicensis) turns and goes beak first at its tormentor. These Flapping Chases are usual in an attack unless the bird flies away before being struck. The pursuing individual will continually alternate, as position on the territory changes, or as motivation changes of as one or other bird tires. The losing bird may get airborne, but does not often fly far, as one might expect. He is promptly attacked again. If both birds get airborne and one lands again almost at once, it dives and the other plunges into the water, from the air, after it. Sawyer (1928) illustrated aggressive encounters in B. islandica.

It is sometimes the case that the victim anticipates the attack to the extent that just as the aggressor is about to surface the victim turns and dives towards him. The two birds may meet head-on midway between the former positions on the water. In one case where this happened, the aggressor reappeared (no longer in aggressive pose) a moment after

diving, farther back than where he had submerged. Another time the male of a pair (which were being attacked) reappeared and swam back to his mate. It seems that the two birds met underwater or that the aggressor saw the intended victim coming for him under water and took evasive action.

As an attacker surfaced under him, a victim suddenly jumped right over the attacker, with a single flap of his wings. On another occasion a fight lasted nearly a minute. Both birds emerged from the splashing of water facing each other. The head of each was half raised (neither the normal low threat, or the fully head-raised position). Then one lunged at the other's head, and seemed to get a grip as the victim turned its head away.

In these fights I do not remember seeing a bird take flight, once a Flapping Chase had started. Clearly to take flight is the easiest form of escape, if the victim is an accidental intruder, and the Flapping Chase must be very energy-consuming. I think it probable that the Flapping Chase over the water requires a faster wing beat than that employed in the normal take-off. Hence the bird is not creating enough lift and cannot get off the water. Fights end either by the birds diving apart, or by one bird ceasing to chase the other. When this happens the loser drifts away a few feet, and quickly does the Upwards-Stretch ♦ Wing-Flap ♦ Head-Shake ♦ Tail Wag sequence. This is almost at once mimicked by the winner of the bout. This seems to have an appeasement signal value. It is a sign that the incident is closed. Munro (1939) writes that "usually after such a performance the male which had been the pursuer would stand upright and shake his wings, curving them forward in front of his body". He is

probably wrong in implying that the winner generally initiates this activity.

Sawyer (1928) described a fight in B.islandica: —

"a pitched-battle, breast to breast (two males); very loud splashing the only demonstration apparent, the water flying and both birds rising about clear of the surface two or three times; it (the contest) lasted about twenty seconds, then each (contestant) joined a waiting female (some yards away) and all four indulged in much head bobbing."

Munro (1939) wrote of an encounter in the same species "swimming rapidly towards each other and then meeting standing upright and striking with their wings."

I once recorded that an adult male charged one of the more persistent of three juvenile males (of B.islandica) which were doing the Kick a number of times at his mate whom he was pumping. The female was Jiving. The male, when he charged them, had the head held higher above the water than in the normal threat position and only opened the beak at the last moment.

On another occasion a courting pair were interrupted by an intruding male who chased the female (flapping) over the water. The female darted back and forth doing rapid submergences, and coming up facing another way, an interesting form of escape that I have not seen in males. Only after she had passed her "mate" about five times did he make a jab at the pursuing male, with his beak. Finally the female flew off with a third male. On another occasion mixed up motivations were likewise observed. A male was courting a female (Rotary Pumping + Threat), but then dove at her, and both flew into the middle of the lake. The male then returned to his territory. Most probably he already had a mate and was courting promiscuously, or mistook her identity.

If a female is nearby a fight ends in a Triumph Ceremony. If territory neighbours have been fighting, it is possible it may not matter if the male won or lost the encounter. A male was once seen to do Rotary Pumping after a fight although no female was in sight.

Surreptitious Encroachment

In Oxyurca jamaicensis (and ? in Anatini and Bucephala) I have seen a pose which resembles the aggressive pose, but which has a defensive motivation apparently, in part at least. It is the opposite extreme of the "alarmed" position, but might represent a state of intention escape by diving, rather than flight. This aspect of motivation remains to be analysed further.

Heinroth (1911) evidently saw this position in B. clangula for he wrote (in transl.) that "if anxious to escape observation without resorting to flight, they swim away rapidly with the head held forward, almost on a level with the water, and the body 'sunk' so that the tail is out of sight". Since he also described the "alarm" position and Threat, it is unlikely that he was confusing the above posture with the latter. Thus it seems that escape motivation, or intention, can be expressed in two ways, the one used when the bird is well-aware that it is under observation, the second used when the bird believes itself to be camouflaged, or otherwise unobserved.

In this crouched, or flattened posture, the bird is evidently attempting to make itself invisible. It assumed the posture when it appears that the bird knows that the area, in which it is, is in the territory of another bird. It evidently desires to stay there, but is aware that, if detected, it will be attacked. It is a conscious intruder, on the defensive, but with no intention of fleeing (at that moment). This is a very anthropomorphic concept, but human beings are often aware of behaving and thinking in this way; it might be regarded as a surreptitious encroachment, with the

intention of gain. Chances are strongly against success, and the individuals are aware that an attack, if provoked, will result in their being defeated. In goldeneye this situation of being forced to enter the territory of another bird does sometimes happen. In 1955 the first brood onto Sorensen Lake was defended by a particularly aggressive female. Two females were still incubating, however, in trees one on either side of the lake, within the brood territory of the aggressive bird. The two incubating females liked to land on the water in front of their nests, after feeding elsewhere, before flying up to fly to the nest itself. But they were always attacked. Unfortunately I did not record their behaviour, but a situation where surreptitious encroachment has advantages is illustrated by these incidents.

The form of motivation involved in this behaviour, has not so far as I know, been recognised in animals, though it would appear to occur in primates, and in the play of a number of mammals it forms a frequent element. There is no valid reason why birds should not be capable of this subtle type of offensive behaviour as well. Perhaps the dominant aggressive component is expressed by the flattened attitude, but the restlessness of the bird, turning from side to side, looking all around itself, and often taking shelter behind a snag or other part of the environment, suggests that the bird is aware that an attack is likely. If the attack comes, the bird will, I think, fly away.

When a duck is aware that an attack is immanent, and is more frightened than otherwise, it will go into the "alarmed" position with raised head.

Expectancy Look ("Alarmed" position)

The difference in circumstances between this pose and that assumed in the fore-going section probably lies in the "alarmed" bird, either being uncertain of the whereabouts of the aggressive bird (but knowing there is one), or being uncertain if an aggressive bird, which it can see, is going to press home an attack. In the case of the surreptitious encroachment the intruding bird does know where the territory owner is, but also knows that the territory owner is not yet showing signs of aggressive intent.

When "alarmed" goldeneye swim with the head held high, as when they are curious about man. The Expectancy Look is however seldom, if ever, seen in a border conflict between equals. Millais (1913) wrote: "If observant of danger at a distance and about to rise, the neck is straightened and the head held up high, with the crest somewhat raised." Phillips (1925) wrote "alarmed and swimming away from a danger-point the body is deep in the water, the tail dragging or submerged and the bird ready for an instantaneous dive or jump.

The "alarmed" head-raised position may not itself, be an intention movement of escape, since when actually struck from below, the victim seldom actually flies. Attacks are followed by Flapping over the water.

Attacks are instantaneous events. The victim may suddenly find himself being lifted out of the water by the beak of the attacker planted firmly in the middle of his undersides. Only the behaviour of the aggressive bird, at a distance, indicates his attentions. Sometimes the sight of him alone will make a potential victim fly away, sometimes his diving will be sufficient stimulus, sometimes the victim is sufficiently uncertain

that he will not fly until actually struck from below. In all three cases the bird may be in the head-raised position which is an indication of alarm or uncertainty but is possibly not, of itself, an intention of flying. One moment the bird is sitting on the water, next it is Flapping over the water (unless it decides to fly) before the attacker presses the attack home. The only true intention movement (such as one might find in a terrestrial bird or animal) is that of moving slowly (swimming) in a direction away from the aggressor. This indeed occurs when the victim is alarmed. It is a frequent accompaniment of the Expectancy Look. Here a true gradation from no movement through various speeds to fastest swimming rate possible is found. But there can be no intermediate between flying away and sitting on the water, for the doing of the one is a direct violation of the other. This distinction between intention flying and intention swimming or walking is important, for in the latter the intentions movements are weak forms of the movement itself.

The Expectancy Look is also a sign of curiosity, an increased awareness or sensitivity to the environment, and it is used sometimes when facing towards a disturbance, and even when swimming towards an object that is interesting the bird. A special case, that is of interest in the study of the motivation behind the Expectancy Look, is when the female has been temporarily parted from her brood. She assumes the Expectancy Look in searching for them, and here the movement expresses a desire to find something (the brood), and of going towards it, rather than away from it. The Expectancy Look is not, I assume, motivated by escape tendencies of a tendency to fly under these circumstances and this is why I prefer the

term, Expectancy Look, to intention escape or intention flying.

The Expectancy Look is assumed under conditions of alarm or curiosity. It enables a wider view of the environment to be obtained. It is natural that it should occur when a bird expects an attack upon it from below. Whether or not it is the intention movement of flying, as well, is not known, nor whether it can be regarded as an expression of escape tendencies. The pose is resembled, in ritualised form by the Head-Up and Head-Raised courtship postures of the two species of goldeneye.

INTER-SPECIFIC AGGRESSIVE BEHAVIOUR

Attacks by B.islandica on other species, as noted during my study in the Cariboo District of British Columbia are interesting for two reasons: —

- (1) Phylogenetic relationships of the victims, to B.islandica
- (2) Circumstances of the attacks, and the light such attacks may throw on territory in goldeneyes.

At this stage all that can be noted on the first score is that Mergini are frequently attacked, Aythiini are attacked fairly frequently, while Anatini have not been observed under attack, although six species breed on or around the lakes.

The following table is a summary of the species attacked: —

TABLE 1

Tribe	Species	No.of species breeding on lakes	Attacker (Sex)	Attacked (Sex, or young)
<u>Mergini</u>		2		
	<u>Bucephala clangula</u> (migrants)		M + F	M + F
	<u>Bucephala albeola</u>		M	M
	<u>Melanitta perspicillata</u> (migrants)		M	M
<u>Aythiini</u>		3		
	<u>Aythya americana</u>		F	M + F
	<u>Aythya affinis</u>		M	M
<u>Oxyurini</u>		1		
	<u>Oxyura jamaicensis</u>		M + F	F + y
<u>Anatini</u>	nil	6	-	-
<u>Miscel- laneous</u>				
	<u>Fulica americana</u>		M + F	y

Some extremely vehement attacks were made by drake goldeneye on other species while the mating territory was in existence. This was especially the case on a small slough where there were no other B.islandica territories. B.albeola and Oxyura jamaicensis (female) were seen to suffer violent and persistent attacks there. Except for the incident between B.islandica (female) and B.clangula which was only a case of momentary Threat as the ice was melting in 1955, the bird involved in all the other attacks by female B.islandica was the first one to bring off her brood on either lake in 1955 (first seen at the north end of Sorensen Lake on June 16). Her brood territory was a narrow strip of water at the tip of the lake, and included the water immediately in front of a natural goldeneye nest, and also in front of a nesting box (occupied by incubating females) on opposite shores of this part of the lake. She spent much time harrying the two females of her own species from these two nests, whenever they came off to feed, so that they had to fly half way down the lake to open water. She made it very difficult for them to return to their nests, and they were continually being chased in flight around the shores of the lake.

Below are more detailed accounts of the various interspecific encounters, by species: —

American Goldeneye (B.glangula)

This was only seen on migration in May, in small parties. Does not breed in the Cariboo District.

The encounter was on May 4th, 1955 on the lagoon of Westwick Lake, the day the ice was melting. About half a dozen pairs of B.islandica were sitting around on the ice or swimming at the edge of it. All were

highly irritable and as the stray migrating drake B.clangula landed on the water a drake B.islandica landed almost on top of him and both submerged. On re-emergence both flew. The drake B.islandica was seen in Threat posture a number of times more, but the B.clangula did not fly, or look apprehensive, until the B.islandica drake came up under him. The migrant merely fed during the brief intervals when he was undisturbed. A short while later the B.islandica drake deserted him to attack a pair of his own species. Clearly this period of the year is the most critical in the establishment of territory, as the water opens up and is occupied.

Bufflehead (B.albeola)

A few pairs breed on these lakes, and stay throughout the summer, but in May a larger number are around, apparently on territories which they later desert, and in courting parties. In 1955 courting parties were frequently seen but only one brood was brought to the lake. In 1956 two pairs remained on Sorensen Lake for almost a week and I thought they were going to establish themselves, but they disappeared.

On a small slough occupied by only one pair of goldeneye I was told that in 1954 a pair of Buffleheads had nested in a tree only a few yards from the nest of the goldeneye at the edge of the water (Mary F. Jackson, pers.comm.). Terrific fights were seen between the drakes of the two species. In 1955 only the goldeneye nested there. However on May 11th I observed a female Ruddy Duck being violently attacked. A pair of Bufflehead and a single Bufflehead drake were also present on this slough. The single drake Bufflehead became the object of aggression by the drake of B.islandica. When the goldeneye was some ten yards away the Bufflehead

would fly, and either escaped or landed somewhere else, but in one case when they landed the goldeneye was only five yards away. The latter then dove and the Bufflehead flew and again landed. Then the goldeneye flew and the Bufflehead swerved away across the slough--the pursuer landing near his female for awhile before renewing his attack.

On another occasion, two days later, on Sorensen Lake, a goldeneye attacked a Bufflehead under water; the latter did not fly as the bird came up (as a goldeneye would usually do), but was actually levered partly out of the water. The attacker then flapped his wings, and the Bufflehead about five feet away also did so. Then the goldeneye assumed the Head-Up position opening and closing the beak. The Bufflehead bathed and wing-flapped and the goldeneye dipped the head below the water and flicked it.

On May 17th, 1956 a drake goldeneye in full Threat dove and a juvenile male and a female Bufflehead flew. The attacker came up only a short distance towards them, however, immediately after they flew. It looked very much as though he saw them fly, from below, or that he was not intending an attack.

Surf Scoter (*Melanitta perspicillata*)

Seen only in small groups on migration at the end of May. These parties may stay, usually in the middle of the lake, for some days.

Two attacks on these scoters were seen. The first was a fight on the water followed by a dive, and the scoter flew (paddled over the water) on May 20th, 1955. The second occasion a drake goldeneye came up right underneath a drake scoter, which jumped away. The goldeneye remained on the

surface in a threatening posture only a foot or two away from it and another pair of scoters. It then swam slowly away and did the Upwards-Stretch movement without the Tail Wag.

Redhead (Aythya americana)

A breeding species, nesting in the marshes of Scirpus at the ends of, more sparsely along the sides of, the lakes. Apparently only weakly territorial, themselves, for groups of drakes and females are seen in the middle of the lake, all through the breeding season.

The female B.islandica on Sorenson Lake flew at a pair of Redhead on one occasion, dove and forced both Redheads to fly down the lake.

Lesser Scaup (Aythya affinis)

A very common breeding species in the area. Nests are found out in the grasslands. Like the Redhead appears weakly territorial.

A drake B.islandica started 100 yards away from a pair of scaup on June 11th, and making three dives towards them, came up under them three times in succession after he reached them. On the first two occasions the scaup merely moved a yard or two away over the water, but upon the attack being repeated a third time they flew away. After the first submarine attack the drake scaup stretched his neck up in an "expectancy look" pose. It is worth noting that at a distance a Lesser Scaup has the general form of B.islandica --- dark purple head and white flashy flanks.

Ruddy Duck (Oxyura jamaicensis)

This is one of the commonest ducks nesting at Westwick and Sorensen Lakes. It nests in the marshes, which are localised and only occur in any

depth near the inlet or outlet at the end of each lake. These marshy fringes are not the favoured stretches of water for goldeneye territories, which are most numerous along the parts of the lake fringed by grass-range. Nevertheless the Ruddy Duck frequently gets in the way of a goldeneye, and is in no way immune to attack from it.

Vicious attacks were made on a female on the small slough mentioned earlier (by the drake goldeneye mentioned in the section on B.albeola). A female Ruddy Duck (none nest on the slough) was forced to seek refuge among fallen logs just below the nest occupied by the female goldeneye. The male did not intensify his attacks, when she was this close to his nest, implying that it was the territory alone that counted and the nest had no extra valence for him. Later on the Ruddy Duck was seen out in the middle of the lake clearly in a very defensive posture, its body very compressed when on the surface, swinging round and keeping a sharp watch on the drake goldeneye while diving for food. In one part of a fight between them the Ruddy Duck was almost turned over backwards by the goldeneye.

In chases the drake goldeneye flew after the Ruddy Duck and landed where she dived, sometimes pivoting around as he landed, as though he knew which way she had travelled under the water.

On another occasion the female goldeneye at the NW end of Sorensen Lake did five dives or so from a considerable distance, with increasingly threatening crouches, towards a drake Ruddy Duck at the tip of the lake. At last he noticed, swam in towards the reeds and then dove. The female goldeneye remained nearby for a minute or two. Her young were scattered over the middle of this part of the lake.

On July 3rd a remarkable case of intolerance was watched from the female goldeneye having her territory at the north end of Sorensen Lake. This bird was also very intolerant of other duck as well as of other female goldeneye. Following an attack on a young Coot (see under that species) she was seen flapping over the water, flying and diving after a drake Ruddy Duck, with at least half a dozen encounters witnessed. The Ruddy Duck apparently got tired, as he did not fly after the first two or three encounters and flapped over the water with his wings. Later still a pair of Ruddy Ducks appeared from the reeds in attendance on one downy (apparently newly hatched). All three ducks swam along the edge of the reeds towards the north west end of the lake, accompanied by two or three other drakes who courted vigorously with the frothing-up-of-the-water movement. One drake performed the paddling-over-the-water act which often precedes or follows the "frothing" of the water. On this occasion the "paddling" occurred either before the "frothing" or quite separately, but not after "frothing".

An hour later the female goldeneye attacked the pair of Ruddy Ducks and routed them, "and then proceeded to keep the young Ruddy duckling under water (it dived in defence) for 1-2 minutes and seized it by its nape when ever she could. I did not see it again and it did not join its parents who finally fled to the reeds. Occasionally when the goldeneye had the duckling by its neck the female Ruddy rushed hunchbacked across the water at her, but seldom would have got that near, and the goldeneye would turn and jab at her and she and the male (who did little but accompany the female and do courting movements ("frothing")) most of the time would turn and flee from the goldeneye."

Doubtless had there been more than one downy in the Ruddy Duck brood, no death might have occurred, but as it was the attack of the goldeneye was

concentrated on one individual which was, be it noted, the downy not the adults.

Coot (Fulica americana)

On May 4, 1955, during one of its long dives towards a B. clangula a drake B. islandica was seen to come up under a Coot. On July 3rd, 1955 just before the incident with the Ruddy duckling mentioned above, the female nearly killed a two to three week old Coot.

"The duck was, I think, holding the young Coot below the water or else diving after it, for the duck was often almost, if not wholly submerged. The Coot then came to the surface and the goldeneye swam hard after it pecking at it or holding it. Her Stage 2 ducklings gathered round at this and did the nod greeting. The female duck left the Coot immobile on the surface after two or three minutes of harrying. The Coot was immobile for a couple of minutes as the ducks drifted away, and then raising its head from the crouched position swam rapidly into the reeds."

Discussion

The case of the goldeneye on the small slough attacking a female Ruddy Duck was of particular interest for periodically it would break off the fight for about five minutes, and then take up an aggressive pose again. This indicated not only that the whole slough was its territory, and that it tolerated no other diving duck in the area, but also that at highest intensity of stimulation (forced proximity to another duck even of another totally unlike species) an exhaustion of its reaction specific energy occurred, and its aggressive motivation was quickly exhausted every ten minutes or so, taking some five minutes to build up again to a point where an unlike species within its territory was an irritant again.

This is quite unlike the behaviour of a goldeneye on a larger lake, where the attacked bird can escape to another part of the lake. In this case the stimulus is quickly removed and the aggressive motivation quickly declines. On a slough this is not the case and it appears that the continued presence of the stimulus results in a much higher level of latent aggressive motivation, which apparently can ^{no} longer be expressed by the motor pathways after a certain time, resulting in a refractory period of some kind. For when a short rest has been had the aggressor once more rushes into the attack. Meanwhile the irritant has still been present and presumably acting upon the nervous system. One gets the impression that the motor path is quite easily exhausted. The nearest analogy, which is rather a good one perhaps, is of bouts in boxing. The fight is still on, but the desire to punch the other guy has to be controlled during the intermissions, and because of the frequent rest periods the fight can go

on much longer. Without them the contestants would become exhausted much sooner.

In Territorial birds of course there is no great advantage in attacking every bird in sight, and indeed though aggressive encounters on the borders of territories are frequent, each one seldom lasts any time as the loser swims or flies away. Thus a sudden and fierce exhibition of Threat or actual aggression is effective.

Evidently on small sloughs, however, where another duck is unable to escape to open water at all (and so requires considerable beating-up to be persuaded to fly off to another slough or a larger lake) there is a greater resistance to be overcome. When a goldeneye drake attempts in such cases to expel an intruder from a one-territory slough, the fairly rapid fatigue of the efferent path in the central nervous system results in sharp but brief bouts of activity followed by a refractory period. The greater stimulation that evidently occurs and greater intolerance towards other birds that is shown has survival value if territorialism is useful, and is to be maintained, by drakes having territories with long shorelines as in small sloughs, or narrow water boundaries, as in the arms of a lake.

FIGURE 7.

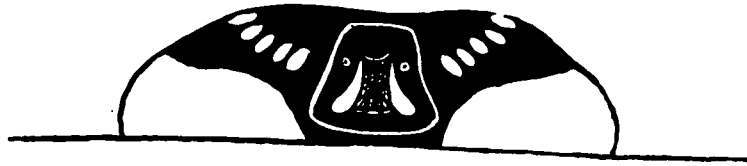
B. islandica (B. C. population)

LAYING NECK ON WATER ("THREAT" POSTURE)

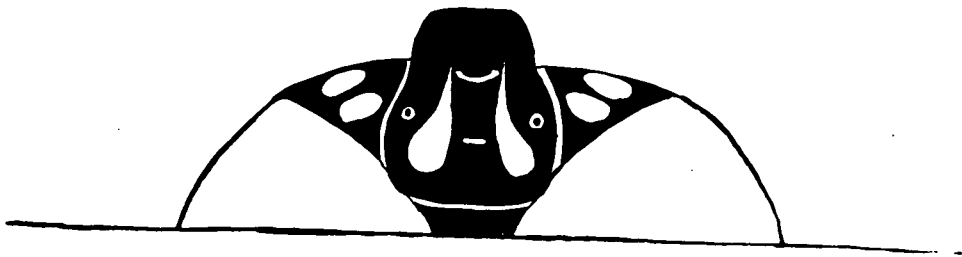
Artists drawings by M.T. Myres, from field sketches.

Water-level views of an aggressive drake.

- A. Distant View. The head is lowered to the water and the back of the bird is seen rising above it. The white windows are prominent in series in the black back and wings.
- B. Close-up View of Aggressive Drake. The top of the head now rises above the contour of the back, the wing windows are less prominent, the head being outlined rather less against the black dorsal regions as against the prominent white flanks. The white face crescents and golden iris are prominent, and "mask"-like in appearance.
- C & D. Side Views. In C. the bird is less highly motivated than in D. The white of the neck still shows, and is divided from the white of the flanks by a black shoulder flash. In D. the neck is lowered below the water, the beak perhaps tilted a little more up. It may (?) be opened with lower mandible on water (or in courtship only?). There is one white flank patch.



A.



B.



C.



D.

COURTING DISPLAYS

GENERAL ACCOUNT

The only detailed or accurate account of display in B.islandica is that by Sawyer (1928). As explained earlier I did not read this paper until after I had completed my field observations. It will become apparent, in what follows, that our separate accounts corroborate each other very well. Although Sawyer did not specifically name any displays he did separate them in his own mind and illustrated them in two pages of figures. Unfortunately text and figures fail to agree owing to a number of typographical errors. These are detailed in Appendix 1, for the sake of completeness. It needs only to be stated here that Sawyer's illustrations are excellent.

I have as yet, seen very little of the display of B.clangula in the field. But there is obviously much to be derived from comparing the displays of B.clangula with those of B.islandica since they are closely related species and occupy mutually exclusive breeding ranges. The literature of display in B.clangula is quite large, but it covers comparatively few of the discrete display movements and is the work of those untrained in ethological observation or theory. However it has been felt that a complete review of this literature on B.clangula would be worth while if only to clear the background for further study. It has been necessary sometimes to read between the lines or to reinterpret observations in light of recent knowledge, but on the whole the literature descriptions can be broken down into discrete displays.

The Literature of *B.clangula*

The reason that displays of *B.clangula* have been described more frequently in the literature than those of *B.islandica* is that *B.islandica* is confined to British Columbia and adjacent regions and Iceland, while *B.clangula* winters throughout the popular ornithological hunting grounds of western Europe and the Atlantic seaboard of the United States.

The earliest accounts of the display are those of Brüggemann (1876) from Germany (cited in Phillips, 1925) and of Gilpin (1880) from Nova Scotia. The latter wrote "the male throws his purple head far backwards till it rests upon his back". Heinroth (1911) published an important paper on the ethology of the *Anatidae*, but he had devoted but little time to *B.clangula* and merely wrote (in transl.) "the drake with a jerk throws the head.....far back onto the back".

But most accounts merely describe one of the many courtship displays of this active species. Curiously the most extensive descriptions come from the period just before the First World War. Townsend (1910) stimulated William Brewster to write up his observations on wintering goldeneye near Boston, Mass. He described a number of discrete displays, which he observed one day in February 1909, in a paper which he read to the A.O.U. Congress in Washington in 1910 (published 1911). This is the only paper to date in which an attempt has been made to name discrete displays and is much the most detailed in its descriptions of the displays.

Millais (1913) added little that was new to our knowledge of golden-eye display when he published his great work on the British Diving Ducks, except an apparently exaggerated account of the Post-coition display.

Nor did Phillips (1925) add anything that was original in his Natural History of the Ducks (except an account of the seldom seen, "Backwards Swimming Display"). Bent (1925) and Kortright (1942) merely make a few quotations from the literature. Isakov in Dementiev et al (1952) evidently takes his account from west European authors, and his illustrations are copies from Bernhardt (1940).

Papers which have something to add to our knowledge of the display of B.clangula are those of Boase (1924), Bernhardt (1940), and Johnsgard (1955). Munro (1939) in his important paper on the American Goldeneye in British Columbia had nothing to add to the scant account in Munro and Clemens (1931).

By far the most comprehensive summary of the displays is that in The Handbook of British Birds (Witherby et al, 1939). This account, compiled from the literature by F.C.R. Jourdain and B.W. Tucker goes a considerable way towards isolating the distinct postures and movements, but does not attempt to name these movements, which would give them the authority of distinctive nomenclature.

Nomenclature

Comfort Movements, like flying, swimming, eating and drinking are activities which every bird has to perform, and ones which are found in all species with little variation in form. Because of their biological necessity they are deeply inherent in bird behaviour patterns, and for reasons of functional efficiency they have a similar appearance from species to species. The taxonomic value of sexual displays, however, lies in the

fact that they have no adaptive function, and are developed to express specific differences.

However, closely related species will tend to have displays which though recognisably different in form, were at one time (when the species had not yet differentiated from one stock) similar or, rather, the same. Much interest lies in identifying homologous displays. Identification necessitates analysis not only of form but of motivation and function "meaning", and occasion of occurrence (Baggerman et al., 1956). If it can be shown that these latter are similar then the variations in form can be explained as secondary, and result from the same forces that separated the species. On the other hand, similarity in form of two movements, in different species, may not be an indicator of a common origin. Convergence may have occurred, and the way to show whether this has happened or not is to analyse the situations in which the two displays occur, and their function or signal meaning. Unfortunately this stage of goldeneye behaviour studies has not yet been reached. Until it can be shown, by analysis, that movements are homologous, and should have the same functional nomenclature, it is necessary that distinct descriptive names should be used, for similar displays in different species. This important principle was pointed out to me by Dr. Frank McKinney (in litt. 1954).

Thus an attempt has been made here to give the most suitable names to the various movements or postures. The rule of priority should, wherever possible, be used. However there is no virtue in perpetuating a name which is no longer descriptive, or which has a functional significance which is still undemonstrated. Thus the term used in the trans-

lation of Lorenz (1951-52) for the females twisting of the head, from side to side, should never have been called "Inciting" in the first place. We do not know whether it has the meaning "I belong to you" directed at the male she is meeting or following, or "See here, I am mated to this male", directed at other males. It so happens that in eiders (Somateria) a display occurs in this context which consists of two quite different parts (McKinney, M.S.), which probably have two rather different motivations. In goldeneye the behaviour of the female takes two forms of which the "Inciting" (here called "Jiving") is one. Possibly the "Deep Jiving" posture is from the same stock.

Another example of confusion is that of "Pumping". This is used by Lorenz (in transl.) to describe the up and down movements of the head by both sexes in the Prelude to Mating, in Mallard (Anas platyrhynchos). In Bucephala I first used this term for the rotary movement of the head of the drake in B.islandica. It is conceivable that the two forms of Pumping might have the same origin, but until we know one way or the other the movement in B.islandica must be known as "Rotary Pumping". If they prove to be different movements the names may then still stand, since they are distinguishable, and specific, which "Pumping" by itself would not be.

Another example is that of the "Masthead" of B.clangula (as here re-defined) which resembles the "Neck-Stretch" of Aythya vallisneria (Hochbaum, 1944), but we do not know that they are homologous. Indeed I am uncertain in my own mind what the homologous movement in B.islandica may be (possibly the "Water-Flip"). Their signal functions may not be the same, even if there is phylogenetic relationship. By contrast, when the

signal functions, and occasions, of the various movements, are known we will be using the same Functional name for quite unlike movements in many cases. Thus the crouched "Threat" posture of A.vallisneria (Hochbaum, 1944) has the same function (namely intention of aggression if certain circumstances arise) as the "Laying Neck on Water" posture of B.islandica. This latter posture greatly resembles the "Sneak" posture of A.vallisneria which does not apparently have a threat function.

By distinguishing descriptive names between species there is an avoidance of confusion should the function of a named display have to be revised. For example if the "Laying Neck on Water" posture of B.islandica were to be called the "Sneak", as it might, it would be presumed that the "Sneak" also was aggressive in function, which apparently is not the case.

The illustrative material and descriptions

Certain of the figures are taken from my own film of B.islandica, But as stated earlier it was preferable to make a comparison with B.clangula if this were possible. I have had the great privilege of being allowed to make use of pictorial illustration from a film of B.clangula taken by Charles Walcott and Benjamin Dane, and of a short film taken by Dr. Frank McKinney at the Wildfowl Trust, Slimbridge, Gloucestershire, England. The latter film contained shots of B.islandica (Icelandic stock), and B.clangula (both American and European races).

Naturally, while making drawings from these films I have been able to compare B.clangula display sequences with those I know from field observation and film of B.islandica. It must be stated categorically

here, that the opinions expressed in the following descriptions are mine and mine alone. They do not necessarily represent those of the persons who took the films. It will however be of considerable interest to compare the descriptions made here, with those that will be found in Walcott and Dane's forthcoming paper (in preparation) on B.clangula and B.albeola.

The Courtship and Coition displays.

For the sake of convenience I have separated those displays which are seen in the courting party and between the pair on territory (without mating), from those occurring in the coition sequence, alone or for the most part. Thus Pre- and Post-Coition Steaming are clearly found only in the mating sequence. The Wing and Leg Stretch are found almost exclusively in the coition sequence, but occasionally at other times (they are almost impossible to tell apart from the comfort movements they so closely resemble either in a courting party, or even when they occur in isolation). Rotary Pumping, and to a lesser extent Bowsprit Pumping and the Kick Complex of displays are seen to a certain extent in the coition sequence, prior to mating, but are a much commoner feature of courting parties. Indeed B.islandica and B.clangula tend to differ in the degree to which these movements may be found in mutual or communal courting situations.

As will become apparent Rotary Pumping is the most frequent display element in B.islandica. But a movement from a different complex, the Head-Throw, is the most important in B.clangula. This species has a more highly differentiated Kick Complex than has B.islandica, but its pumping

movement is apparently less differentiated. The Masthead has not been identified in B.islandica, unless it be the same movement as the Water-Flip.

Thus in most of the courtship displays the two species differ quite considerably in the form, the relative frequency, and the occurrence of each display. It took me some considerable time to realise that apart from the coition sequence (Wing and Leg Stretch, Water-Flip, Jabbing, and the two forms of Steaming), the only sexual display found in courting parties, which takes exactly the same form in the two species is the Head-Up or Head-Raised (with Neck-Withdrawn) posture-movement sequence. Whether this is a basic courtship movement which has not differentiated, but has been replaced (as a criterion for species recognition, by more differentiated displays), or whether it was the last basic display type developed before the species diverged, or whether it has a somewhat generalised and unspecific signal function, is not yet certain. In both species it is more closely allied to the pre-coition displays than to the pair-~~ing~~-forming and pair-maintaining displays. It is not as frequently seen as Rotary Pumping or the Head-Throw.

I have distinguished the following male courting displays in the order in which they are described: —

<u>Complex</u>	<u>B.islandica</u>	<u>B.clangula</u>
<u>Head-Up Complex</u>	Head-Up---Neck-Withdrawn	Head-Raised---Neck Withdrawn. Alike
<u>Kick Complex</u>	Pseudo-Kick) Kick)	Head-Throw) Head-Throw-Kick)
) not unlike) very distinct	
<u>Pumping Complex</u>	Rotary Pumping	Bowsprit Pumping Not unlike
-----	-----	Masthead
-----	-----	Backwards Swimming

The female's repertoire of displays is restricted by comparison. She has two regular displays, Jiving and Deep Jiving directed at the opposite sex and an Invitation to coitus, which is a static posture displayed at the mate. Often the male is not ready for coitus when she assumes this posture and the preliminary⁷ to mating may continue for as long as 20 to 30 minutes. She has no post-coition display though she regularly performs Splash Bathing movements, as does the male.

THE FEMALE

There are three actions which are characteristic of the female alone, Jiving, Deep Jiving and the Invitation to Coitus. The last will be deferred until the Coition Sequence. However the female may also perform, in weak or infrequent form, some of the courtship displays of the male. Deep Jiving (B.clangula at least) has resemblances (probably non-relational) to the Head-Throw-Kick in one of its forms. Jiving is only seen in the female, and is the main movement with sexual motivation in female goldeneye, as in many other ducks (= Inciting display of Lorenz). The circumstances of female use of other displays is very uncertain. It remains to discuss the literature on them.

B.islandica

I have observed Rotary Pumping by the female in the field. This is not however very common and is described in the sections on inter-female and Brood behaviour. It is a form of greeting display, and appears to have a similar function in B.clangula. The Water-Flip is commonly performed in B.islandica.

B.clangula

In the literature a number of displays are attributed to the female. It is of interest that the chief of these is the Bowsprit position, which is believed to be the homologue of Rotary Pumping in the other species. It evidently also has a greeting function. The next most commonly described of the displays, chiefly found in the male, is the Masthead. There is some little evidence that the Head-Throw and/or the Head-Throw-Kick may occasionally occur in weak form, but it cannot be ruled out that

the "females" in which these displays were supposedly seen were not immature males. The alarm posture resembling the Head-Raised posture is presumably found in the female as it commonly is in B.islandica.

The Bowsprit performance in the female has been described as follows

(B.clangula): —

In one instance the female made display by extending the neck with head in line at an angle of about 45 degrees, (Boase, 1924).

She dips her bill; splashes water sideways with it; protrudes her neck at an angle of 45 degrees (the "bowsprit pose" of Brewster); she stabs the zenith; kicks up water behind her; and as I say, rolls and extends her wing. (Gunn, 1939).

....the females. The latter were also active, jerking with the neck, making drinking movements, lying low on the water, and swimming up to the males. (Bernhardt, 1940).

a female, first nod, next crouch, and then take the bowsprit pose! This behaviour on her part created intense excitement among the attendant drake who....crowded close about her... (Brewster, 1911).

Display has also been used as a welcome to newcomers. In one case, two individuals judged to be females....showed great excitement at the approach on the wing of a male....the two 'females' called quar-quar and held the head and extended neck stiffly upwards at a steep angle, the head feathers raised, and one bobbed the head by repeated retractions of the neck, calling. (Boase, 1924).

The Masthead is described above when Gunn (1939) refers to "stabbing the zenith". In another passage Townsend (1910) describes it as occurring in response to the Head-Throw of the male: —

....the female, although usually passive, sometimes responds by protruding her head close to the water in front, and then bringing it up so that it also points to the zenith. Further than this I have not seen her go.

He admits the possibility in the spring that young males are involved

but states that he is convinced that females do actually perform this act.

Boase (1924) writes: —

The female, which had been watching the male with chin on the water, and neck retracted, replied by jerking head and neck in line upwards at a steep angle, holding the final extended position for an instant, and returning to normal. These displays were repeated several times.

Although Gunn (1939) above says he has seen the female kick up water, he denies that she has the Head-Throw. Boase (1924) says that he did not see the Head-Throw from the female. Phillips (1925) remarks that a "curious hollow groaning note like owhh was heard from a female by Harper on the Athasbasca, which seemed to stimulate the male to throw back his head on to his rump". Brewster likewise believes the female stimulates the males to display, by some action of hers. He writes: "she might occasionally single out and obviously encourage one of them by approaching him closely and bobbing her head up and down a few times. To this salutation he would immediately respond by a corresponding action before beginning his more elaborate performances again.", and as remarked earlier (quoting from Brewster, above) and later (under Head-Throw) the Bowsprit posture seems to stimulate the Head-Throw.

Mr. Gerald Legge had two pairs and an immature female in captivity.

He is reported in Millais (1913) as writing: —

At the same time she suddenly throws up her head and neck until the bill is quite perpendicular, and at the same time she makes a loud call, ('very loud and harsh') quite unpronounceable, and quite distinct from that uttered by the male. She also kicks with both of her feet, but does not kick the water so high as the male....the kick is done with both feet, one after the other, in quick succession....It is usually after the young bird has chased her elders....the drake approaches his duck and does his full show and kick, and the duck seems to follow in imitation. I have, however, several times seen the old duck show when she has not been pursued by the young bird.

Millais (1913) also says that the female may advance towards her mate with "head and neck outstretched, and somewhat similar in attitude to that of the male." and that "both sexes make use of a hoarse kraa-aa as a call, the male being somewhat louder than the female....I have heard the female make a low note like wah-wah when talking to her young".

Phillips (1925) describes the call of the female as a "loud guttural churr-ing noise not often repeated. I have heard her give vent to a squeaking ach or heck uttered sharply on suddenly being surprised on the water with her young brood. Again the harsh note of alarm may sound like the quaak of a surface feeder, very loud, but coarse and rough. Harper (M.S.) heard a note like cuk-cuk-cuk-cuk, quite different from the ordinary grating grrrk when four or five female were circling through the woods hunting for nest-cavities."

Jiving

This is the response of the female to courting activity by the males. It occurs on territory when a male rejoins his female, either when he returns from a boundary dispute, or when she rejoins him on other occasions. It thus appears to have the meaning "I belong to you".

It occurs in courting parties and is expressed in such a way that it appears the female is repelling some of the males, with the meaning "See here, I am mated to this male". In such situations Jiving may lead into a short rush with the beak open at another male than the preferred one. It need not be assumed that Jiving is aggressive in motivation, however, since the female is capable of aggressive threat in the form of the Laying

Neck on Water posture of the male, and may even be capable of a "Gesture of Repulsion" from this position. Boase (1924) writes of the female making short runs at the male "with head and neck in line extended horizontally--this is, of course, an action common to many ducks". Jiving often occurs between a pair when another male is threatening to attack a pair.

In this movement in B. islandica the female lowers the head forwards but the head is some way off the water. She then swings it sharply from side to side, first one way, then another, in broad sweeps of considerable amplitude, so that she faces right around towards other males in her wake. This usually occurs when the female is following a male swimming ahead of her in a courting party. In a courting party the extreme lateral position of the Jive comes, very often, to be directed at another male than the one she prefers. If a female has no chosen partner she may Jive at all following males. When the female is behind the male of her choice he is usually in the Head-Up position, Head-Turning, rather than Rotary Pumping. On territory she may also do it as she comes to meet him, and then swing into line beside or behind him, while he makes Rotary Pumping movements. If a male approaches too close she may rush at him with neck stretched forward and beak open. In extreme form the rear of her body may swing out of line from the direction of movement, and her body may come side on to the following male. This may, I think, lead into a jab towards him. But this is exceptional. However it raises the question of the signal intention of the movement, and its orientation. After Jiving the female Tail-Wags emphatically. Once when a female was disturbed from the shore by the observer she swam out towards her male and Jived as she approached him.

A female who had three times refused coition to a courting male, began Jiving, behind her male, after they had both dived and he had begun Rotary Pumping after surfacing. Shortly afterwards she was driven away by another male. In one very peculiar instance Jabbing was observed performed, by both birds, at the rump of the other. It seems that the birds were not paired and that an element of aggressiveness took charge in an otherwise heated courtship sequence. It ran as follows: — Both birds dove and the female upon surfacing did the Upwards-Stretch movement and then Jiving (low croaking as she did so). The Jiving became so violent that she came alongside the male from behind and then faced away from him at the extreme of the outward movement. He turned at right angles to follow. Once she jabbed him in the side of the rump during the Jiving. She as often turned towards him from in front of him. He would jab then at her rump as she turned (and she once at his). Then he took up the Threat posture and dove twice at her. She had to scoot away. As he came up he once seized her rump feathers and a flapping chase ensued over the water. He dove again and she flew. He followed and during this flight swerved up at her once. She avoided this and they circled together. He came back to his territory and she landed close inshore 300 yards away. On two occasions the Upward-Stretch with Head-Flick immediately preceded Jiving.

This movement is found in the Anatini, being the only display about which the common homology in the two groups cannot be doubted. As discussed earlier Lorenz referred to it as the "Inciting" movement (in transl., 1951-52). It seems likely that light on both Jiving and Deep Jiving will come from comparison of goldeneyes and surface-feeding ducks with other groups

e.g. scaups and eiders. McKinney (M.S.) cites Hoogerheide (1950) to the effect that in Somateria mollissima "the two components of inciting are not fused into the one movement as they are in many Dabbling Ducks. The duck stretches threateningly toward one bird and then chin-lifts repeatedly toward 'her own' male." This is a very important discovery.

Sawyer (1928) writes "The extreme example is a snaky movement of the neck as the head is swept forwards and backwards, from extreme side to side of the bird, in a generally horizontal plane". He illustrates this in
 o Figures 19 and 21-23 on Plate 3 of his paper. Mary Jackson (M.S., 1952) describes Jiving as follows: —

The head is held erect and the bill describes an arc in which the following positions may be identified: (1) Bill horizontal, pointing straight ahead, neck relaxed; (2) Bill pointed downward toward the water at an angle of 30 degrees, and toward the right, neck outstretched; (3) Bill horizontal, pointing straight ahead, neck relaxed; (4) Bill pointing downward toward water at an angle of 30 degrees, and toward the left, neck outstretched; (5) Bill horizontal, pointing straight ahead, neck relaxed. Thus the bill describes a horizontal angle of nearly 180 degrees, and a vertical angle of about 30 degrees.

Deep Jiving

I have no field data on this movement in B.islandica though it probably occurs. However Figure 8 shows this movement in B.clangula taken from Walcott and Dane's film. It appears to resemble the second half of the Head-Throw-Kick Position 2, in that the neck is sunk below the water, beak pointed steeply upwards, and there is a rounding up of the rear of the body and a considerable paddling (or kick) with the feet. It seems to be directed at one particular male, and appears to be threatening in function (though females can also assume the Laying Neck on Water posture, especially towards other females when they have broods).

Gunn (1939) has described Deep Jiving in B.clangula as follows: —

She has one curious little performance which is never seen in the male, and which I may describe by an extract from my notes. "A movement by the duck when attracting the attention of the drake; usually associated with periods of 'lying along' the surface. The head is slowly and completely submerged and then carried forwards in a curve having an upward direction, so as to reappear with the bill pointing upwards at an angle of 45 degrees. As soon as the eyes are clear of the water the movement is arrested, and this position of the head is retained while the whole of the neck is out of sight. At the same time the stern is well elevated in a humped-up way, the heels being exposed though the tail is not lifted from the water. The bird then is more or less in the position taken by a Great Crested Grebe chick which has been bullied by a stronger brother, and, after making his escape by diving, rises and peeps to see if 'the coast is clear'. This pose forms part of an active display by the female bird; and, as such, differs from the common attitude of solicitation, when she half sinks her body and lies extended flat along the surface of the water."

Brüggemann (1876) wrote (in transl.) of B.clangula that: —

The female bends itself completely flat on the water while it lays the head down on the same. From time to time it bends the neck contortion-wise downwards and points the spread out tail feathers downwards into the water, while it makes its whining (Winselnde) or purring (Knurrende) voice, heard in reply to the call of the male.

It seems possible that this is a description of Deep Jiving. Boase (1924) also believed that a call was uttered by B. clangula in this pose "swam around him with chin on the water and neck almost submerged, the body being sunk low; they appeared to be calling, but wind made the sound inaudible."

FIGURE 8.

B. clangula (American population)

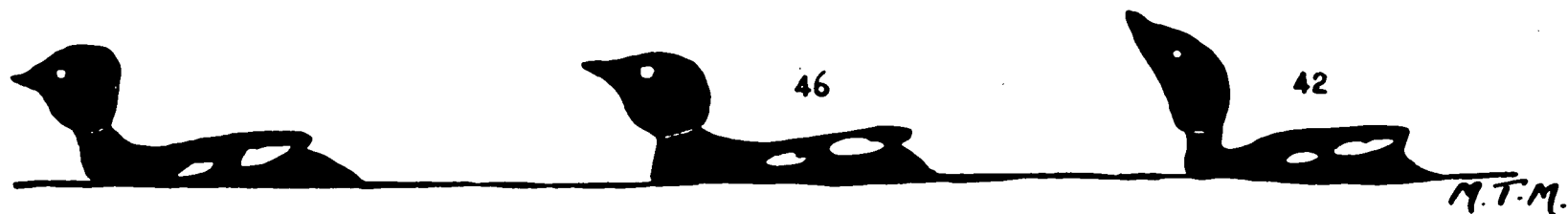
DEEP JIVING

From a film by Charles Walcott and Benjamin Dane.

Read from right to left.

The neck is sunk below the water, and there are signs of a kick owing to the elevation of the rear of the body. The movement resembles the late phases of one form of the Head-Throw-Kick.

24 frames/second. Shutter Speed 1/48th second.



THE MALE

Head-Up---Neck Withdrawn (*B.islandica*)Field Descriptions

The main posture consists of the neck being stretched vertically upwards and maintained in this position. The beak is held horizontal (Figures 9 & 10). The male gives a clicking sound from his bill which is opening and closing all the time. The noise is presumably caused by contact of the mandibles, and thereby differs from the noise made in the Laying Neck on Water pose which occurs during Rotary Pumping, and in which the bill is kept open. The head is turned slightly from side to side while it is held up in this position (Fig.10): "there is no movement in this position except a 'startled' sideways twisting of the head from right to left and vice versa".

While in this position the neck is frequently drawn back quickly (Fig. 9., Frames 10-11), and shortened, so that it is brought between the shoulders. It is held here for a moment, and then the head is elevated again more slowly (Fig. 9., Frames 18-22) and the neck straightened (Fig. 9). It is of interest that in 1955 I did not recognise this as a discrete movement, although it was described in my field notes. However in 1956 I observed the withdrawing of the neck (or bending of the neck) in the Redhead (*Aythya americana*) and shortly afterwards recognised it for what it is in *B.islandica*.

The Neck Withdrawn position is only assumed momentarily in the course of the Head-Up display. My notes record that : "they would also slowly stretch and lower their necks as in Rotary Pumping. There seem to be two components here — a slow forward pump and a vertical courtship pumping

proper.". In another case I recorded (tape): "began to pump at the female (high pumps with very little amplitude). In this position the high position resembles the Expectancy Look. In the high position the beak is sometimes opened...continually opened and shut...". Sometimes the withdrawing of the neck is not a fast jerk but a slower movement. There is an angled aspect to this movement on such occasions-- a lowering of the up-stretched head into the shoulders and raising it again to the head-stretched position. This low motivation movement sequence has considerable resemblance to Rotary Pumping, as well as to the Head-Up---Neck-Withdrawn movement. It remains to be discussed what form low motivation Rotary Pumping may take (possibly in the high-up pose). But it seems that Rotary Pumping may intergrade into the Head-Up---Neck Withdrawn posture-movement display. Juvenal males may perform the Head-Up---Neck-Withdrawn position.

The resemblance of the Head-Up position to the Expectancy Look pose has been mentioned earlier. It seems likely that the former has derived from the latter. However it is now a highly ritualised movement, frequently seen in courting parties. Very often more than one bird may be seen doing it at any one time. The Head-Turning which accompanies the Head-Up position, and the ticking noise, is a constant feature and also adds likelihood to the suggestion that the Head-Up---Neck-Withdrawn display originated in the Expectancy Look. On one occasion a male realising that another male was directing a submerged attack upon him, began swimming towards his female with neck raised and (?) courting weakly (Rotary Pumping). A distinct quacking was heard from his open bill "while in this position of 'alarm'", and it seems that the position is essentially one which increases

the visual field (head raised, and the turning of the head) of the alarmed bird. Whether this pose has any resemblance to the beginning of flight has not yet been analysed, but it is a fact that if the attack is pressed home, or if the bird is alarmed sufficiently the Expectancy Look position (or Head-Up position) is followed by flight. We may look therefore for elements of escape motivation when it is observed in a courting party, although mimetic stimulation seems to be one cause for its occurrence there. The Head-Up position is maintained even when the female is submerged.

The movement also has resemblance to the Head-Turning which is interposed between the Head-Throws of a male, when a female is following a B. clangula drake. There is a suggestion from one observation that the Head-Up position is a releaser of Jiving, which commonly accompanies the Head-Turning, by a following female of B. clangula. Furthermore the neck is withdrawn into the shoulder in B. islandica no less than it is in the Kick and this backward position of the head is considered to be equivalent to the extreme head-on-rump position of B. clangula in the Head-Throw-Kick. There may be a connection here therefore. On the other hand B. clangula has an identical pose to that of the Head-Up (Head-Raised----Neck-Withdrawn) so that the Head-Throw cannot be said to be the exact equivalent of the Head-Up position. The Head-Throw is evidently the equivalent to the Pseudo-Kick.

However in B. islandica the Head-Up (Neck-Withdrawn, the Pseudo-Kick and the Kick, are much more alike than are the Head-Raised (Neck-Withdrawn), Head-Throw and Head-Throw-Kick of B. clangula.

Literature Description

Sawyer (1928) illustrates this pose. He writes "head bobbing and

elaborate neck pumping and stretching are the most outstanding actions; these motions are grotesque and spectacular; as, for example, in the sudden upward thrust of the head," (See Figures 10-11, Plate 3 in his paper. He also says that "the drake often or usually gives a continued short quack in throwing the head back and while in the attitude which ensues", which is the Head-Up position. Mary F. Jackson described (M.S. 1952), a movement which she called "Head-wagging": —

The head is held level, with the bill horizontal, and the neck stretched out (means up) as far as possible. The head is then moved backward and forward (means sideways) through an angle of about 135 degrees, with the slightest momentary pause at the end of each "wag", so that the entire pattern appears to be slightly jerky. The body is carried high on the water throughout.

Head-Raised---Neck-Withdrawn (B.clangula)Film Description

This movement resembles the Head-Up position of B.islandica almost exactly (compare Figs. 11 & 12 with 9 & 10). Curiously enough it has not been specifically named before, nor has it been seen very often. The head appears to be held a little further backwards in the Head-Up position than in B.islandica. The contour of the head and front of the neck and breast from bill-tip to the breast at the water-line traverses a smooth half-S. The bird gives the appearance of leaning back a little (like a man looking down his nose) i.e. the bill is tilted a little upwards from the horizontal. In this position the beak is opened and closed (Fig. 11, Frames 35-37, and Fig. 12, Frames 2-4 and 29-32).

The position is assumed from the Normal resting position (a little forward and the neck a little more stretched than usual), by the head being withdrawn into the shoulder, and then reflected forwards and upwards off it, thus raising the angle of the bill a little and extending the neck. From this extreme position the head is periodically withdrawn onto the back. The movement is rapid (Fig. 11, Frames 11-13, Fig. 12, Frames 13-16). The head lies much further down the back than in B.islandica and beak tilted upwards resembling the Head-Throw-Kick (Position 2) instead of horizontal as in Head-Up position. The raising of the head afterwards appears as though it may be as rapid. The beak is opened and closed 2-3 times between each withdrawing of the neck. There is Head-Turning (Fig. 12) as in B.islandica.

It appears from scrutiny of Walcott & Dane's film that if the female

is behind him, the male will swing his body from side to side, or will turn his head from side to side, while calling. In this position it appears that the neck is less frequently withdrawn--a comparable position to that found in B.islandica, in which it is withdrawn rather less often, and in which the head may be turned from side to side more frequently.

Most usually the movement is made towards a female from behind her, but if the female turns to go with him, he then turns to lead and is then in front of her and facing away from her. Then Head-Turning replaces the Neck-Withdrawing rather more. This could be because the Neck-Withdrawn position is less readily seen if done in front of the female. Head-Turning is then more visible and (?) the white face patch becomes visible on each side alternately (this is not the case however in Post-Coition Steaming in which Head-Turning also occurs). When swimming behind the female the male may be a little at a slant away from her so that the Neck-Withdrawn position is visible to her.

Orientation is indicated here, to be important in the genesis, moulding, and selection of movements. If each sex in each of two species behaves and is responsive to subtly different orientation situations, and signal-exposure is dependent on these we can explain how the Neck-Withdrawn position has become more frequent in B.clangula and Head-Turning more frequent in B.islandica. Further analysis alone can tell us whether these first impressions are in fact correct. Meantime they are worth recording.

Literature Description

Both literature descriptions (Boase, 1924 and Bernhardt, 1940) say that the head feathers are puffed out. The best description is found in

Bernhardt (1940) in which the orientation is indicated and the exact following of the female (turn by turn) by one or more males is emphasised. Also the withdrawing of the neck is indicated by the phrase "continually stretching their necks": —

Seven males swam around a female continuously stretching their necks; they swam back and forth with elevated crests; if the female changed her direction, the males did so also, like commandos. Each is determined to outdo the others...

This description describes exactly a similar action observed in the Lesser Scaup (Aythya affinis) by myself, and I think I have seen it in Melanitta sp. as well. It would be possible to argue that the description was of the Bowsprit pose, but I doubt if it were, for Boase (1924) has also apparently described the Head-Raised position: —

The head feathers of the male were raised, making the head appear large; the head was held rather higher than in the normal attitude, and, swimming near the female, the males displayed as follows....

and he goes on to describe the Head-Throw, which may evidently be introduced into a sequence of Head-Raised (Neck-Withdrawn) positions. Head-Turning is not mentioned however.

FIGURES 9 & 10.

B.islandica (Icelandic population)

HEAD-UP WITH NECK-WITHDRAWN

From a film taken by Dr. Frank McKinney at Slimbridge,
England

Figure 9.

Side View

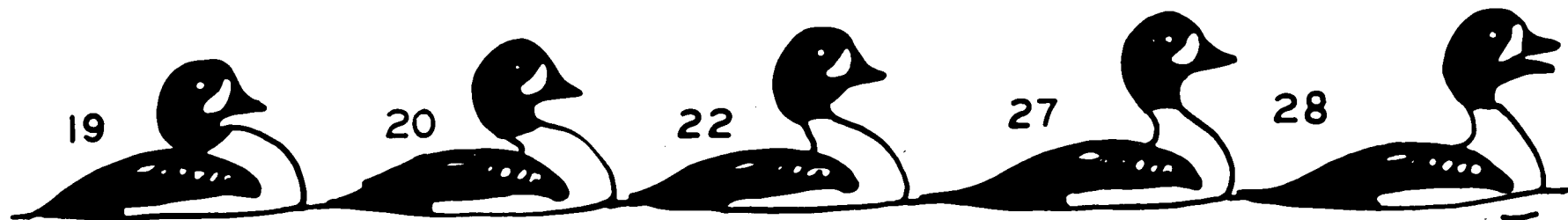
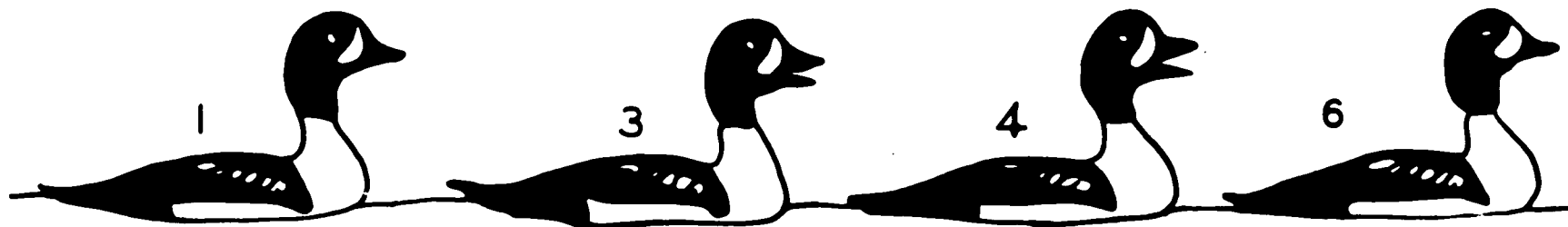
Frame 1.	Head-Up position
Frames 3 & 4	Beak opened
Frames 6-9	Beak closed
Frames 10 & 11	Neck being withdrawn
Frames 11-18	Neck Withdrawn position
Frames 18-22	Head being raised to Head-Up position
Frames 22-28	Head-Up position
Frame 28	Beak opened

Figure 10.

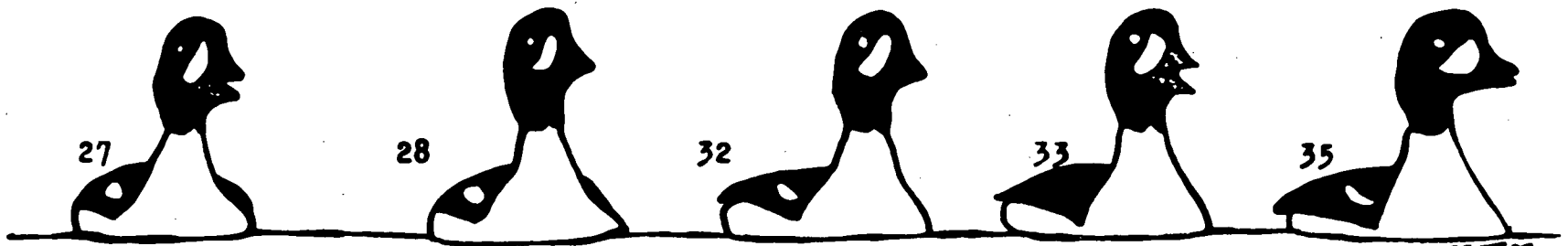
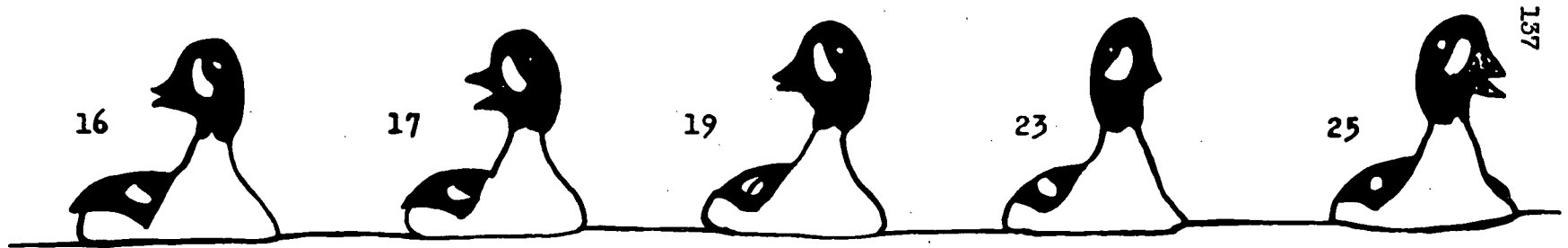
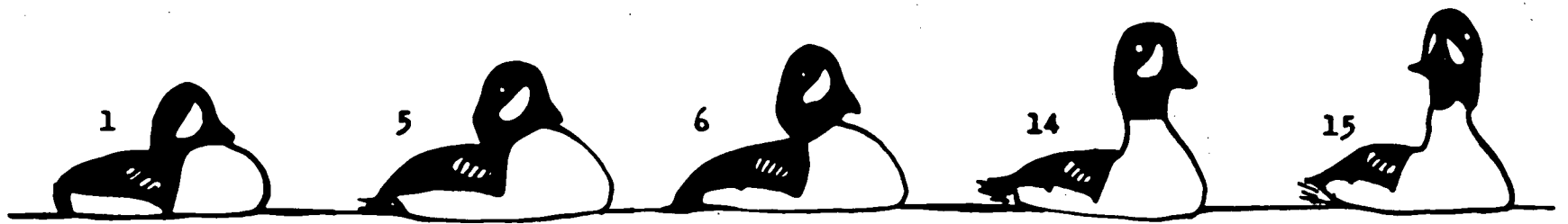
Front View with Head-Turning

Frame 1	Neck Withdrawn position
Frames 5-14	Head being raised to Head-Up position
Frame 15	Head-Turn to right
Frame 16	Beak opened
Frame 19	Beak closing
Frame 25	Beak opened when head directed forwards
Frame 27	Beak closing
Frame 33	Beak opened and Head-Turn to left
Frame 35	Beak closing. Head turned fully to left

16 frames/second. Shutter Speed 1/32nd second.



M.T.M.



M.T.M.

FIGURES 11 & 12.

B. clangula (American population)

HEAD-RAISED WITH NECK WITHDRAWN

From a film by Charles Walcott and Benjamin Dane

Figure 11. Side View

Frames 1-10.	Head-Raised
Frames 11-13	Withdrawal of Neck
Frames 13-15	Neck-Withdrawn
Frames 16-18	Head-being raised to Head-Raised position
Frames 19-38	Head-Raised position
Frames 35-37	Beak Opened

(In Frames 25-38, the body of the bird was hidden by a wave).

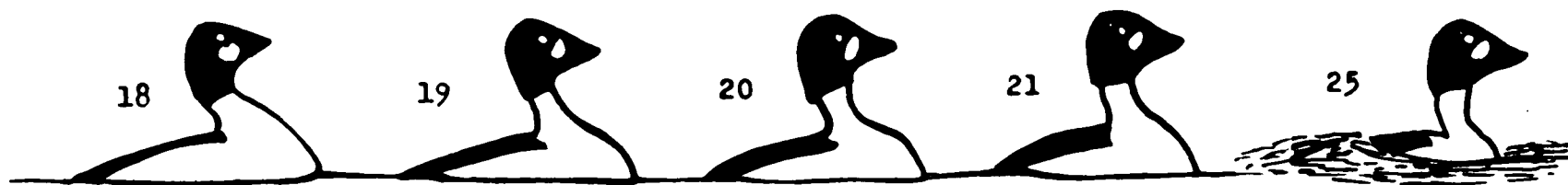
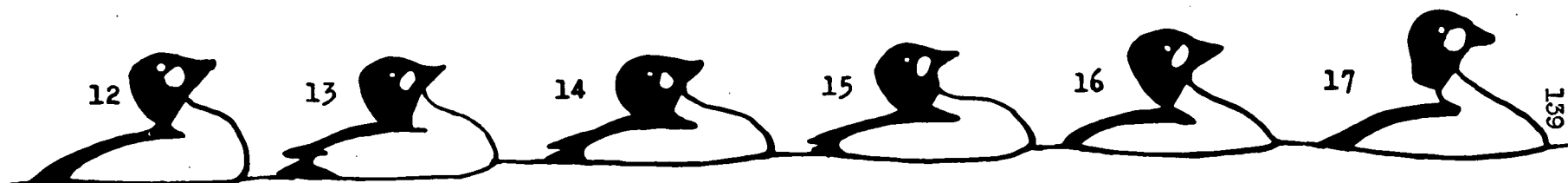
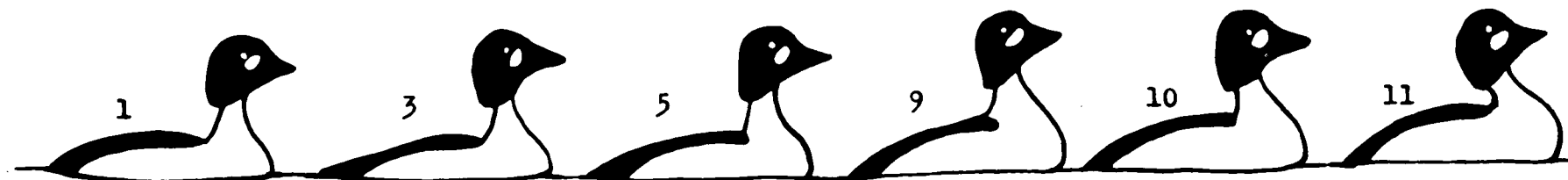
24 frames/second. Shutter Speed 1/48th second.

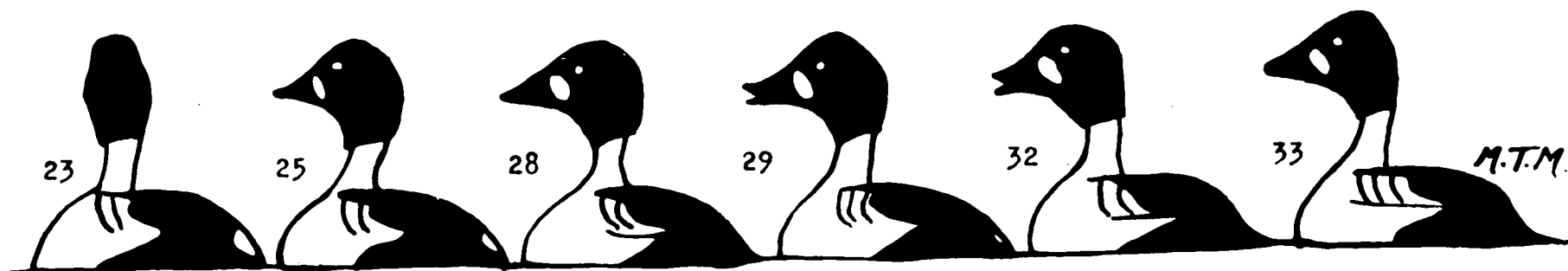
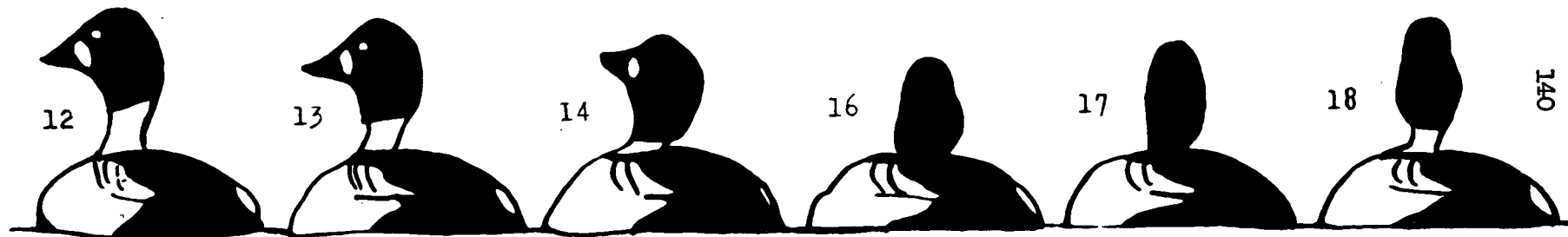
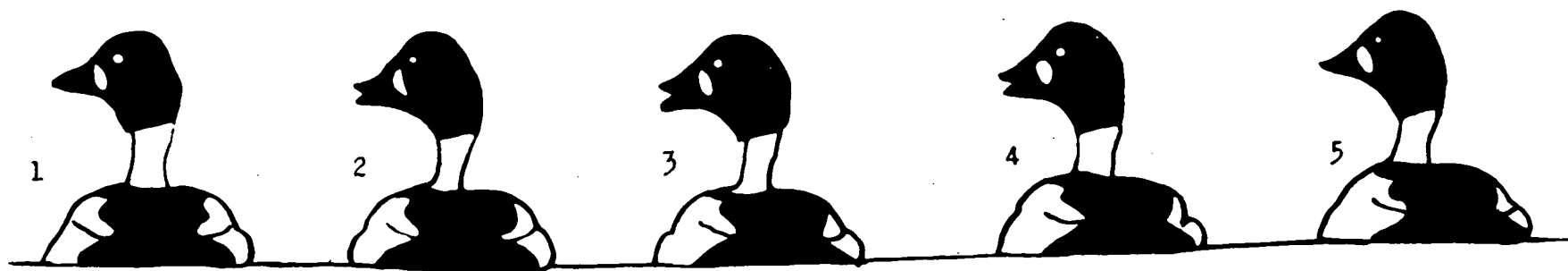
Figure 12. Rear View with Head-Turning

Frames 2-4	Beak open
Frames 14-18	Neck-Withdrawn
Frames 29-32	Beak open

At the beginning and end of the Neck-Withdrawing movement the head faces away from the observer. The beginning and end of this sequence is therefore with Head turned to the left.

? 24 frames/second and Shutter Speed of 1/48th second.





Pseudo-Kick and Kick (B.islandica)

In the first year of my study I was unable to separate these movements. Both movements are very rapid and hard to describe, and in my recordings they appear merely by name whenever they occur. I have not personally recorded either movement on film, but have been able to make drawings of both from a film of Icelandic birds taken by Frank McKinney at Slimbridge.

These two movements are not as distinct, or as extreme, as are the Head-Throw and the Head-Throw-Kick of B.clangula which are quite different from each other, and take a much more rigid and amplified form than do either of the equivalent movements in B.islandica.

The Pseudo-Kick

In the Pseudo-Kick the feet are kicked but do not break surface. In one place I described it as a "lifting of the head back and up not quite onto the shoulders and with beak held almost vertically upwards. It is a rapid movement both up and down and the upper position is not held. During the movement the bird calls--like the quack of a duck". The film (Fig. 13) shows that the head is lifted from the resting position upwards, then swung backwards until it is being held stiffly over the back at an angle of 45 degrees, beak being held not quite vertical. The beak is then opened and evidently a stroke of the legs occurs for the breast sinks into the water. A Head-Flick follows the movement as the head moves forward and then back into the resting position. A point of interest brought out by the film is that in the Pseudo-Kick (but not in the Kick proper) the rear (raised) position of the head, the tip of the back, and the head as a whole, are tilted over sideways towards the female, giving the male a distorted

appearance, as seen from behind or in front (Figs. 15 & 16a). There are slight indications that the beak is opened twice, i.e. before the kick (Fig. 13, Frame 4) as well as after it. This may also occur in B.clangula in the Head-Throw-Kick (Fig. 20, Frame 26, and Fig. 21, Frame 11).

The Pseudo-Kick thus resembles the Neck Stretch of Aythya vallisneria (Hochbaum, 1944), the Masthead of B.clangula, and in weak form might resemble the Water-Flip of both B.islandica and B.clangula. In B.clangula the Head-Throw (without a splashing of water behind) is distinct from the Head-Throw-Kick. In B.islandica the Pseudo-Kick seems to be different from the Kick, and is probably homologous with the Head-Throw of B.clangula.

The Kick

In the Kick the feet are convulsively thrust backwards, as in B.clangula, in such a way that a shower of spray is produced behind the bird. The film (Figs. 14 and 16b) shows that the head is thrown back and up in the same way as in the Pseudo-Kick, but is dropped onto the middle of the back between the wings (as compared with the rump in B.clangula). This takes place as the bird sinks into the water, as the propulsive movement of the foot takes place. I once noted that: "The head is thrown back as though merely by the force of the jerk of the feet", which in B.islandica occurs when the head is still elevated (Fig. 14, Frames 9-11). In B.clangula the head is not, however, thrown back by the force of the jerk, for the head is laid on the rump before the feet are even brought forward (Fig. 21, Frames 6 & 7). The sinking action of B.islandica is also quite distinctive, for in B.clangula the rear of the body is elevated by the kick of the feet and the neck is thrown forward, often to sink well below

the water. The actions differ in timing too, for the beak in B.islandica is opening at the same time as the propulsive movement is taking place (Fig. 14, Frames 10-15) while in B.clangula the kick occurs before the beak opens. The head does not appear to be tilted over sideways in the Kick as it is in the Pseudo-Kick. The movement ends with the head being thrown forward with a slight flick sideways (Fig. 16b, Frames 13-15).

Mary F. Jackson (M.S., 1952) managed to compile a fuller description of the Kick in the field, than I was able: —

The head is thrown rapidly up and back until the back of the crown and occiput touch the back between the wings, and the bill is vertical, pointing upwards, with the mandibles slightly parted. The throat at this time is somewhat inflated and swollen...As the head is thrown back, the bird utters a short, soft, somewhat guttural note...The head is immediately returned to its normal position...At the same time the bird usually kicks back vigorously with both feet, raising a splash of water several inches above the surface.

The Kick is clearly homologous with the Head-Throw-Kick of B.clangula.

Literature Descriptions:

Sawyer (1928) wrote that "a frequent act of the drake is the backward kick which sends a spurt of water backward and upward in the wake of the swimming bird" (Fig. 2 on Pl.3 in his paper). Munro (1918) mentions the backward kick. A photograph by Phillipa Talbot-Ponsonby is reproduced in the 4th Annual Report of the Severn Wildfowl Trust (1950-51) in which the opening of the beak (and production of the call) is seen to be contemporaneous with the kick of the feet. This is not the case in B.clangula, in which the call occurs when the head is being raised from the forwards position after the kick. We also see the high position of the head above

the back which is the most posterior position of the Pseudo-Kick in this species.

Phillips (1925) points out the difference between the Head-Throw-Kick of B.clangula and the Kick of B.islandica. He wrote: "The principal difference is that the whole performance in the Barrow's is less exaggerated and the male does not throw the head nearly so far back". He then quotes from Brooks (1920) who wrote: "The most common form of display in the drake is the 'swallowing' or 'gulping' action, this may or may not be followed by a kick which throws water up behind...Once in November I watched a lone drake going through the whole performance by himself--water-kick and all." Perhaps the Pseudo-Kick should, by priority, be called the "Swallowing Action", but it would tend to imply a form of drinking which it is not.

Munro (1939) described the Pseudo-Kick and Kick as follows: —

When displaying the male throws back the head with a quick jerk until the bill points backward, or merely stretches the neck upward to its greatest extent, or makes a succession of quick bows. Usually the head movements are accompanied by a quick backward thrust of the foot that may send spray flying. These actions vary in intensity and have numerous modifications.

So like Brooks, Munro also did not distinguish the Pseudo-Kick (or "Swallowing") display from the Kick display. There can be little doubt that they are elaborations of a single primitive display, as mentioned under B.clangula. In B.clangula the two movements are rather more distinct than in B.islandica, though in both the Kick is the essential distinguishing feature.

Origin and Circumstance

The origin of these movements is completely uncertain in either species. The Head-Throw of B.clangula is found in many other ducks (Aythya and

and Mergus). The opening of the beak appears to be rare, and is only found in like circumstances in the Head-Up position and in Threat. The back-throwing of the head is found in the Neck-Withdrawn position from a resting or raised position of the head. In both the Masthead of B. clangula and the Water-Flip of both species the head is lifted back from a low position, with the beak extended forwards over the water. A kick of the feet is only otherwise found in the Deep Jiving of the female (Fig. 8). In this position the neck is below the water, as it is in one form of the Head-Throw-Kick of B. clangula.

The movement is found in four differing kinds of situations: —

- 1). Courting Parties, 2). when another drake flies over one on the water, or lands near him, 3). in Isolation, often after landing on the water, 4). in the Coition Sequence.

(1). In courting-parties on lakes in the Interior, the Kick is seen more frequently from first year, juvenal, males than from any adult males (who may however perform it, or mimic juvenal birds as they do it). The juvenals are unmated, of course (and in more female-like than male-like plumage). When they perform the act it is often immediately followed by another bird doing it (often an adult). Some sort of social stimulation appears to be involved, as it is with other displays in Bucephala.

A juvenile male following a female did the Kick and then an Adult male behind her did it as well. Shortly after the juvenal was Rotary Pumping and scooted through the water for a second ("probably an incipient Kick"), and then did another Kick.

- (2). When a drake flies over, or past, a drake on his territory the latter sometimes does the Kick. At other times they may assume the Threat

posture. It is not known yet if a threat position is assumed before the Kick is performed. On one occasion two juvenals were seen to do the Kick as an adult male flew low over them. Since they were neither mated nor on territory it seems that the Kick display does not have threat motivation in these circumstances.

I have a number of records of the Kick being performed either just after a drake lands on the water, either by himself or another drake nearby.

Two males and one female landed on the lake, and the second male began Rotary Pumping vigorously. A third male landed, threatened the second male and performed the Kick display at him. Then it swam away in the Expectancy Look position.

Two males were flying together and landed a little way apart. One then dove at the other which flew, landed not far away and almost at once did the Water Flip and the Kick. Soon afterwards another male landed near a pair, the male of which dove at him. The intruder flew, landed and performed the Kick. The tape recording continues: "The owner male dove at him again and he flew--to the far end of the lake and landed 15-20 yards from a pair. The male of the pair went into Threat. The intruder did the Kick again, nothing else and then dove" (Cummings Lake, May 16, 1956).

One time a male did the Kick as an intruding female landed on his territory. Another time when a neighbouring male flew an adult male nearby did the Kick twice. The stimulus of a bird flying, taking off, or landing is most clearly illustrated perhaps by an occasion when an adult male after threatening a group of goldeneye did the Kick display just as

a Baldpate (Anas americana) which rose from the water nearby began to call, as they do in flight.

(3). Once an adult male landed alone on the lake and did three or four Pseudo-Kicks in a couple of minutes, with some Water-Flips, and preening.

(4). The Kick, or perhaps more likely the Pseudo-Kick with its head-orientation towards the female, may be seen in the preliminaries of the Coition Sequence.

Unmated birds perform the Kick most commonly, adults often in reply to a juvenal. The movement is performed in courting parties under these circumstances. It may occur in isolated birds also however, but is as often seen in birds as they land either alone, or close to other drakes or pairs. It often follows an aggressive incident in which the performer has beaten a retreat. The indications seem to be less that it is a form of aggression, than that the display has a "greeting", "advertising" or "appeasement" significance.

Head-Throw (B. clangula)

Even Brewster (1911) appeared unable or unwilling to distinguish the Head-Throw from the Head-Throw-Kick. They are however distinct stereotyped movements and probably have different signal functions. Brewster's name for them "Folded Duck-Skin Pose" no longer has any valency in the language, and has been replaced by more universal terms, descriptive of the actions.

Field Description

I have little experience as yet, of this movement. I have watched it, however, at 73-Mile Lake, Cariboo Highway, during the spring migration of 1956. A courting party was observed containing both males and females. In the Head-Throw the head was thrown back onto the rump, often so that the nape feathers dipped behind the tail into the water, the chest being raised and the beak held vertical or backwards some 10 degrees. In this extreme position the beak was opened and a call emitted and then, after a pause, the head was rapidly brought forward to the normal position again. The legs were held out sideways. The action was repeated over and over again.

Preceding this convulsive movement, or alternating with repetitions of it, the head was turned very rapidly, from side to side, showing each face patch in turn. This is nowhere mentioned in the literature. It resembles the Head-Turning that occurs in the Head-Up position, and in the post-coition display.

Film Description

Walcott & Dane's film shows that the Head-Throw begins with a vertical lifting of the breast, and stretching of the neck, so that the head is elevated (Figure 17). The neck is then kinked, and the head rotated, so that the head and neck are brought back and lie on the rump. The movement resembles Position 1 of the Head-Throw-Kick, but is quite unlike the more common Position 2 of the Head-Throw-Kick. The head is held for about one second (22 frames) in this position, and almost as soon as the position is assumed the beak is opened and is held open for 5/6th second (20 frames), closing as the head starts forward again. This holding of this position is much longer (about 3 times as long) as it is in the Head-Throw-Kick (Position 1). The Head-Flick occurs before the head reaches the normal resting position.

In an extreme form the Head-Throw is continued, and the head is carried forward into a Forward Position resembling the Bowsprit position (Figure 19) but there is not usually any Bowsprit Pumping from this position. In one instance on the film of the sequence Head-Throw—Forward Position—Bowsprit Pumping—Head-Throw—Head-Flick—the Head-Flick was delayed to the end, and did not come in its usual position at the end of first Head-Throw. This is evidence that the Head-Flick is an indicator of the end of this motor element. The Forward Position is therefore a normal variant at the end of the Head-Throw proper.

The Head-Turning between Head-Throws (Figure 18) may be very energetic, and is especially frequent when the male is swimming in front of the female, leading her. The face-patches may perhaps be exposed alternately. As seen

from in front there is a very sudden break between the extreme posture of the Head-Throw (when the head is on the rump and the tip of the beak alone shows black over a mountain of white chest), and the clearly exposed sideways flicking of the black head over the white breast as the bird returns to the normal resting position (Figure 18). This same Head-Flick would also be very visible from behind.

Literature Descriptions

This movement is the one most commonly described in the literature as "the display" of the goldeneye (with the Head-Throw-Kick as a variant). It has been described by Brüggemann (1876), Gilpin (1880), Townsend (1910), Brewster (1911), Heinroth (1911), Boase (1924), Phillips (1925), Munro & Clemens (1931), Munro (1939), Bernhardt (1940), and Johnsgard (1955).

It is illustrated in Brewster (1911--in which the head is not placed far enough back, and the beak is turned backwards at too great an angle), in Scott and Boyd (1954, p.6.,--again not in the most extreme form), Phillips (1925,--tail shown as spread which is probably incorrect), Bernhardt (1940) and Johnsgard (1955).

Brüggemann (1876) was the first to describe the Head-Throw (in transl.):

The male ruffles the crest up, snaps it suddenly onto the back and emits a loud sound, almost like quaätsch, while in the mean time it makes one energetic thrust movement with the rear end of the body and feet. Alternately it lays the crest flat down and stretches one or the other wing wide out. This play usually lasts about five to ten minutes.

Again and again it is pointed out that the goldeneye has the most spectacular of all duck displays. Johnsgard (1955) writes that "the goldeneyes have developed the head-throw to its extreme", and compares this movement

of B. clangula with the similar movement found in the courtship of the mergansers and the Aythya. Boase (1924) wrote "the male threw the head and neck back, the nape touching the tail, immediately recovering and jerking the head in line with the extended neck held stiffly vertical". Gunn (1939) says "his astonishing 'jack-knife' movements...when he flashes his fluffed-out head on to his back, holds it there for a second, and then as quickly snaps it forward again." Alford (1921) wrote: —

The most acrobatic display that I have ever witnessed is that of the male Goldeneye....With a terrific jerk--sufficient, one would suppose, to dislocate its neck--the head is thrust upwards to the full extent of the neck, with the bill closed, then bent sharply backwards until the tip of the mandible touches the tail. The next second, and with equal force, head and neck are jerked forward again to the normal position, with bill agape, the bird uttering at the same moment a loud squeak, not unlike the sound produced by the creaking of rusty hinges, and splashing the water behind it by the force of the convulsion. The whole performance occupies but two seconds.

Munro and Clemens (1931) description gives an idea of the marionette-like quality of the movement: "First one male then another would jerk back the neck convulsively as if pulled by a wire, until the neck was lying on the back with the bill pointing up or even backward. Then the same convulsive jerk would bring head and neck back to normal position."

The rearmost position of the Head-Throw is more extreme in B. clangula than in B. islandica and the head is held on the rump statically longer in the Head-Throw than in the Head-Throw-Kick. Townsend (1910) wrote: "Sometimes the head is held on the rump for several seconds before it is snapped into place". Brewster (1911) wrote: "The living bird would ordinarily remain in the attitude just described from half a second to a

full second or perhaps two seconds, but rarely longer than that".

Heinroth (1911) wrote that during this action the head is made more noticeable by spreading of the feathers of the head. In the Head-Throw-Kick this has been noticed more often.

Brewster's (1911) description is the most complete: —

Back thrust of head and neck ending in the folded duck-skin posture. Sometimes made from the mast-head posture but far oftener directly from the normal position, by a single uninterrupted upward and backward swing of the head and neck; this movement was so swift and sudden that I often failed to follow it...At its termination the neck lay extended along the back and so very flat and close that it was scarce noticeable. The head showed conspicuously enough, resting apparently on the occiput at a point anywhere between the middle of the back and the rump, with widely-parted mandibles pointing straight upward...At the close of this brief period of inaction the head and neck would swing forward, usually less rapidly and abruptly than when carried backward, sometimes pausing for a moment when the mast-head posture might be taken, but, as a rule, continuing to move without decided halt until the normal position was resumed.

Townsend (1910) also apparently believed that the Head-Throw could be assumed from a "Masthead" pose (breast elevated, neck stretched upwards, call emitted). After describing this he continued "the head is then quickly snapped back until the occiput touches the rump. whence it is brought forward again with a jerk to the normal position." Evidently Brewster was doubtful that the Masthead was often a part of this display, and since he did not distinguish the Head-Throw completely from the Head-Throw-Kick we may assume that he only saw the "Masthead" pose only on occasions when the kick of the feet was present. It is true the head, as it goes back, is lifted off the back and then placed down onto the rump, but no call is emitted until the head is in the latter position.

Most usually the Head-Throw ends with the head being returned to the normal sitting position. In some instances the head is raised off the rump with the neck stretched and stiff, so that as it rises to the vertical the Masthead pose is assumed. This is however only to be mistaken for the true Masthead display if a static view of the most upright position is seen, for the head is not poised here, but continues to swing on forwards into a "Bowsprit" pose. But here again, since oscillations of the head do not seem to occur on these occasions, the forward position is not to be confused with the true Bowsprit display (which it only resembles in a static view).

Boase (1924) writes of this relaxation from the head on rump position "immediately recovering and jerking the head in line with the extended head held stiffly vertical". He talks of a call urr in this last position, but was probably hearing only the call accompanying the earlier phase of the Head-Throw. In another instance the same author wrote as follows: —

The display began as before with the upward extension of the neck and the swing back so that the nape touched the tail, but, held there an instant and instead of the up-thrust of the rear of the body (Head-Throw-Kick), the head and neck were jerked up in line vertically, and a call quee-reek uttered, then a relapse to normal.

Boase writes that this display was repeated several times, but as there is no mention of a kicking motion it seems evident he is describing the Forward Position following the Head-Throw.

Johnsgard (1955) is clearest about the Forward Position. "The head is then rapidly brought forward to its normal position, or perhaps more commonly to about a forty-five degree angle. The bird holds this position, with neck extended, for several seconds".

"Stretching of the trachea of syrinx"

We need to discuss the form of the call, and the supposed origin of the Head-Throw in the necessity to stretch the trachea or syrinx to produce the call.

A call is emitted from the open bill when the head is laid on the rump and as the head is moving forward again. Brewster (1911) was unable to decide exactly when it occurred. Both he and Townsend (1910) claimed that they had seen the movement unaccompanied by any sound but this seems improbable. The call is variously described. Heinroth writes (1911.transl.): "While he returns the head into the normal posture one hears a fairly loud 'creaking note'." Bernhardt (1940) speaks of a 'creaking note' also (Knirrlaut). Johnsgard (1955) after describing the submergence of the posterior half of the body wrote: "at the same time they utter a double note, zzee-at, which in quality reminds me of the cry of a Nighthawk (Chordeiles minor)". Townsend (1923) talks of "a harsh and rasping double note, vibrating and searching in character and expressed by the syllables zzee-at."

Heinroth (1911) discussed the contorted position of the Head-Throw in relation to the production of the call that is associated with it. He wrote as follows (transl.): —

Obviously this peculiar head and neck movement is necessary for the production of the courtship call, which is demonstrated, if by nothing else, by the exceptional structure of the windpipe. It should again be mentioned here that the trachea and the bulla ossea of the drake Clangula is built completely differently from that of the other Fuligulinae; it reminds one very strongly of the Merginae.

Lorenz (1941, transl. 1952) perpetuates this explanation. After describing the exaggerated 'burping' movement of the Garganey (Anas querquedula)-- a

form of 'head-throw' he writes: "The similarity with Bucephala certainly rests upon convergence, which has arisen from the necessity, found in both forms, of stretching the bone-drum to a high degree". But he has not expanded this theme, and there seems to be considerable evidence to show that it is not correct. The question is whether the call developed first and forced the exaggeration of a less extreme movement, or whether (as seems more likely) the movement developed first and the call was differentiated later. The Head-Throw--or something resembling it in actual body form--is found not only in B. clangula but also in Mergus and even in Aythya vallisneria (Fig.2). Allen's account of the Canvasback (in Bent, 1923) reads as follows:

The call consists of three syllables, ick, ick, cooo, with a little interval between the second and third. When the first two syllables are being produced the bird opens his bill slightly and then with considerable force appears to inhale quickly, jerking his bill as he does so. It appears as though this sudden inhalation abruptly closes the glottis so as to produce the two rather high-pitched, sharp, quick, ick, ick notes. Accompanying these notes the back of the neck swells and the feathers rise as though a gulp of air were being swallowed. Immediately, however, it seems as though exhalation occurred with the bill closed, accompanied by a low cooo like a muffled bark or distant moo of a cow....Accompanying this note the chin swells out for an instant with a curious swelling about the size of an ordinary marble.

Very frequently this note was accompanied by the head-throwing performance, already referred to, the ick, ick notes being given when the head was thrown back, and the cooo when the head was brought forward again, the swelling on the chin being noticeable as the head assumed the normal position.

Hochbaum (1944) called this movement in the Canvasback the "Head-Throw". He writes, significantly for our purpose, that the ick ick notes do not carry for any great distance. The cooo note which is louder, "an asthmatic groan which, on a still day, may be heard half a mile or more". When heard

close-to it appears as a split note, cu-oo¹. When many birds are courting at a distance it "seems soft and dovelike". He points out furthermore, that "This note, in part, or in full, is given frequently without the head-throw. When thus offered it is accompanied by a short, forward thrust of the head, while the neck is arched slightly backward. A conspicuous swelling appears on the chin the moment the sound is uttered."

Thus the fact that the Head-Throw is identical in the Canvasback and B.clangula (and also in Redheads, (Aythya americana), and scaups, as well, according to Allen--in Bent, 1923), but the notes are different, indicates that the notes as such have no part in determining the movement for the notes are different and are determined solely by the form of the trachea and the force of air (and stops) behind it. That the Head-Throw is not a necessity for the appropriate air blast to be created is indicated by Hochbaum's statement that the cooo call (the ick, ick syllables are probably included in his meaning) may be given in the absence of the Head-Throw movement. The movement is not therefore a necessity.

Furthermore since the Head-Throw takes the same form in B.clangula and A.vallisneria, but the calls differ, the movement must (if they are related genera) be older than the call (in the same way that a movement is older than the plumage characters displayed by it). Presumably stretching (or some other action) of the "bone-drum" (syrinx presumably) is part of the production of the note, since a swelling of the throat appears in the extreme position. But that the movement of the head onto the rump is necessary to produce the required tensions or muscular actions on

the trachea (as suggested by Heinroth and Lorenz) seems improbable.

The swelling of the neck is found also in Anas querquedula.

Lorenz (transl. 1951-52) describes it as follows: —

Then while the head is brought back in a sweeping curve to the normal position, a loud rattling noise is belched out, during which the stretched windpipe springs, like the cord of a bow, to the front of the neck, lifting a high fold of skin. This is invariably followed by drinking.

The rejection of any phylogenetic relationship between the "Head-Throw" of the Garganey and Aythya, and Bucephala and Mergus, needs to be re-examined. There are three common features a). the movement, b). a call being emitted c). the swelling of the neck as the windpipe springs forward. If the movement is not a functional correlate of the call, then the combination of all three items being found in two groups which are unrelated is highly improbable. In Aythya the call may be given in a normal posture, but there are apparently no other elaborations. In the Mergini the Head-Throw-Kick appears to be an elaboration of the simpler Head-Throw display. In A.querquedula drinking follows the "Laying of the Head Backwards" (as Lorenz describes it), but drinking does not follow in Aythya or Bucephala.

To explain such a situation it is only necessary to suggest that Aythya represents a central stock from which the Mergini have derived and retained the essential postures, while A.querquedula is a species linking the Aythiini to the Anatini. In view of other considerations about the Surface-Feeding Ducks (Anatini) such an hypothesis is not impossible.

Head-Throw-Kick (*B. clangula*)

-This movement has considerable resemblance to the Head-Throw and presumably has differentiated from it. It is similar to the Kick of *B. islandica* but as with the Head-Throw it is a neater movement than either of the equivalent postures in *B. islandica*. As noted by Brewster (1911) the head lies on the rump for a considerable portion of the whole movement in the Head-Throw, but in the Head-Throw-Kick it is held there only for a very short period. It is this, with the propulsive movement of the feet, and the position of the head in the second half of the movement which (in *B. clangula* at least) distinguishes the Head-Throw proper from any version of the Head-Throw-Kick.

Field Description

I have seen this movement only once, during the spring migration of 1955. I described it as consisting of a convulsive movement of the legs back, and the head up. It was like a sudden spasm, as its arresting (end) was as quick as its start. It seemed probable that the head was held on the rump for a shorter time than it was in the Head-Throw.

Film Description

Walcott and Dane's film illustrates that this movement may take two rather different forms (though perhaps there are intergrades). In both the head is thrown back onto the rump, as in the Head-Throw, but its duration there is curtailed. But the two forms start and end in different ways. The common element is the violent propulsive movement which gives the two movements their common name.

Position 1. (Figure 20).

In this form the breast is elevated, and the head and neck are erect before being swung backwards and placed on the rump. This resembles the Head-Throw but the head remains on the rump only about one-third of the time. The rear of the body is then humped up as the feet are drawn forward ventrally, and there is a downward pressure of the feet at the start of the kick. The wings show as a projecting spur beyond the rounded angle of the body. At this time the head is brought forward and lifted off the back at the end of the foot-stroke and the beak, which has been facing 10 degrees backwards when the head is on the rump, remains in this position. The head is flung forward until the breast and front of the neck form an upright line, but since the beak is still being held 10 degrees back, from the vertical, the position is very striking. The throat appears very swollen (bulging forwards) and the beak is opened. Then the head is lifted back and up at about 10 degrees back from the vertical. As the beak closes the head is rotated, so that the beak returns to the horizontal, and the Head-Flick follows. The bird then relaxes into the Normal resting position. The whole sequence only takes 2 seconds.

Position 2. (Figure 21).

In this form the head is not elevated, before being thrown back, and does not reach the rump. It is drawn between the shoulders more rapidly than in Position 1, and remains on the back about half the time that it does in Position 1. The rear of the body is humped and the tips of the wings appear as in Position 1. The head passes forward until the neck it-

self is right underwater. The head is then lifted back, with beak open, as in Position 1. Head-Flick and relaxation follow. Owing to the shorter time taken to assume the extreme backwards position this sequence only took 1-1/3 seconds (31 frames).

The forward movement of the head, in both forms, occurs as the body angle is inclined decidedly forward, and the mass of the body is behind the neck, i.e. forward propulsion. But the head should really be flung backwards mechanically by the kick of the feet. It does not do so, and its forward passage implies that it is rigidly stiff and that the protracting muscles are contracting strongly.

Literature Descriptions

It is evident that almost everyone has regarded this movement as an extreme form of the Head-Throw, and undoubtedly they have the same derivation. The head-Throw-Kick now has a quite different form (and timing) from the Head-Throw even in the portions of the sequence in which the kick of the feet is not the dominant motion. It is also evident (as was mentioned for B.islandica) that the behavioural context, in which it occurs, differs somewhat from that in which the Head-Throw occurs.

The first part of the Head-Throw-Kick (to the head-on-rump position) may resemble the Head-Throw exactly. As the head passes forward the rear part of the body and tail are raised, as the feet are brought forward, and then thrust backwards. Spray is then thrown up behind the bird. The Handbook of British Birds quotes H.Wormald, and Phillips (1925), as saying that the kick of the feet may occur as the head is still moving backwards.

There is doubt whether one of both feet are kicked and, if both are involved, whether they occur together or successively. The head is raised, after the kick, to a forwards position and then lifted up and back.

The second half of the head movement (forwards) may however be different, the neck being brought forward and actually lowered into the water, bill pointing upwards (rather like Deep Jiving in the female), before being elevated as before.

Accounts of this movement begin with Gilpin (1880) who talks of water being "thrown into mimic surf by their play". Millais (1913) wrote: "The third action is to drop the head...suddenly between the shoulders, the bill still pointing heavenwards, and to kick...so as to throw a jet of water high in the air behind the bird." Brewster (1911) describes the movement as follows: —

Just as the paaap was uttered--or perhaps a fraction of a second later--a slender shower or spurt of water...might often be seen rising immediately behind the bird to a height of one or two feet which, indeed, I saw plainly more than once, jerked out of the water..Owing to its force and direction the kick caused the hinder portions of the body to sink perceptibly in the water for an instant, after which these parts bobbed still more obviously upward...

Phillips (1925) wrote that sometimes when the head was snapped back (he did not distinguish the Head-Throw from the Head-Throw-Kick) the bird "shoots itself forward by a rapid kick of both its bright red legs, which results in a spurt of water showing behind the bird for a distance of several feet". In fact, of course, the kick does not begin until the head is already on the rump, but if the showing of the red feet has signal value this is a major point of distinction of the Head-Throw-Kick from the Head-

Throw. It is possible also that the spray, per se, has extra-corporal signal value. Townsend (1910) likewise emphasised the colour of the legs. He wrote "As the head is returned to its place the bird often springs forward, kicking the water in a spurt out behind, and displaying like a flash of flame the orange-coloured legs."

Townsend furthermore adds that there are "many variations of this curious action" and goes on to delimit the Head-Throw proper and a movement which reads as though it were the Masthead, or the elevated pose of the head at the beginning (of Position 1) or the end of both forms of the Head-Throw-Kick. Phillips (quoting Brewster, 1911 and Boase, 1924) also suggests a Masthead-like posture. Boase (1924) explains that the movement starts from the Normal position, with neck retracted, and how the neck is "suddenly extended upwards, the head remaining normal to the neck, a back-throw of the head and neck so that the nape touched the tail, the neck being arched over the back." The Masthead-like pose at the end of the Head-Throw-Kick is described by Johnsgard (1955) who wrote: "A second typical action is a partial head-throw, where the head is rapidly jerked upward to a position directly perpendicular to the water, usually accompanied by a frenzied kick that splashes water far behind". This reads like a description of the Kick of B.islandica, but it is also a description of the elevated pose assumed at the end of the Head-Throw-Kick. The beak is not opened as the head is raised and goes back, but it is opened in the elevated pose at the end of the movement. Indeed Brewster's description of the Masthead pose probably applied to this for he said the beak was open in it. As explained later the name has been reapplied to a similar pose (but different display).

Boase (1924) describes the Position 2 as follows: —

followed by an up-thrust of the tail, the bird resting momentarily on the base of the neck in the water, and a resumption of the normal posture.

This is illustrated by Bernhardt (1940) who states that the tail is fanned. He wrote that the head is suddenly thrown onto the back where a "creaking note" (Knirrlaut) is uttered—" and jerks the head and neck well forward, at the same time spreading the tail and shooting a stream of water out behind with the feet." I know of no other reference to the spread tail, except the illustration by Allan Brooks of the Head-Throw (in Phillips, 1925). Bernhardt (1940) also illustrates the position of the feet in another figure. After breaking surface they are seen to be placed quite a bit lateral to the body. Boase records that the whole performance is carried through with a swing and great rapidity.

Bernhardt (1940) wrote that the "creaking note" is uttered "not only when 'throwing out' the throat as I assumed earlier, but also in the dorsal position of the head, and indeed with opened bill". Boase mentions a "call or grunt". Gilpin (1880) mentions a "short shrill cry comes...from his upturned bill". Millais wrote: "At the moment of throwing back the head the call keek-kee is emitted, but sometimes it is given after the kick". Brewster (1911) described it as a "short vibrant paaap, not unlike that of the Woodcock but a trifle more prolonged and also less harsh and incisive. It reminded me somewhat of the blast of a penny trumpet, less forcibly of the wheezy quack of a drake Black Duck...It was sometimes doubled (paaap-paaap) and occasionally trebled (paap-paa-paa) ...syllables were each shorter than the normal single call and otherwise slightly different".

Millais (1913) mentions that the head feathers are puffed out during this movement, even more than in the Bowsprit.

Discussion

We do not know if the call is different from that which accompanies the Head-Throw, or whether no differentiation has yet taken place (as compared with the movement). The occasions on which the movement is found have been discussed in the section dealing with B.islandica.

Munro and Clemens (1931) wrote: "The males did not face a female when displaying thus. The action seemed entirely mechanical and would be indulged in just as freely by members of a band composed entirely of drakes". This raises the question of whether this movement has primarily a courtship or "greeting" or other significance. This has already been discussed in the description of the Kick in B.islandica.

There is some confusion as to whether one or both feet are kicked during this movement. Bernhardt (1940) in his illustration confirms that both feet perform the kicking movement together. Millais (1913) wrote that they "kick once alternately with both feet". Brewster (1911) wrote: "When, as occasionally happened, the jet was doubled in volume, and also apparently somewhat divided at the base, I thought that the bird had made simultaneous use of both feet". This implies that Brewster thought that the more usual form was a kick with a single foot. However this would presumably have the effect of turning the bird's orientation through some degrees. There is no indication that this happens. Rather it may be suggested that both feet are always kicked, but that occasionally one

breaks surface a little before the other so that two jets of water are produced, one a little ahead of the other, while normally the jets are following equal and parallel paths and appear as one from the side. If alternate beats do prove to be the more usual on the other hand this would presumably be a reflection of the alternate foot paddling of the ducks during leisurely swimming.

B.clangula differs from B.islandica in that in both the displays of the Kick Complex the head is laid back on the rump, and in that the two displays are more clearly differentiated. The kick in Head-Throw-Kick has the effect of raising the rear of the body and throwing the neck forward and down, while in B.islandica the whole body sinks and the neck does not get forward into a "Deep Jiving" pose. There must be considerable differences in the way the foot-stroke is made between the two species. There does not appear to be any tilting of the head sideways in either display in B.clangula, as there is in the Pseudo-Kick of B.islandica, in which the head does not come in contact with the back at all. The origins of the displays is not known, but the Head-Throw is found in Mergus and in Aythya and may be a very old display. The call is not coincidental with the kick in B.clangula as it is in B.islandica. The need to stretch the bone drum of the respiratory tract has already been discussed in the discussion of the Head-Throw.

FIGURES 13-14

B.islandica (Icelandic population)

PSEUDO-KICK & KICK

From a film taken by Dr. Frank McKinney at Slimbridge,
England

Figure 13. Pseudo-Kick (Side View)

Though a kick of the feet occurs it is not as violent as in the Kick, and the bird merely bobs on the water, not sinking as far as in the Kick. The head does not reach the back between the shoulders. A Head-Flick ends the sequence.

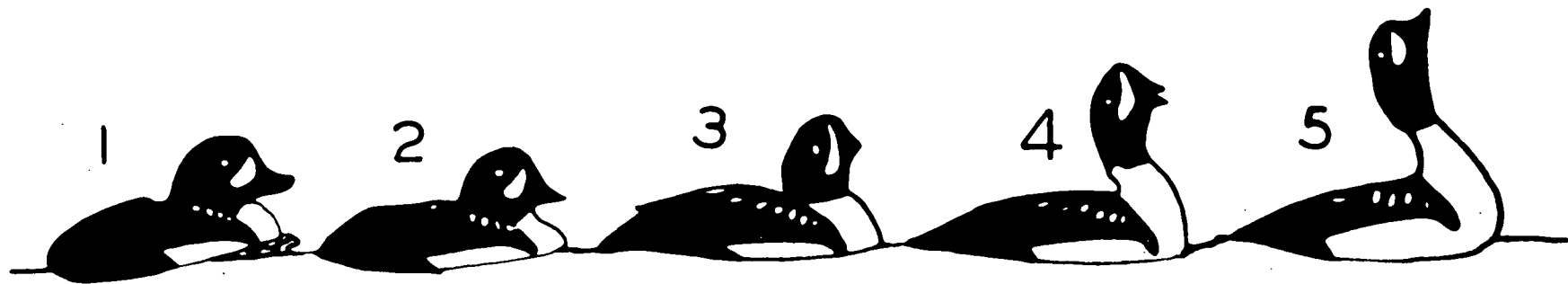
Frame 4	Beak opened
Frames 5 & 6	Neck extended up and back to full extent, beak apparently closed
Frame 6	Rear of body is humped up as feet are brought forward for the Kick of the feet.
Frames 7-10	Body sinks in water, beak open.
Frames 11-13	Head-Flick as head passes forwards
Frames 14-15	Head drawn back and down into Normal resting position.

Figure 14. Kick (Side View)

The head comes to lie on the middle of the back, not as far however as in the Head-Throw-Kick of B.clangula. The body sinks much deeper than in the Pseudo-Kick.

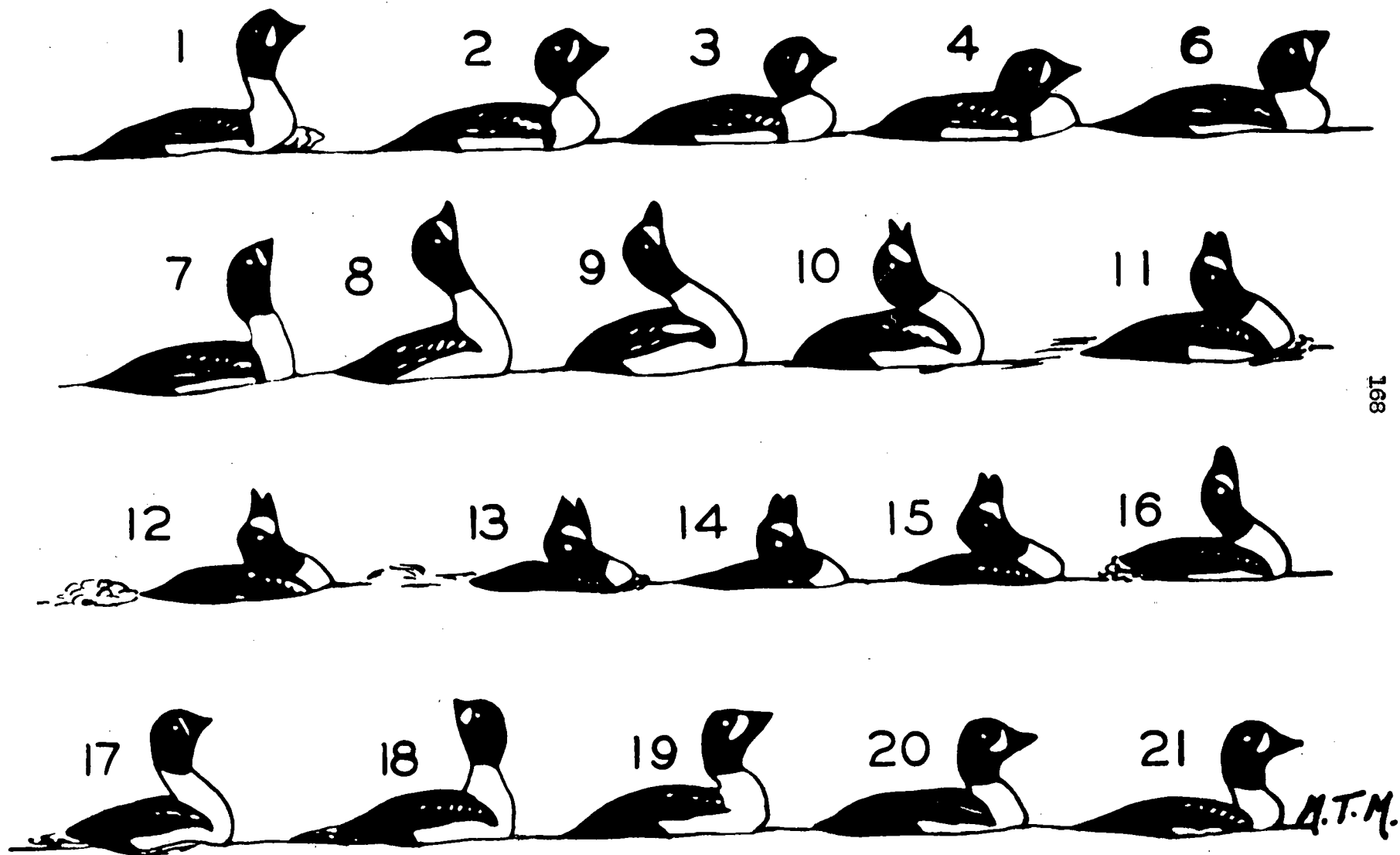
Frames 3 & 4	Head is drawn sharply into the shoulder
Frames 6 & 7	Head is elevated forwards
Frames 8-12	Head is thrown back between the shoulders (and beak opened while the head is still passing back)
Frames 9 & 10	Feet brought forward and rear of body humped.
Frames 11-14	The Kick causes the sinking of the body (as compared with <u>B.clangula</u> , in which the rear of the body remains elevated)
Frames 15-17	Body rises
Frames 17-19	Head-Flick

16 frames/second. Shutter Speed 1/32nd second



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FIGURES 15-16

B.islandica..(Icelandic population)

PSEUDO-KICK & KICK

From a film taken by Dr. Frank McKinney at Slimbridge,
England

Figure 15.

Pseudo-Kick (Rear View)

Shows tilting of the head towards the female to the
right of the male.

Figure 16.

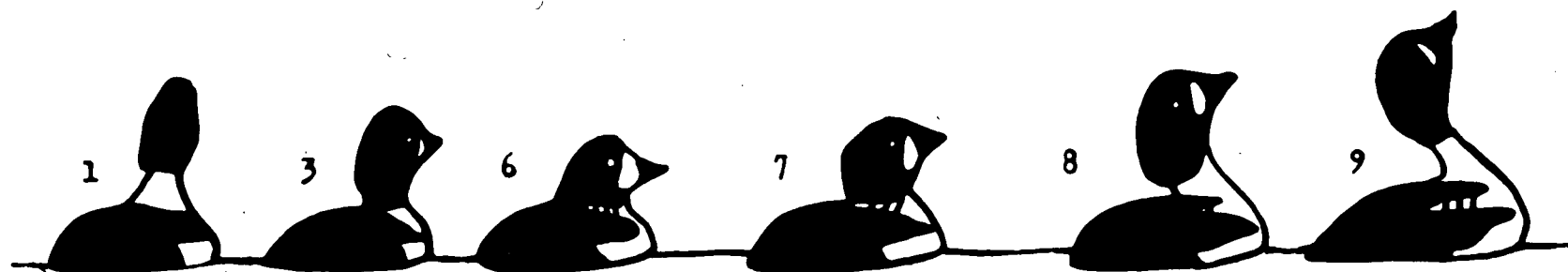
A. Pseudo-Kick (Front View)

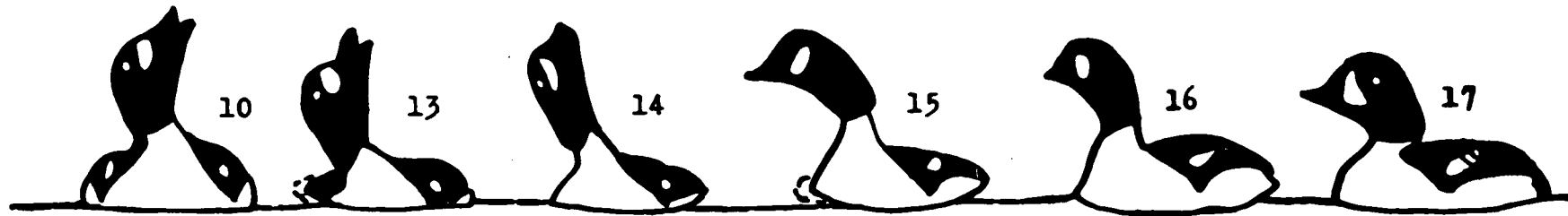
Shows tilting of the head toward the female to the
left of the male

B. Kick (Front View)

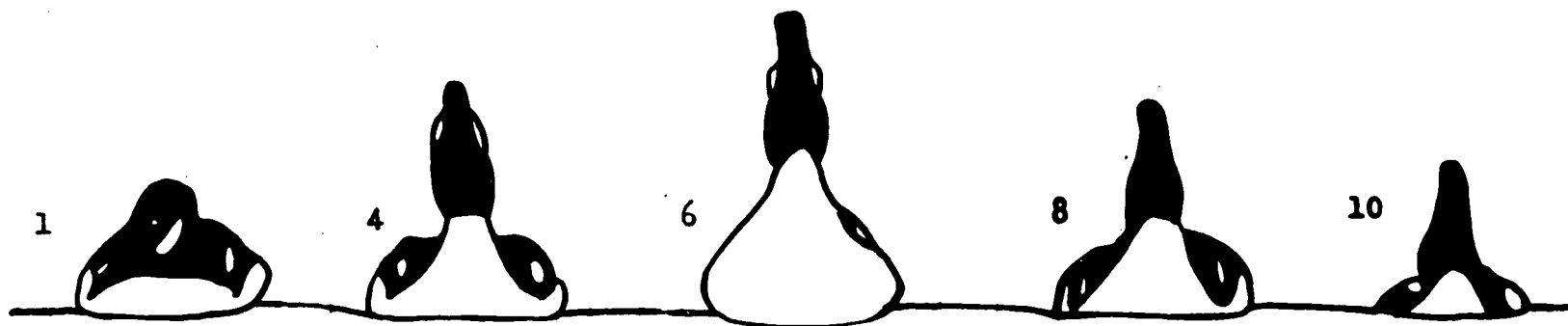
Shows the Head-Flick at the end of the movement
(Frames 13-15). Any tilting of the head that may
occur, occurs only in the extreme position (Frames
10-12 only).

16 frames/second. Shutter Speed 1/32nd second.





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FIGURES 17-19

B.clangula (American population)

HEAD-THROW

From a film by Charles Walcott & Benjamin Dane

Figure 17. Side View

The head and neck are lifted (Frames 2-5) as in the First position of the Head-Throw-Kick (Fig.20). The head remains on the rump for 22 frames (Frames 7-28). The beak is open from Frames 10-29. There is a Head-Flick (Frames 32-35).

Figure 18. Front View.

Frame 1. Breast appears as a mound of white from which the beak may be seen projecting upwards.
 Frames 10-12 Head-Flick at the end of the Head-Throw.
 Frames 28-40 1st Head-Turn to right
 Frame 45 Centre position held between Head-Turns
 Frame 48 Head-Turn to left
 Frame 67 2nd Head-Turn to right
 Frame 81 Centre position after 2nd turn to right
 Frames 83-85 Movement of head back towards rump during 2nd Head-Throw.

Figure 19. With Forward Bowsprit Position

The head is laid on the rump for 22 frames, as in the normal Head-Throw (compare Fig.17). Instead of being drawn forward into the normal resting position (compare Fig.17), the head is lifted up and forwards into the Bowsprit pose, and held there for nearly 20 frames. It is then drawn back into the shoulder with a Head-Flick. That this Bowsprit pose is part of the Head-Throw is evidenced by the delaying of the Head-Flick until after it, and to the apparent fact that Bowsprit Pumping does not occur.

24 frames/second. Shutter Speed 1/48th second.

1.

2.

4.

5.

6.

7

10.

13.



28.

29.

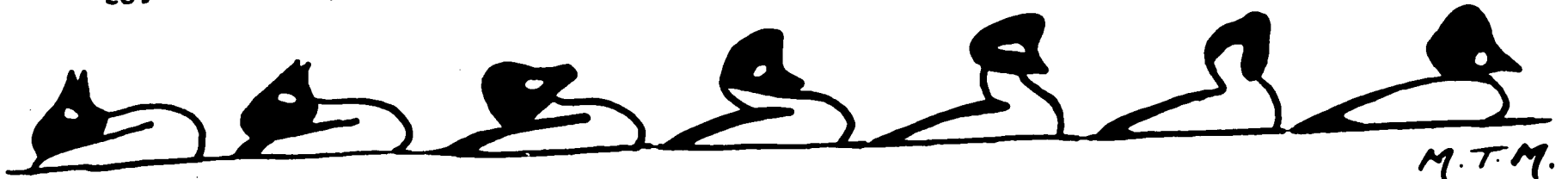
30.

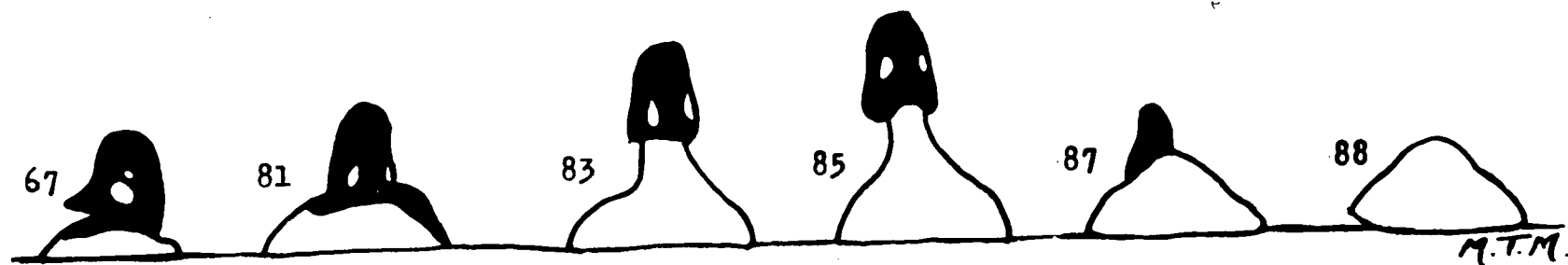
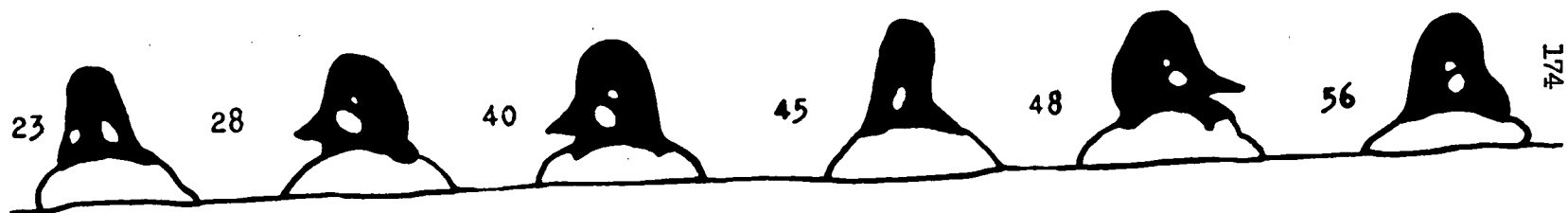
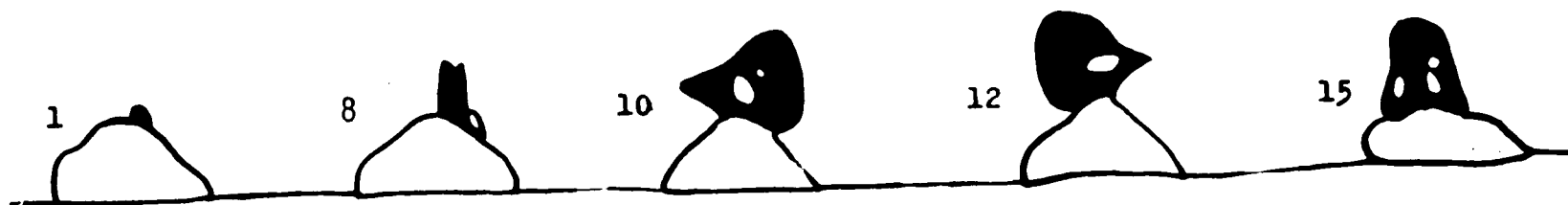
31.

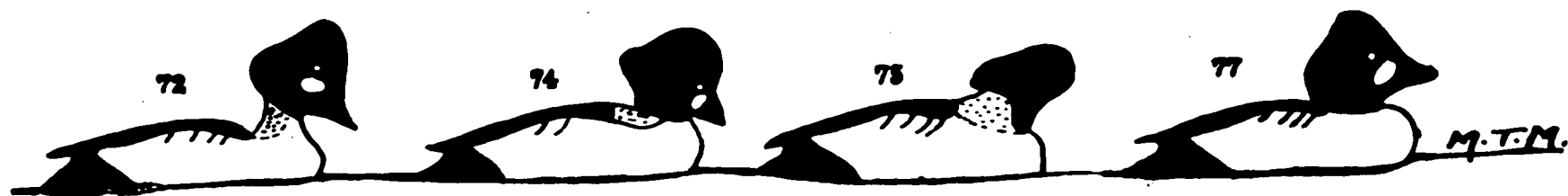
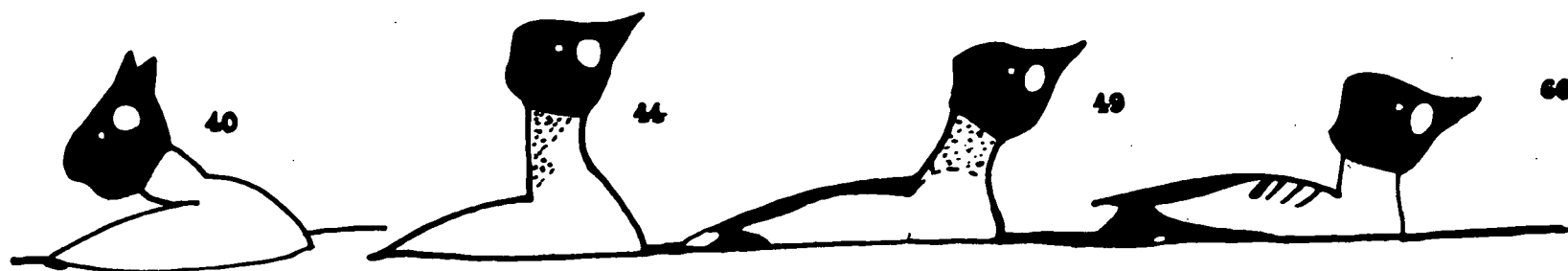
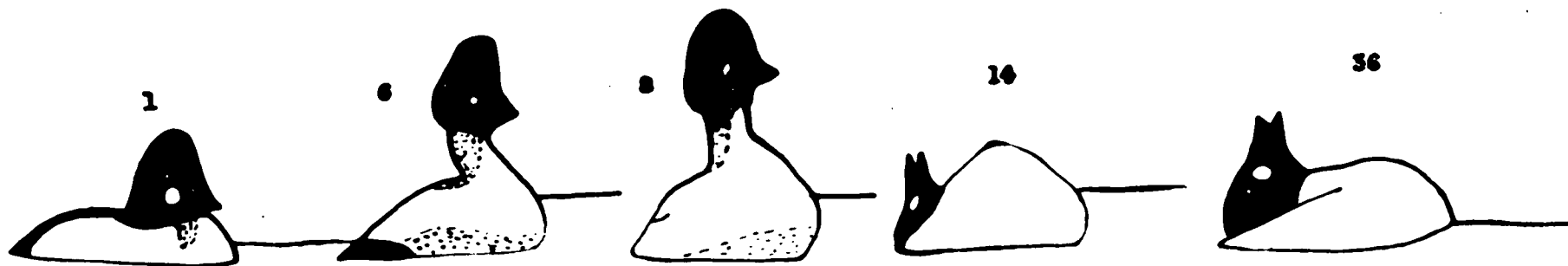
32.

33.

35.







M.T.M.

FIGURES 20 & 21.

B. clangula (American population)

HEAD-THROW-KICK

From a film by Charles Walcott & Benjamin Dane

Both frames start with the same two individual birds (Frame 2, of Figure 20 = Frame 1 of Figure 21). In Figure 20 the farther of the two is followed through Position 1. In Figure 21 the nearer individual is followed through Position 2 and completes the movement in about $\frac{1}{2}$ the time taken by the bird in Figure 20.

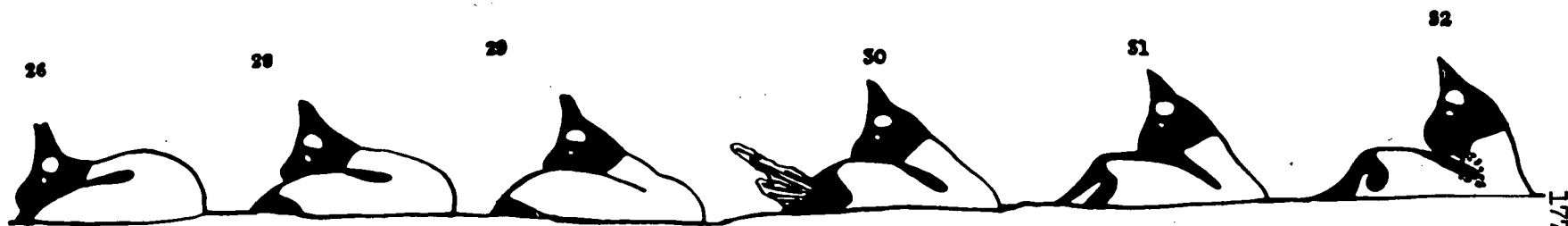
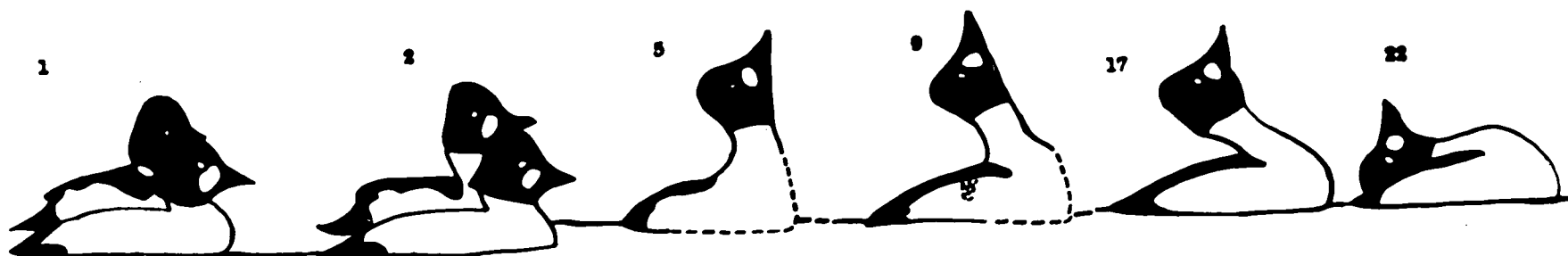
Figure 20. Position 1.

The head is lifted up, on extended neck, as in the Head-Throw. The head is held on the rump from Frames 22-29, which is one-third of the time in the Head-Throw. The only sign of the beak being opened in this position in either Figure is in Frame 26.

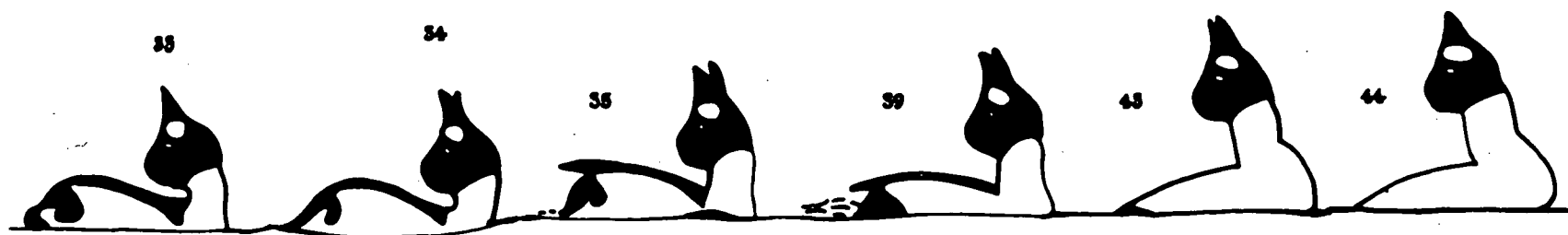
The rear of the body is drawn in in Frame 30 (when the first and main Kick occurs and the head begins to move forward. The rear of the body remains humped until Frame 35 when the wing becomes visible as an acute projection beyond the contour of the body. A second kick appears to occur in Frame 39, and the head is then elevated from the lowdown forward position which it has reached. The beak closes. A Head-Flick ends the sequence (Frames 47-50).

Figure 21. Position 2 (less extreme).

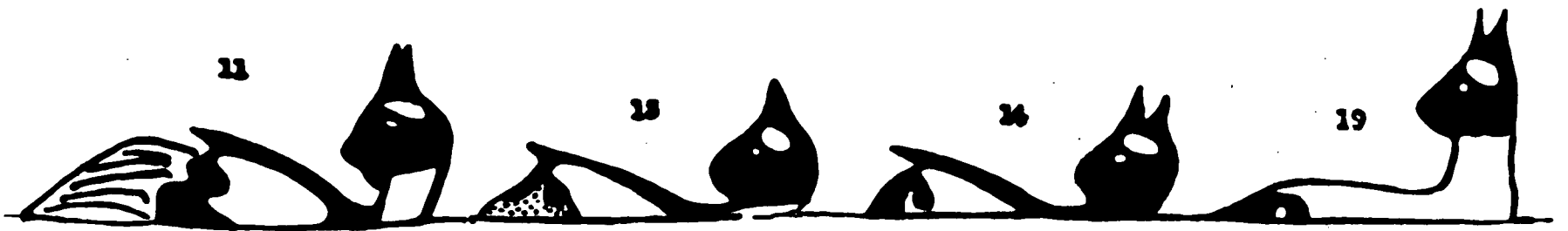
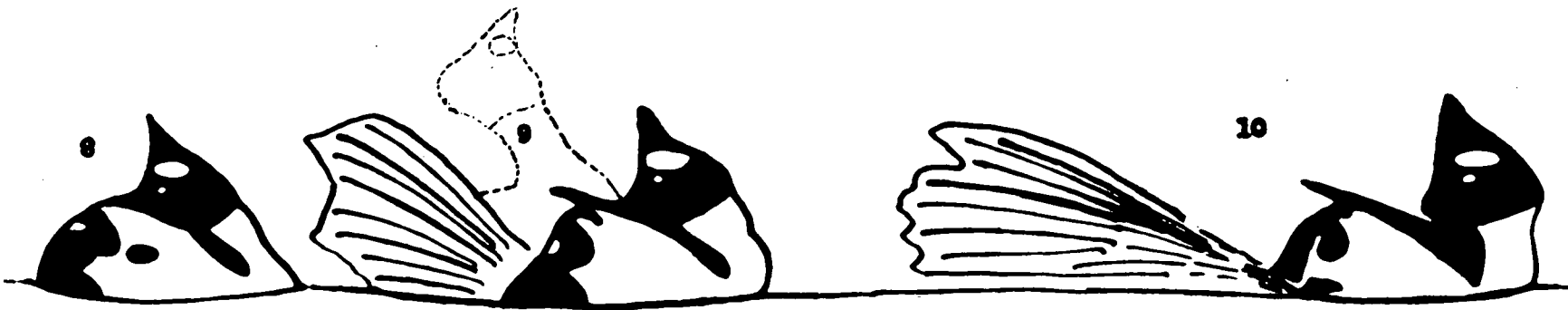
The Head is not elevated at the beginning of the movement, but is drawn directly into the shoulder, not as far back along the back as Position 1. The head is held on the back for an even shorter time (Frames 5-6) and the beak is not opened. In Frame 7 the feet have been brought forward and the rear of the body is humped. In Frame 9 the wing appears as an acute projection as the feet break surface. The equivalent position at this time in Position 1 is shown by a dotted outline (the head still passing backwards). The head and neck pass even farther forward than in Position 1 and the neck is submerged (Frames 13 & 14). From this position the head is raised (beak open) and a Head-Flick (frame 25) ends the sequence. The bird in the foreground in Frames 22 and 25 is the female. The beak appears to be open in Frame 11, as well as later.



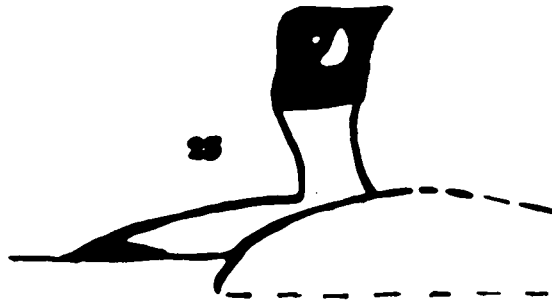
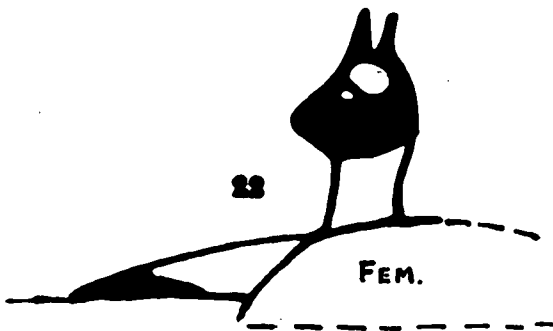
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M.T.M.



M.T.M.



Rotary Pumping (B.islandica)

This movement (it is hardly a posture, as the movement is continuous) is the most frequently performed of all displays in B.islandica, whereas the Bowsprit Pumping of B.clangula is much less common than other displays, in particular the Head-Throw. Rotary Pumping varies in intensity to a considerable degree and has at least one variant form.

Field Description

The common form is illustrated in Figure 22, and analysed in Figure 26, in which the path of the tip of the beak is traced. The head is lifted back and up from the resting position, then lifted forward, by rotation of the stiffened neck, until the neck is at an angle of about 75 degrees, then undergoes a gradual lowering and contraction of the neck into a semi-crouched position before being lifted back and up again. The path traced by the beak is pear-shaped. The neck is considerably straighter and more upright (neck axis at a steeper angle in the forward position) than in B.clangula.

The speed of the movement varies greatly, as does the number of rotations. It seems that when birds are either on territory, or the sexual motivation is weak, only Rotary Pumping occurs. The male will give but little jerks of the head (hardly recognisable as pumping) and this may go on for as long as 45 seconds. The movements may be very slow, or even be stopped temporarily while the male is almost motionless, with the head held high ("Head-Up" pose), as he watches the female. In the high up position the beak may be opened, and it is possible that we have here an intergradation of motivation with that of the Head-Up----Neck-Withdrawn position (discussed earlier).

Motivation is increased, either through some sort of feed-back in the true courtship sequence or because of an increase in aggressive motivation e.g. after a territorial boundary dispute, when a triumph ceremony occurs. The speed of rotations of the head (Rotary Pumping) is increased and of fuller amplitude, and there is a head forward (Laying Neck on Water) posture, which is frequent at this time (Figure 23).

In this "Threat" position the male makes a faint ticking or clicking noise. The beak is held wide open continuously at an angle of about 30 degrees (contrast Head-Up position) and the noise is produced either by a tapping of the tongue against the mandibles, or by exhalation through the syrinx. The ticking sound occurs in bursts of 4-5 clicks and greatly resembles the noise made by a pair of hand-operated hair clippers. The slight pause between bursts might be due to a pause for breath. Since the sound appears to be a broken series of stops it seems just possible that it is produced by a current of exhaled air, rather than by the tongue.

This form of Rotary Pumping is very regular. The number of head rotations before thrusting the head forward is fixed and few, reduced usually to two between each forward thrust of the head down to the water. We thus have a sequence: Pumping, Pumping, Threat, or PPT, PPT, PPT, PPT. At such times the Head-Flick which normally accompanies the Threat attitude (occurs during it at intervals) may occur while the head is in the head-raised position of the Rotary Pumping (Figure 23), between periods of Laying the neck along the water. This is an indication that the laying of the neck along the water has a truly aggressive motivation.

An example of the aggressive intermixture is seen in the following record: a male flew towards a female, and the mate of the latter threatened him, with a ticking noise, and the head in the Threat posture. This continued while the mated male did Rotary Pumping towards his female. He was making the ticking noise both while in the Threat position and also while pumping (it is not known if the beak was held open the whole time in this latter position). This aspect of Rotary Pumping, which Sawyer (1928) illustrated, namely the beak open during the movement, is not usual during pumping, and acts as a possible link with the Head-Up position, in cases of extreme stress or excitement. There is seldom any likelihood of such an individual becoming involved in a fight, for he is usually the territory owner.

Rotary Pumping is often performed by an intruding pair, when threatened by a territory owner, as the threatened pair swim away from the aggressor. In these cases the pumping by the threatened bird is quite violent but the head is held high and is not lowered to the threat position.

Once when a pair landed on the water the male began Rotary Pumping with head held high. Then into Threat, flew, landed and came up head-on with another male which went into a position resembling the Head-Up position, and flew with a different female. The aggressor did Rotary Pumping and the threat position a number of times, and then performed a considerable amount of preening i.e. even after the victim had flown away the aggressive motivation was still high, as was the sexual motivation expressed by Rotary Pumping.

Threat in Rotary Pumping

T h e T r i u m p h G r e e t i n g C e r e m o n y

After an encounter the male returns to his female. Rotary Pumping is the primary display he exhibits but very often the PPT, PPT, PPT; PPT sequence is added. The female responds on these occasions (and on other occasions when the male is doing Rotary Pumping towards her) by Jiving, and even occasionally a few pumping motions herself as they first meet. The return of the male to the female deserves to be regarded as a "Triumph Ceremony". Delacour and Mayr (1945) say that this mutual display is confined to geese (where it consists of similar movements by both male and female), but in its motivation and pair-bonding function the Triumph Ceremony of goldeneye is exactly similar, even though the movements of the two sexes may differ (the female can and does do Rotary Pumping, however, on occasions). It occurs after nearly every encounter. Whether the threat attitude is assumed as the male goes to meet his female or only when they are swimming alongside each other I am not sure. The female shows no sign of being intimidated by the male, however and she Pumps as they go towards each other (= Greeting in downies) and Jives when she come alongside or behind him. Sometimes the male may direct his Threat outwards towards another male. It is very rare indeed that the male attacks his own female.

There is a suggestion here that in the case of the Laying Neck on the Water posture which occurs during Rotary Pumping, on such occasions, there is no aggressive or flight motivation at all in respect of the female, although the Rotary Pumping itself is being directed at her. The aggressive

motivation present in the Triumph Greeting Ceremony is not, apparently, directed at the mate, but at third parties, whether present or not. All that is seen is Rotary Pumping, Threat and occasionally beak-opening in a high position of Rotary Pumping (?Head up position, with escape motivation).

In ethological theory aggressive elements in courtship behaviour towards the female have been explained as either indicating a past conflict situation (which has been ritualised in the intention movement of attack as a courtship display) or as indicating that aggressive motivation is still actually present during a courtship sequence. But need this be the only conflict (as discussed in the Introduction), and need the aggressive postures be necessarily directed at the mate, rather than at third parties? It is not hard to think of analogies from human behaviour in which the presence of the female, and/or an adversary, leads to greater degrees of sexual activity with or without aggressive activity associated with it, than when the female is absent. The Triumph Ceremony is just such a situation in ducks. There is no indication that the female accepts the actions of the male as being a threat to herself, although the Pumping which she may mutually perform with him, or the Jiving, may have the function of appeasement.

Circumstances in which the motivation of another bird (e.g. in a courting party) arriving on the scene, is not made clear at once, or is not known to other birds, requires a greeting ceremony with appeasement function. It is possible that the Kick display has such a function for it occurs at times when a bird is a new arrival, or is about to land near some other birds.

Individual Distance

In any discussion of the aggressive content of sexual displays one must clearly consider the nature of "individual distance", both as regards the origin of the displays, and as regards their present day motivations. Goldeneyes pair on the wintering grounds and are not there being more than slightly aggressive towards each other. They move around alone, in pairs, or flocks (of from a few birds to hundreds, or even thousands---eiders). Courting activities occur in groups and, at this time, the individual distance of the male is very small. The birds swim close together and, individual distance being small, most displays are derived from conflict situations which have been expressed as displacement preening, bathing, stretching or drinking. It may have an aggressive element, as in Rotary Pumping with the Laying Neck on Water attitude, or an escape element (Head-Up position), but these are not the only displays. This is because the individual distance (which is defended) is at that time so small that the necessity to curb and ritualise aggression in courting parties is slight. Indeed it seems that it is only a favoured male who seems to go in for any great aggression against its neighbours in a courting party (at least in scoters) i.e. the individual distance is suddenly increased as the female pays attention to him.

Nevertheless the Threat position in Rotary Pumping may be an essential element if individual distance increases on the breeding grounds. When males clash on territory Rotary Pumping towards the female may need to be alternated with Threat towards the intruder to keep him away. Thus Threat may come to reinforce the pair bond, while still having valency for an intruder.

Unlike gallinaceous birds that have a 'lek' and in which we might expect the displays to derive from aggressive postures, for the lek is both courting ground and a territorially divided area, the ducks as a whole have very few courtship postures which originate from aggressive postures. As discussed in the introduction the tensions which may have given rise to displacement preening and to comfort movement displays are those between the sex drive itself and escape. These displays are commonest in the pre-coition sequence. It is true, nevertheless, that threat appears commonly to be included in the performance of Rotary Pumping, and that the Head-Up position may be the intention movement of flight. It is of interest therefore that Rotary Pumping is the most common mutual display, or display by the male towards the female while on territory. At this time the individual distance of the male has increased to several acres.

Literature Descriptions

Mary F. Jackson (M.S., 1952) described Rotary Pumping as follows: —

The head is slightly tilted backward until the bill points upward at an angle of 45 degrees to the vertical. Then the head is pumped up and down four or five times in rapid succession, by alternately straightening and bending the neck into an S-shape.

Sawyer (1928) illustrated the movement (with the beak open) in Figures 6-9 of Plate 3 in his paper. He includes in this the Threat posture (beak open). He writes: "head bobbing and elaborate neck pumping and stretching are the most outstanding actions" and then refers to the Head-Up position. He goes on "In many of his gestures the neck is extended to a surprising length. With neck stretched upward the bill may be opened and shut at one to three second intervals in repeated low quacks. I

think this is more common during rivalry, but I have noted it when the drake seemed to be courting a certain female". As explained earlier it is not my experience that the beak is open very commonly during Rotary Pumping. Plate 9 in Stonor (1940) shows Rotary Pumping and the Laying Neck on Water position which accompanies it.

Bowsprit Pumping and Bowsprit Position (*B. clangula*)Field Descriptions

I saw this movement, on two occasions, in the Interior during the spring migration (in which *B. clangula* crosses British Columbia to its breeding grounds east of the Rocky Mountains). The movement is quite clearly comparable to the Rotary Pumping of *B. islandica* though, from still photographs of any stage in this movement, it would be impossible to compare them. When the movement of the head is seen in the field, however, the oscillation of the head is seen to be quite similar in timing.

The movement was seen between a pair in 1955, and was observed to be in the form of a forward and upward movement along a plane 25 degrees from the horizontal. In the forwardmost position the neck axis (to the waterline) forms an angle of 50 degrees. The effect of this forward, and upward, elongation of the neck is that the beak appears to be longer, and more finely pointed, than in *B. islandica*. This effect is also accentuated by the gentler slope of the front part of the skull in *B. clangula*. At 73-Mile Lake on April 30, 1956, the Bowsprit Pumping was seen to be followed by the Head-Throw a number of times. In the field the movement gives, at first, the impression of being backwards and forwards, but is later seen to be actually following an elliptical path (Figure 26). It could be derived from exaggerated oscillations of the head during swimming, such as occur when the bird is alarmed and is trying to hold the head still for a good view while swimming (as a chicken does when walking).

Film Description

The Bowsprit Position may be assumed in three ways: 1) from the Head-Throw (Figure 19), by the head being passed forwards of the normal resting position, 2) via the Forward Scoop (Figure 25), or 3) from the Normal resting position.

Only in the last case is the head pumped while in the Bowsprit position (Figure 24). In the other cases it is held statically in the Bowsprit Position ~~for~~ some time. It is never assumed from the Head-Throw-Kick, another feature that distinguishes that movement from the Head-Throw.

The Forward Scoop movement resembles that leading to the Masthead position, but with a different directional form. The head is lowered forwards from the Normal position and a scooping movement is made over the water forwards. The head then goes up to a 45 degree angle, or is raised a little higher and then lowered an imperceptible fraction (as in the Masthead), and appears by faint forward and backward oscillations to be held in this position under tension. The Bowsprit Position may be held for about 1 second (20 frames) The head is then drawn back into the shoulders. A Head-Flick follows. Even when the oscillations are very weak the Head-Flick follows the Forward Scoop and Bowsprit pose, and is an indication that the movement is a true display.

From the Normal resting position the Bowsprit position is assumed (apparently) directly by lifting the head forwards, and upwards, at some 25 degrees. When the pumping is very pronounced, the neck also bends a little and the movement then has a considerable resemblance to that found

in B.islandica. During Bowsprit Pumping the back of the crest is raised, forming a cobra-like shield, and the contour of the head is sharply angled against the neck. The white face patch is greatly enlarged. This treatment of the head feathering occurs also when the position is assumed in other ways but no oscillations (pumping) occur. It distinguishes the movement from the Masthead in which, if anything, the head feathers are smoothed.

The Bowsprit occurs chiefly, it seems, when the male is approaching another individual, and has come quite close to that bird. It appears to have greeting function as it does in downies of B.islandica. It may also be associated with Head-Turning in the Normal position. There is a suggestion from Walcott and Dane's film that the Bowsprit position is a releaser of the Head-Throw in other males; indeed I saw this myself a number of times on April 30, 1956. The Bowsprit position (static at least) may be assumed by the female, and so the female herself may be able to release the Head-Throw.

Analysis of Pumping

Figure 26 illustrates the path of the beak tip as traced from film sequences, and modified (slightly) in the light of field observation. The movement takes the beak-tip through a smaller traverse than in B.islandica and thus gives the impression (generally) of being a slower rotation. The path is a crude ellipse, as compared with a pear-shape in B.islandica. The head is held much farther forward, and lower down, than in B.islandica, the eye being held at only just over half the height from the water in the extreme forward position, that it is in B.islandica. In B.clangula the angle of pumping is a plane of 25 degrees from the horizontal, as compared with

a mean plane of about 35 degrees in B.islandica (in which the head passes forwards above the horizontal, but is then lowered at an angle of 70-80 degrees, at first, and drawn back further at an angle of about 40 degrees). The angle of the neck-axis is inclined at 50 degrees forwards of the water-line, as compared with 70 degrees in B.islandica. In the rearmost position of the head (well into the shoulders), the neck axis is much more sinuous than in B.islandica. In B.islandica the head is held much more upright, and much farther back, hence the neck-axis is straighter.

Literature Descriptions

The movement was named by Brewster (1911) who noted the resemblance of the extreme forward position to the prow of a sailing vessel. It has also been described by Townsend (1910), Millais (1913), Boase (1924), Phillips (1925), Bernhardt (1940) and Johnsgard (1955). The Bowsprit Position is apparently illustrated in Brewster (1911), Phillips (1925) and Johnsgard (1955), but only Brewster (whose illustration shows too great a bend in the neck) observed that a similar position was assumed sometimes following the Head-Throw. His descriptions are as follows ("Wounded-Duck posture" resembles the Threat posture): —

Forward Thrust of Head and Neck ending in the Bowsprit posture. The drakes assumed this attitude by suddenly thrusting their heads and necks forward and upward from the normal position (this was evidently the usual way) or by raising them more slowly from the crouching of the wounded-duck posture....On each occasion the bird remained absolutely motionless for several seconds with its neck elongated to the utmost and held perfectly straight and rigid at an angle with the water of about 45 degrees suggesting the bowsprit of a vessel of ancient type....During its continuance the feathers of the head were sometimes fluffed out, but oftener pressed down so

very flat that the head looked scarce thicker than the neck which because of its unusual elongation, appeared abnormally slender. The bill was only slightly opened....When the head was raised to the bow-sprit posture from the crouching or wounded-duck pose the movement was not especially rapid; but when it was thrust directly forward and upward from the normal position the action was so swift and abrupt that my eye could scarce follow it....sometimes take the bowsprit or topmast posture without becoming rigid in it, or maintaining it for more than a fraction of a second....on closely approaching....they often bobbed their heads up and down two or three times in quick succession....

.....As a rule the bird kept silent when in this position, but twice I saw, as well as heard, it bleat. In one of these instances it kicked up water just as it uttered the paaap; in the other this action was omitted.

Phillips (1925) adds that the bill is dipped into the water at intervals from the Bowsprit position. Bernhardt (1940) wrote: "The mating takes place about as follows: the drake swims up to the female, perhaps also swims around her, at the same time stretching the neck obliquely forward. The crest is erect." He described how this led into the Head-Throw-Kick. At copulation he again says that "the drake swims around her with repeated thrusts of the neck". Townsend (1910) may also have seen the Bowsprit when he writes: —

One or more males swim restlessly back and forth and around a female. The feathers of the cheeks and crest of the male are so erected that the head looks large and round, the neck correspondingly small. As he swims along the head is thrust out in front close to the water, occasionally dabbing at it....

He goes on to describe the Head-Throw as though it followed on the Bowsprit.

Perhaps Boase (1924) was also describing the Bowsprit when he says: —

He seemed to make an impression, for, swimming away from the group he was followed by the particular female addressed.... (he) then began a new display, bobbing the head in a curved path by rapid retractions of the neck and was imitated or replied to by the female with a similar performance....

Millais (1913) says that the tail is raised, and the head may be raised to

the vertical, but we may doubt either of these features. He wrote: —

The male approaches the female with his head and neck held stiffly up at an angle of from 60 to 75° , the feathers on the cheeks being much puffed out. He swims, sometimes with raised tail, in a semicircle round her, gradually elevating the bill until it is quite perpendicular".

It is perhaps odd that none of these descriptions except that of Brewster (who appears to have seen all three origins of the Bowsprit pose) is a really accurate account of this common movement.

FIGURES 22 & 23

B.islandica (B.C. population)

ROTARY PUMPING

From a film by M.T.Myres

Figure 22. Simple Form

The head is drawn back, then forwards and upwards, and finally back and down. Compare with Figure 24 (B.clangula) and Figure 26, where the path of the beak tip in both species is traced.

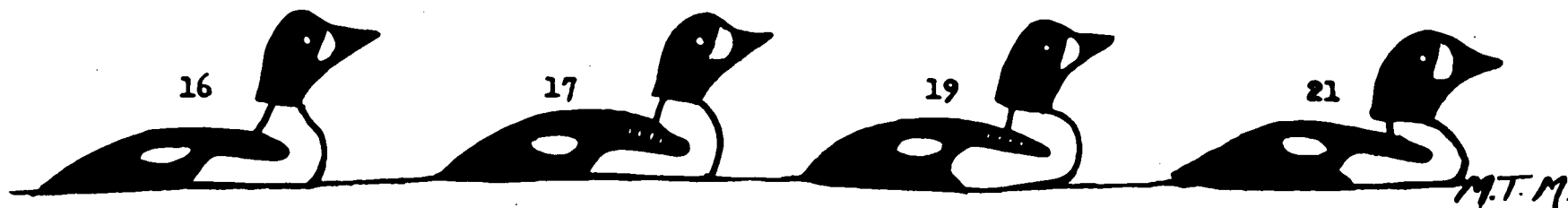
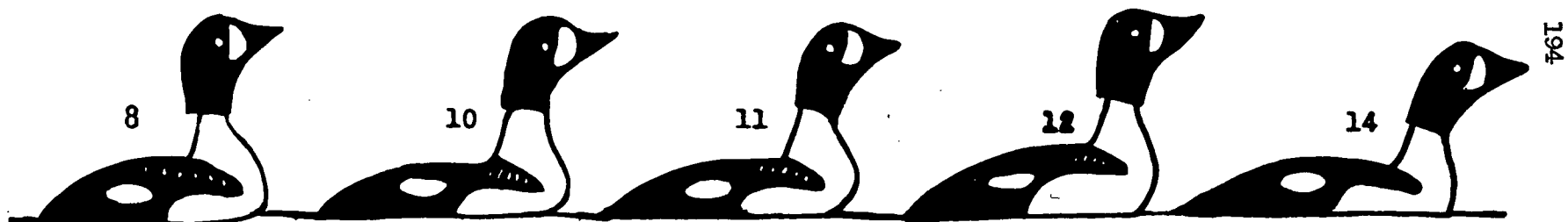
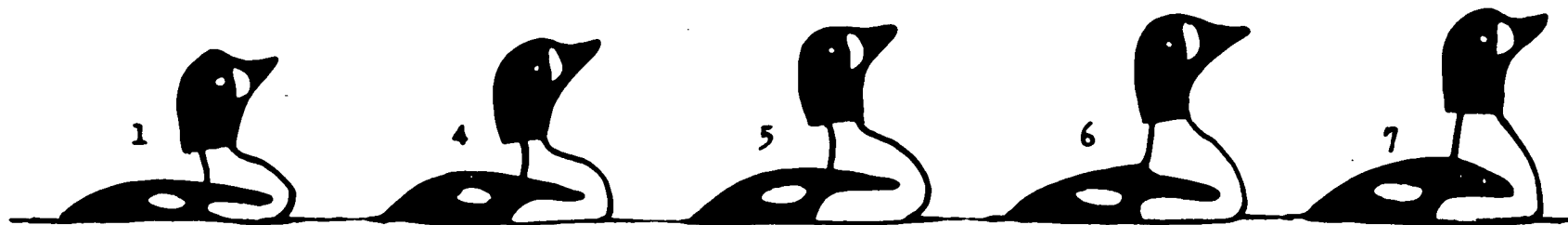
Figure 23. With Laying Neck on Water

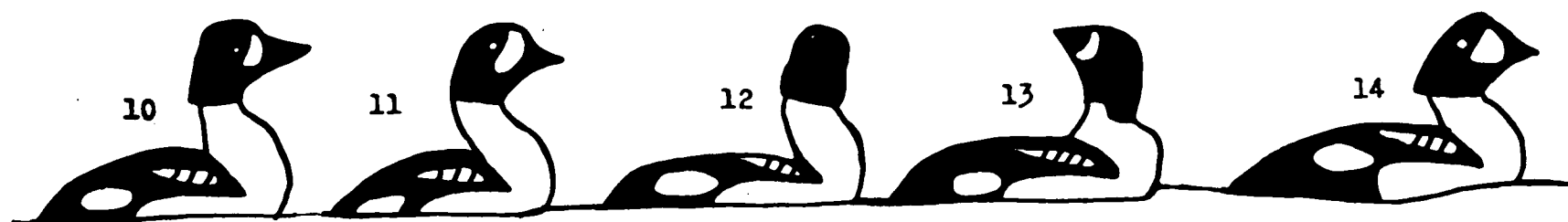
This full sequence of 43 frames was repeated twice over -- making about 85 frames altogether. As the head was passing forwards (and while in the highest position) there was a Head-Flick on both occasions. This led into the lowering of the head to the water. Because of the lowering of the head and neck to the water a different path is traced from that found in normal Rotary Pumping (Fig.26). When the neck is laid on the water as in this case, there is greater aggressive motivation than normal, usually towards a third bird.

The sequence began with normal Rotary Pumping (with the female Jiving), then Laying Neck on Water----raising of the head----Head-Flick----Laying Neck on Water (19 frames), of which the last frame is Frame 1 of this figure. The head was raised, flicked again and layed back on the water (Frame 43). Shortly afterwards the bird dove and may have attacked another bird. The Head-Flick lasted only 1/6th of a second and was not visible in the field.

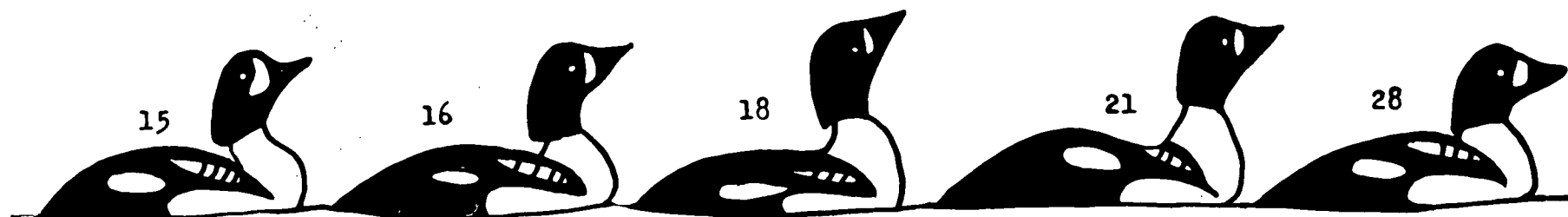
Frame 1.	End of Laying Neck on Water position
Frames 9-10	Head starts forward
Frames 12-14	Head-Flick
Frames 15-21	Head passes forward again in Rotary Pumping.
Frames 28-30	Head is jerked back into the shoulder before going down and forward to water level.
Frames 39-43	Assumption of the Laying Neck on Water position.

24 frames/second. Shutter speed 1/48th second.





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FIGURES 24 & 25

B. clangula (American population)

BOWSPRIT PUMPING & BOWSPRIT POSITION

From a film by Charles Walcott and Benjamin Dane.

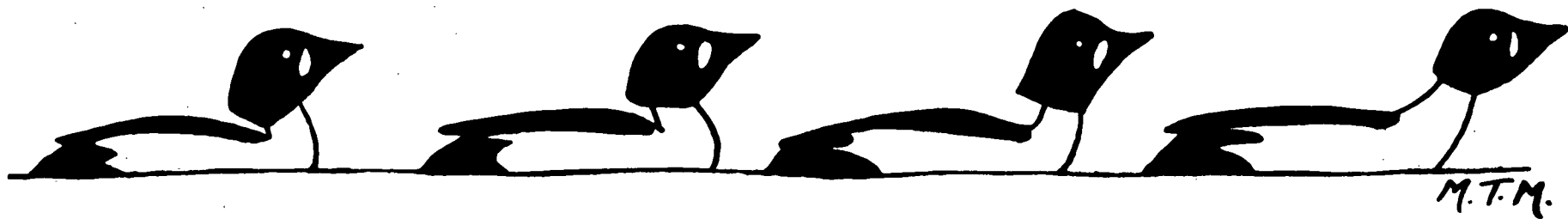
Figure 24. With Bowsprit Pumping

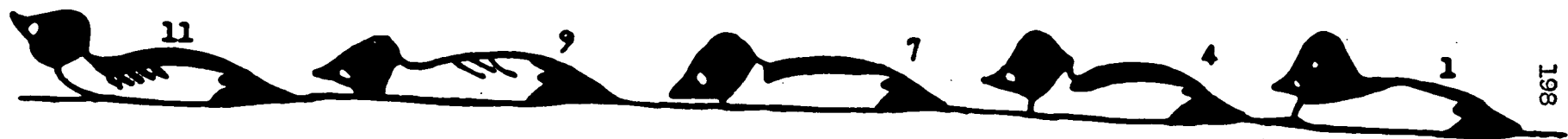
This is a compounded series of drawings to be read from left to right (no frame numbering).

Figure 25. Bowsprit Position static from Forward Scoop

Read from left to right

This is one of two other ways in which the Bowsprit pose is reached (the other--see Fig.19). The beak is lowered to the water (Frames 1-7) and lifted in a scooping motion (Frames 7-11). The Bowsprit pose is maintained for as long as 22 frames (Frames 12-34) and is not pumped. The head is finally drawn back into the shoulder (Frames 34-44).





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FIGURE 26

B.islandica and B.clangula

ANALYTICAL COMPARISON OF ROTARY AND BOWSPRIT PUMPING

Compounded from field notes of both species by M.T.Myres, and from tracings from films by M.T.Myres (B.islandica) and Charles Walcott and Benjamin Dane (B.clangula).

Upper pear-shaped trace (with broken-lined head) is the path taken by beak of B.islandica during Rotary Pumping.

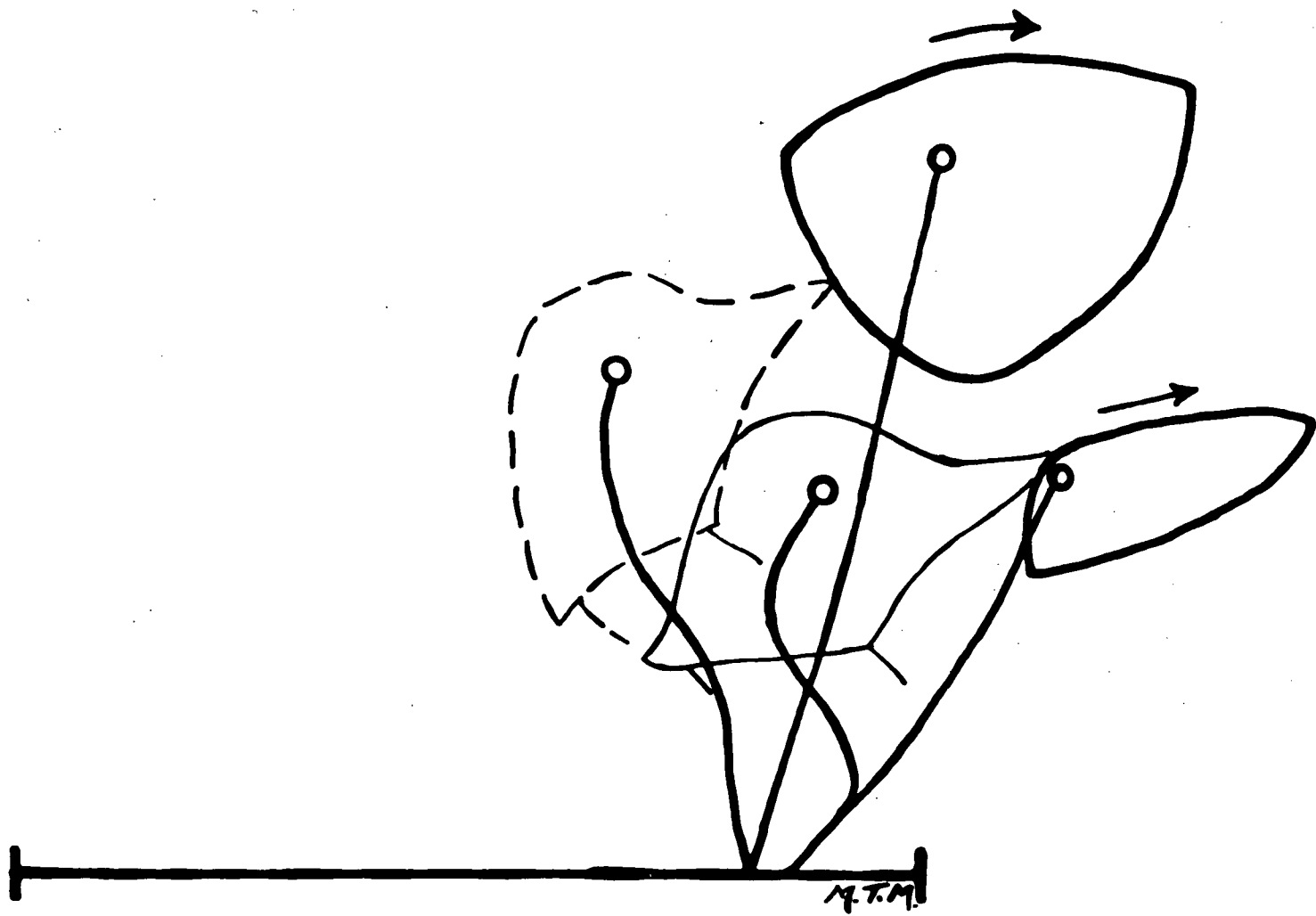
Lower, almost elliptical trace (solid-lined head) is the path taken by beak of B.clangula during Bowspit Pumping.

The path of the beak tip is much wider, and placed much higher in B.islandica than in B.clangula.

The base line represents the length of the body at water-level. The solid lines arising from water level represent the neck-axis of the goldeneye at the extreme forward and extreme backward position of Pumping in each species.

The rearmost position of the neck of B.clangula is most curved, that of B.islandica most elongated. The fore-most position of the neck has a shallower slope in B.clangula than B.islandica.

N.B. the path of the eye could, and should, be traced in a similar fashion. The traces would be placed more nearly over the front of the body, and the shape would be more elliptical in B. islandica, as there appears to be considerable lift of the beak tip in the rearmost position. Thus the NW segment of the beak-tip trace in B.islandica would be absent in an eye-trace.



Masthead (B.clangula)

There is on Walcott & Dane's film a display (Figures 27-29) which I have not seen in B.islandica. It resembles the Water-Flip of both species and also resembles Drinking. But whereas the Water-Flip is chiefly found in the pre-coition sequence, the Masthead, as I shall call it, is found in courting groups. It is usually directed at another bird from the Laying Neck on Water posture, and may have certain aggressive adjuncts. It may vary somewhat in amplitude, depending presumably upon the intensity of motivation.

Film Description

The neck is lowered to the Crouch or may even be dipped into the water at an angle forwards and downwards. It is held here for a considerable time (Figure 27, Frames 1-23), then the head is suddenly jerked up from the base of the neck, as though the tip of the bill had a string attached and were being pulled upon by a playful boy. The neck appears quite stiff and straight. The angle of the beak rises to 60 degrees, or even further and the head is then dropped a little way as suddenly, held at this lower angle for a moment, and then slowly lowered to the water again, as though the string had been allowed to slip. The movement is rapid and jerky and is stiff, almost life-less. The head is held close to the water for as long a time after the movement as before it (Figure 27, Frames 38-92), or even longer. The movement looks much less like Drinking than display of aggressive motivation, although the beak may be actually dipped into the water before the head is raised.

Literature Description

The name derives from that used by Brewster (1911). However it has become evident that Brewster may really have been using the name for the second part of the Head-Throw-Kick. He was not completely clear, it seems, about the movement, for although he says that the "bill was invariably well opened" he also says in the next sentence "oftener than not I heard no sound". That he confused it with the Head-Throw-Kick is evident from his remark that "At the close of this brief period of inaction the bird frequently uttered its paaap and kicked up spray". However the beak is quite definitely not opened during the Masthead display as redefined after Townsend's description (see below). Nor does the Masthead lead into a performance of the Head-Throw-Kick. It is not clearly detectable in B.islandica, although it seems to resemble the Water-Flip in some respects.

Brewster's original description is as follows: --

Upward Thrust of head and neck ending in the mast-head posture. Ordinarily this movement was complete in itself and made directly from---as well as back to---normal position. Occasionally, however, it closely preceded or immediately followed a still longer backward swing---yet to be described. In the pose to which it commonly led i.e., the mast-head pose--- the Whistler's neck might be elongated and straightened as in the bow-sprit posture, and held stiffly erect, or it might be so shortened, and curved that the occiput almost touched the back between the shoulders. In either case the bill was invariably well opened and pointed skyward for several seconds during which the head and neck were kept perfectly rigid. At the close of this brief period of inaction the bird frequently uttered its paaap and kicked up spray, but oftener than not I heard no sound and saw no water fly.

All that can be said of this is that he thought he saw these variations, but unlike the rest of his descriptions which are substantially correct,

he seems to have been rather innaccurate here. Townsend (1910) describes a display which also indicated that the beak was opened at the start of the Head-Throw-Kick. This has not been confirmed however, as indicated above. But in another passage Townsend does seem to have seen the Mast-head. He wrote: —

I have also seen them thrust out the head in front in such a way as apparently to scoop up the water, and then elevate the head, the bill pointing straight up, but closed as if they were drinking the water, although I doubt if this is the case.

It is to be noted that he notices that the bill was held closed in this display. Also that the neck was stretched forward along the water, before the head and neck were rigidly swung back into the almost vertical position.

The Backward-Swimming Display (*B. clangula*)

Phillips (1925) gives an account of a display which he saw, which was otherwise unrecorded at that time. On April 11 one year he was watching nineteen goldeneye at Wenham Lake: —

All of these, except two males and a female, were diving and feeding, but these three were in especially active display. Besides the ordinary actions just portrayed I saw the males with head held stiffly forward (bowsprit pose) for a second or two, suddenly shoot backward for a distance of one or two feet. I cannot imagine how this was done, for there was no way of observing the feet. But this curious action was repeated many times and I feel sure that it must have had some significance.

There is a further mention of this behaviour in Gunn (1939). He states that A. Holte Macpherson described this same display in a letter to him in 1932. I have recently come across a second, unpublished, record of this backwards movement. Mr. Theed Pearse of Comox, British Columbia has kindly allowed me to look through his field notes, and under the date February 9, 1941 there is the following entry for B. clangula: —

The male does not always open the beak wide to display nor always use the foot for splash effect; sometimes he raises the feathers on the top of the head, other times gives a jerky twist of the head.

Another form is to depress the head horizontally to the surface, hunch up the back and move backwards.

FIGURES 27-29

B. clangula (American population)

MASTHEAD

From a film by Charles Walcott & Benjamin Dane

Figure 27. Side View

From the Normal resting position the head is lowered towards the water, and held there for as many as 20 frames. It is then raised until the peak points vertically. The beak is not opened. The head is then lowered to the water again, and held in this position for at least 50 frames. Note resemblance to Water-Flip (Fig.31) of B. islandica and to Drinking (Fig.2).

Figure 28. Extreme Form

As above, starts and ends from a Crouched Position with beak close to water or dipping in it. Difference lies in the degree to which the stretched neck is sloped backwards, and in the elevation of the breast from the water. The movement is very rapid (Frames 17-24 up, and 25-29 down.). The beak is not opened.

Figure 29. A. Front View

Shows the large dark, spatulate, shape of the head above white neck and breast.

B. HEAD-THROW

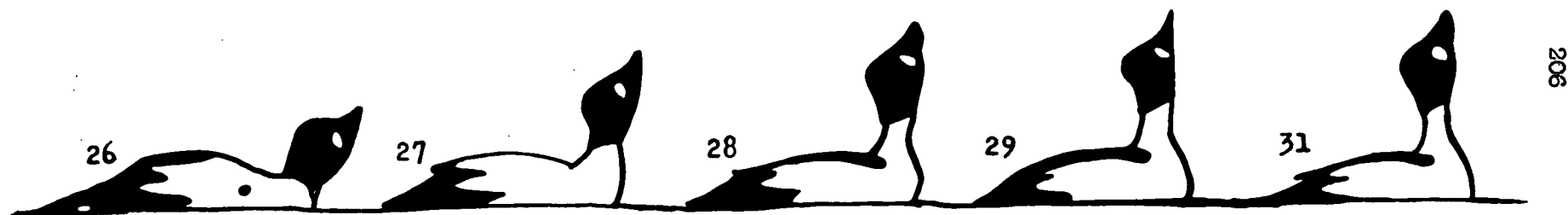
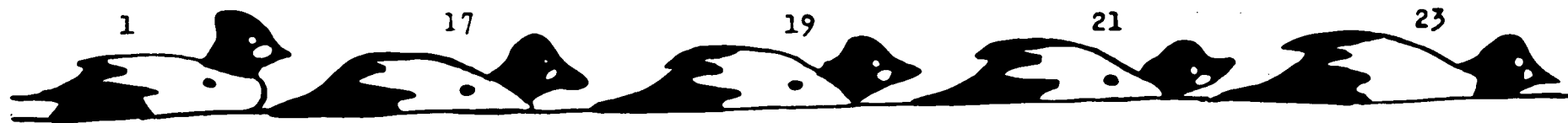
Rear View

Shows head in its extreme posterior position over the rump. The bill points upwards and the white face patches are only just visible, and may not be visible to a female following along behind it. The dark back is tilted back at 45 degrees and the shoulder regions form dark outwardly pointing flanges.

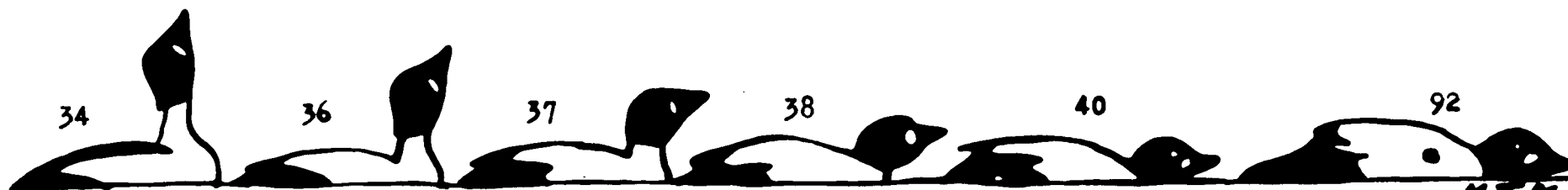
C. With Forward Bowsprit Position

Two views. Frame 1 shows the head passing forward after the Head-Throw. The dark head sits atop a brilliant white neck. Below the square black back lies between white flanks. In Frame 13 the head is static in the Forward position. The length of white neck is greatly reduced over Frame 1.

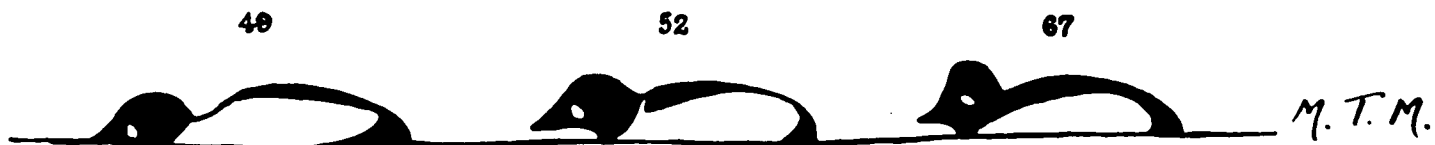
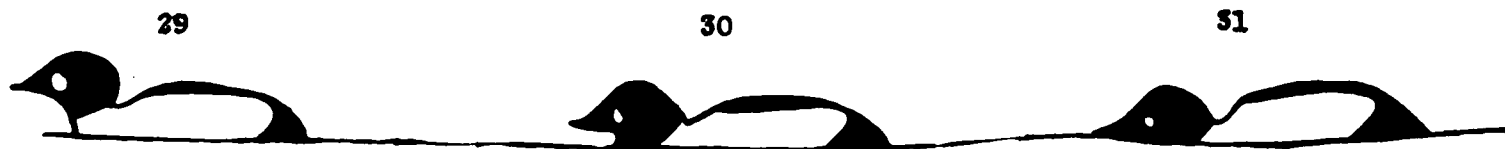
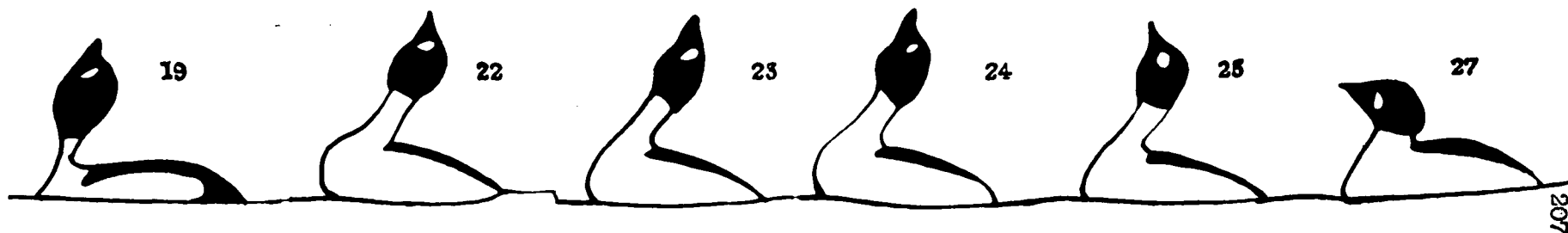
24 frames/second. Shutter Speed 1/48th second.

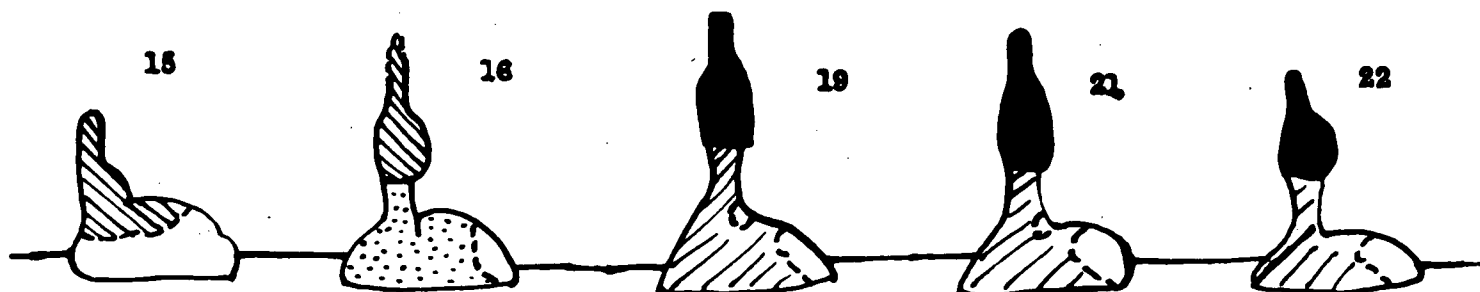


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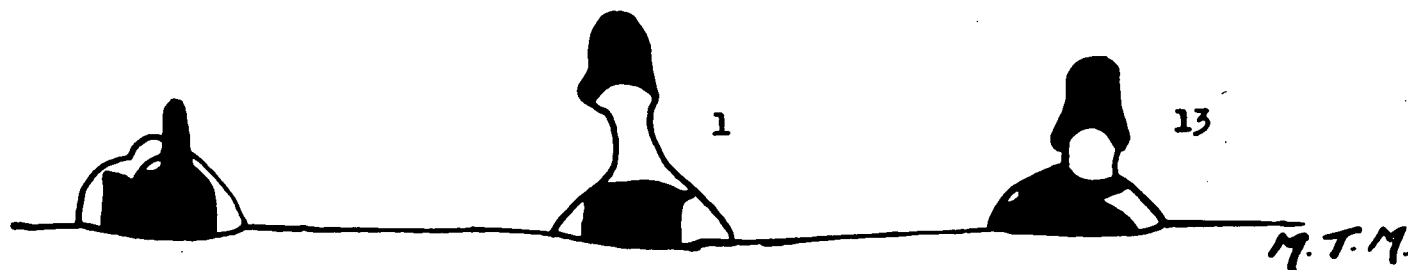


M.T.M.





A.



B.

C.

THE COITION SEQUENCE

The displays separated out from the courting displays and placed here, are those which directly lead to, occur during, or follow, the act of fertilisation. Copulation may be seen as early as February. The coition sequence is often initiated by the female (especially on the sea). She does this by assuming the Invitation to Coitus, and may remain in this position for a considerable period. The male tends to ignore her at first but on the breeding grounds the position is generally assumed after a certain amount of courting activity by the male has taken place.

The Wing- and Leg-Stretch display of the male is much the most certain indicator of a coming mating. However, the Water-Flip (either alone, or in combination with the Wing- and Leg-Stretch) occurs most frequently in the pre-coition sequence as well. The male assumes the Pre-Coition Steaming posture in B.islandica from a lying sideways pose (e.g. Wing- and Leg-Stretch) or from a normal posture after Water-Flips or twitching of the water sideways. Jabbing of the water violently appears immediately to precede the Steaming position in B.clangula (in which also there is a preening movement behind the wing).

The Kick is seldom seen among the displays preceding coition. Rotary Pumping is the most common element in the early part of the sequence when the pair meet on territory (in B.islandica), or when the male starts displaying in a pre-coition sequence. When the sequence is broken off for any reason there is a reversion from the specific coition displays back to Rotary Pumping.

On one occasion a male (? off territory) made three attempts at cop-

ulating. The female scooted away from him each time, but he could not follow in the Steaming position; it appeared too tiring. Failure to mount may result in a reversion to Rotary Pumping. On two occasions both members of the pair dove, and on surfacing the male did Rotary Pumping and the female Jiving, i.e. there may have been the necessity to dive before Jiving could be performed (?).

The Post-Coition Steaming display does not resemble that of Anas platyrhynchos or Aythya vallisneria.

Invitation to Coitus

The "solicitation" posture of the female has been described by a number of authors. In the Mallard (Anas platyrhynchos) the female performs the up and down "pumping" movements (Lorenz, 1941) mutually with the male. In the Canvasback (Aythya vallisneria), however, the female stretches herself low on the water as in goldeneyes (Hochbaum, 1944). Alford (1921) in particular was impressed by the invitation posture of the female and remarked how long the posture could be maintained before copulation occurred (as long as 15 minutes): "With neck outstretched and her body quite limp and apparently lifeless, she allows herself to drift upon the surface exactly after the manner of a dead bird". This observation was made on Vancouver Island in February (species ?).

Bernhardt (1940) wrote of B. clangula that copulation was initiated by the female, who lowers herself flat on the water and stretches her neck well out in front.

Sawyer (1928) illustrated the posture in B. islandica (Figure 20 of Plate 3 in his paper): "to indicate the fact that the females thus often manifest desire without relation to the mood or proximity of any male". He discussed this further as follows: —

"inviting" females to be seen floating like half submerged logs on the pond...For many minutes at a time the bird looks like a rounded piece of driftwood as she lies half submerged for her entire length, including head, neck and bill. She sometimes emits a low clucking call in this attitude...the females, so far as one might judge by behavior, were decidedly more precocious than the males in their desire. With a given pair the female's period begins long in advance of the male's and continues unabated until the male's period, only two or three minutes in duration, is over. It was a common thing to see a half sunken duck float and drift invitingly about a drake for a quarter of an hour or more, while he showed not the slightest knowledge of her existence.

Water-Flip

This movement is placed in the coition sequence because it is here that it is most frequently found, but it does occur between pairs on other occasions, and is even performed by unaccompanied birds. Furthermore the female may perform the movement, not in the coition sequence, but at other times, especially in response to its performance by the male.

The movement (Figure 31) is almost impossible to distinguish from Drinking (Figure 2). In B.islandica the head is dipped to the water and then rapidly the beak is raised to an angle of about 45 degrees (or more). There seem to be a number of postures in which the head dips in a medial plane to the water: the symbolic dip to the water (Water-Dip) the Looking for Food pose, and Jabbing as well as the Water-Flip. But it seems clear from its similarity to Drinking, that the Water-Flip is derived from the comfort movement of Drinking, and that it is more in the timing and repetition of the movement than in its form that it has acquired sexual signal value.

It is distinguished most clearly during the Wing- and Leg-Stretch movement of the pre-coition sequence. The form in this case appears to be a little different as the neck is thrust forwards down to the water in a contorted position, and then sharply lifted. In this forward position from the sideways-tilted posture of the body, the body seems to bob in the water.

The mutual performance of the Water-Flip between the pair (at other times than the pre-coition sequence) is very striking. I once recorded the following sequences in B.islandica: "Six times when the male has done

an Elaborate Water Flip, the female has responded to him by doing the same thing, deriving in the male from something like the Crouch position. Once he responded to an Elaborate Water-Flip initiated by her. Another time he did it though she was dove."

Wing- and Leg-Stretch

This movement is almost exclusively found in the coition sequence, just prior to the act of mounting, though it may be performed for some minutes at a time, then broken off and replaced by other movements, and then resumed.

The male lies on his side in this movement. Most usually, but not invariably his belly is towards the female, gleaming white. He stretches the wing and the leg which are then uppermost, so that the orange leg is displayed against the undersides of the wing, and the snow white breast and underparts are gleaming (especially when the sun is out, since the breast is covered in water-droplets). The wing is stretched slowly backward and then brought forward again, after a pause, for folding. The leg passes back parallel to it, and appears to support the wing (Figure 30). The head is often turned forwards (? always), and pointed out over the water in front. A deep and contorted Water-Flip is often performed while in this pose, when the wing is stretched farthest back the end of the Wing- and Leg-Stretch movement and as the wing is starting forward again.

Sawyer (1928) illustrated this movement in Figures 23 of Plate 2 in his paper. He wrote (B. islandica): —

The first positive indication of his desire is apt to be a peculiar and animated twitching of the water with his bill; then he is apt to stretch, turning over on his side and extending the upper wing and leg--in this he is quite deliberate; pluming of the back feathers follows, and looks like a gesture of ostentation.

Bernhardt (1940) remarked that he had seen a wing-stretching display in breeding pairs. Gunn (1939) thought he was the first to notice this display but Brüggemann (1876) mentions it in B. clangula. Gunn wrote that it consisted in "the exhibition by the drake of the upper surface of his outspread wing while it is supported by his foot. In order to do this effectively, he careens his body and extends the wing that then comes uppermost". He went on to discuss the display further, as follows: —

"There is, of course, a great difference in the advertisement value of the two wing-surfaces for the under is partly "mouse-grey" in colour and shows little of interest while the upper surface is made up of large black and white areas in conspicuous contrast. It follows therefore, that the most complete method of showing his wing-pattern is for him to roll towards the duck and while his back is towards her to spread his uppermost wing. The object in supporting the wing with the foot is, presumably, to enable the drake to retain this somewhat awkward pose with the wing at full stretch, longer than he could in the absence of such a strut; that it serves its purpose efficiently is certain, for, in a back view, his orange-coloured toes may sometimes be seen projecting between the quills. When, as sometimes happens, he makes the mistake of careening away from the duck instead of towards her the exhibition becomes something of a damp squib, for he then shows only the under surface of the wing; but, as a result of watching him over a good many years, I can state confidently that he is much more often right than wrong in his selection of the proper attitude to adopt and wing to extend.

I am sure that in B. islandica it is the belly that is most often exhibited towards the female, though both orientations may be seen. It is possible that there is a difference between the two species in this

respect. Gunn (1939) mentions that the female B. clangula also performs this display. During the coition sequence however the female is posed in the Invitation to Coitus and so I believe he may merely have been describing the comfort movement.

Jabbing, Wing-Preen, Pre-Coition Steaming,
and Mounting and Post-Coition Rotations

Field and Film Descriptions

In B. islandica the male assumes the Pre-coition Steaming position direct from the Wing- and Leg-Stretch position, or there is an interval during which he may be performing Water-Flicks. The Pre-Coition Steaming posture ^{basically} resembles the Post-Coition Steaming posture. The male often has to swim from a lateral to a posterior position in relation to the female before actually assuming the posture, but the speed of motion is considerable during this preliminary orientation. In the Pre-Coition Steaming position the chest is raised very high (white) off the water. The head feathers are bristling as the male races towards the female. It is not easy to see what happens as he mounts, but possibly he brings his feet forwards as he reaches the sloping rear quarters of the female. It is possible that the Water-Flicks are the equivalent of Jabbing in B. clangula.

In B. clangula Jabbing intervenes between the Wing- and Leg-Stretch and Mounting. It consists of a series of violent jabs or dips to the water, downwards in front of the male. It resembles the preliminary dips to the Water found in Splash-Bathing. As the drake B. clangula performs these movements he is moving backwards until he is behind the female.

When behind the female the male turns the head and preens on the back between the wings or behind the half-lifted wing (Figure 32, Frames 1-9) in B. clangula. Then he suddenly lifts the neck stiffly upwards (Figure 32, Frames 9-12) and moves very fast towards the female in a pose resembling that following mating. The head may be rotated back a little (Figure 32, Frames 12-19) and then swung forward again as the drake begins to cover the female. It is noticeable (Figure 33) that the male actually covers the female and treads her down (? she actively sinks herself in addition), before he manages to acquire a grip on the crest feathers of the head. The female is almost completely submerged. In the coition sequence illustrated, the spreading of the tail and wagging of the tail (? origin of Tail-Wag) by which intromission is effected, continue for about 7 seconds (103 frames from Frame 35-Frame 138).

When coition is completed the male slides sideways off the female's back (either side), but continues to hold onto the feathers of the nape. The male begins to paddle with his feet. Since the female is still motionless she acts as a dead weight, and the male's head is dragged back at a sharp angle (Figure 34, Frames 145-149). In the Figure he appears to be dragging the female around him, since he is turning to the right, while she is on his left, but this is an illusion. In fact there is a combination of the female acting as a dead-weight, and the male propelling himself away from the female (outwards) to counteract her weight. The female turns around parallel to him, but since she is almost stationary the male can only turn away from her by traversing a circular path around her, moving backwards. Presumably the leg on the side of the female is beating

more powerfully than the other one. In the sequence illustrated a full $1\frac{1}{2}$ turns are made before the male releases the head of the female and she emerges completely from her submergence in the water. In Frame 200 (Figure 34) it is noticed that the head of the male is placed as far back as in Frame 149, but there is a greater turn of the head, the axis being more upright than it was earlier.

Literature Descriptions

Brüggemann (1876) who saw coition about twenty times in B. clangula describes Jabbing. His is the earliest description of the coition of B. clangula. He wrote (in transl.): —

"Then the male pushes the beak, sneezes into the water, immediately afterwards sneezes again and thus four or six times after each other with always short intermissions. At the same time it moves away to the side of the female swimming up to about two metres. Then it turns suddenly around with a tremendous speed at the female."

Sawyer (1928) mentions "water-twitching" and described coition in B. islandica. Sawyer illustrated the performance in Figures 8-17 of Plate 2 in his paper. He writes of Mounting: "then the upright position is assumed, which marks the beginning of the spurt to the female; the birds are usually within a yard of each other when the spurt begins", and he mentions that an unusually plumaged male (probably a yearling) when trying to force copulation began his Steaming movement "at a distance of some dozen to twenty-five or thirty feet from the intended mate, instead of the customary yard or less". Nor was his performance preceded by the "dabbling, stretching or preening so characteristic".

The Post-coition Rotations are described by Brüggemann as follows: —

"After the pairing the drake holds onto the crest of the female for a few moments and pulls her, turning backwards two or three times in a narrow circle around him while she gives off the previously mentioned call".
Sawyer (1928) also described them as follows: —

"While finally, in coitu, they begin to swim in a very small circle a note is repeated at regular intervals of about a second; I wrote it, "Gr-err-er" or "cr-err-er", and it seemed to come from the female, yet the latter point is in doubt. The middle syllable, high and accented, seems jerked forth. Another note (I thought from the drake) is a low cluck; these two notes were timed with each other so that one appeared an echo...there seems a possibility that both calls came from the same individual. Having circled, as mentioned, two or three times around, the pair separates, each bird swimming away instantly from the spot; dabbling and vigorous bathing begins at a distance of some forty feet on the part of the female, rather farther in the case of the male.

Post-Coition Steaming and Splash-Bathing

The male, upon dismounting swims directly away from the female, usually at an angle forwards in B.islandica. He has his head held high and crest fully expanded (Figure 35 and 36). He grunts as he turns his head from side to side. Once I saw the movement from in front. The head turning was a little twist of the head to the left and right as he steamed away. The difference between this and the Head-Up (in B.islandica) lies in the curvature of the neck axis (compare Figure 9), the long sloping "set" of the feathers at the back of the head, and the fact that the beak is pointed downwards at an angle of 45 degrees. The white face-patches flash jerkily and alternately with small amplitude. It seems probable that seen from behind they would not be visible to the female.

Brüggemann (1876) was the first to describe this display. He wrote

of B. clangula (in transl.) "Then he releases the female and then swims for a few metres in a straight line with neck stretched out vertically, and with breast out of the water, and only by and by does it get out of its exalted state". Millais (1913) figures this display in B. clangula but his figures exaggerates the posture enormously. He wrote: —

..after pairing with the female....a mad rush along the surface of the water for 15 or 20 yards. Whilst doing this he adopts the somewhat remarkable attitude....breast is held high out of the water, and head depressed backward with bill up in the air. He makes the water fly in all directions and not infrequently makes his rush at any other bird that may happen to be near.'

This description compliments the illustration, but is not accurate.

For B. islandica, Sawyer (1928) provided the first description: —

The male's appearance in this swimming away is noteworthy. He has an extremely self-conscious bearing; in the live bird the effect is enhanced to a ludicrous extent by the regular ticktock movement of the bill from side to side. The set pose, the straight course with uniform speed, the mechanical movement of the head--all give every appearance of an automaton, personifying egotism and wound up to run a set course....How...can we explain the remarkable 'proud' swim, so uniform in every remarkable detail, of the male; this especially, since it follows complete consummation of the mating.?

Sawyer illustrates the display in Figure 18 of Plate 2 in his paper.

Sawyer raises the question of the selective value in a post-coition display. Such displays are, of course, quite frequent in animals. The movement in this case is completely stereotyped. Post-coition comfort movements could be understood as an outlet of emotional tensions, and as a normal cleansing activity after the "contamination of bodily contact" (as one might call it) of coition, just as occurs after a fight. In both cases the feathers need to be readjusted from the ruffled condition

that has been brought about. But why a specific ritualised display should be evolved is not clear to me.

After some seconds the male subsides and begins to Splash-Bathe. After an unsuccessful copulation the male did not take on the Steaming posture (nor did the female begin Splash-Bathing as she normally does). Shortly after the unsuccessful attempt a successful copulation occurred and the usual display followed. The female generally pauses a moment after the male lets go of her head and then begins to Splash-Bathe (ahead of him, in time).

Sawyer (1928) remarks "Just after the bathing which follows a mating completely enacted the female is especially given to repulsing intrusive males and females alike". I have not noticed this. Vigorous preening follows the Splash-Bathing for some minutes in both sexes.

Hochbaum (1944) makes **no** mention of a Steaming display in Aythya vallisneria: "After treading the pair part, flap their wings vigorously, preen for a moment and then swim off together."

FIGURES 30 & 31

B.islandica (Icelandic population)

WING- & LEG-STRETCH

From a film taken by Dr. Frank McKinney at Slimbridge, England.

Figure 30 Upper Line

- A. White patches on the upper side of the wing are visible. Sometimes these are exhibited to the female, instead of the white belly and orange legs.
- B. The tipped-over-sideways position is seen, and the extended foot is seen to be using the wing as a backcloth, or is supporting the wing.

B.clangula

WING- & LEG-STRETCH

From a film taken by Dr. Frank McKinney at Slimbridge, England.

Figure 30 Lower Line

A & B. Equivalent positions to above.

WATER-FLIP

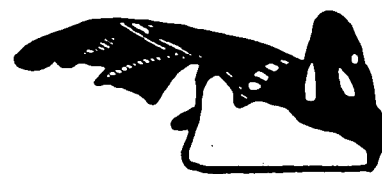
Figure 31.

This individual was performing in a pre-coition sequence. The resemblance to Drinking (Fig. 2) will be noted, and to the Masthead (Fig. 27).

16 frames/second. Shutter Speed 1/32nd second.



A.



B.

222

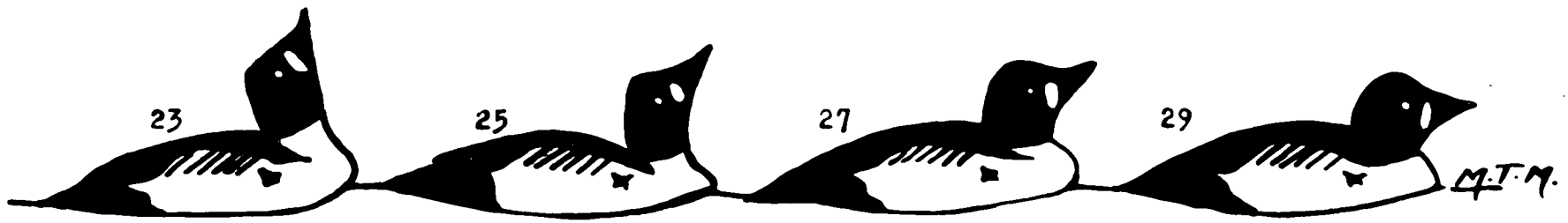
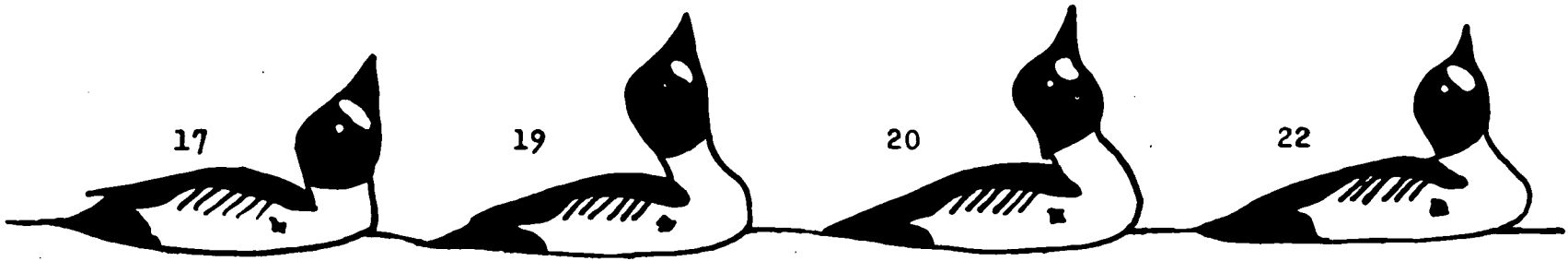


A.



B.

M.T.M.



FIGURES 32-35

B. clangula

THE COITION SEQUENCE

FIGURE 32

B. clangula

PREENING, AND PRE-COITION STEAMING

From a film taken by Dr. Frank McKinney at
Slimbridge, England.

Read from right to left

From the normal position which is preceded by some form of preening (on the back between the wings, or behind the wings) the neck is shot upwards with raised beak and the male swims rapidly towards the rear of the female. The head is first drawn back steeply (Frame 14) and then forwards into a curved posture (Frame 19).

16 frames/second. Shutter Speed 1/32nd second.

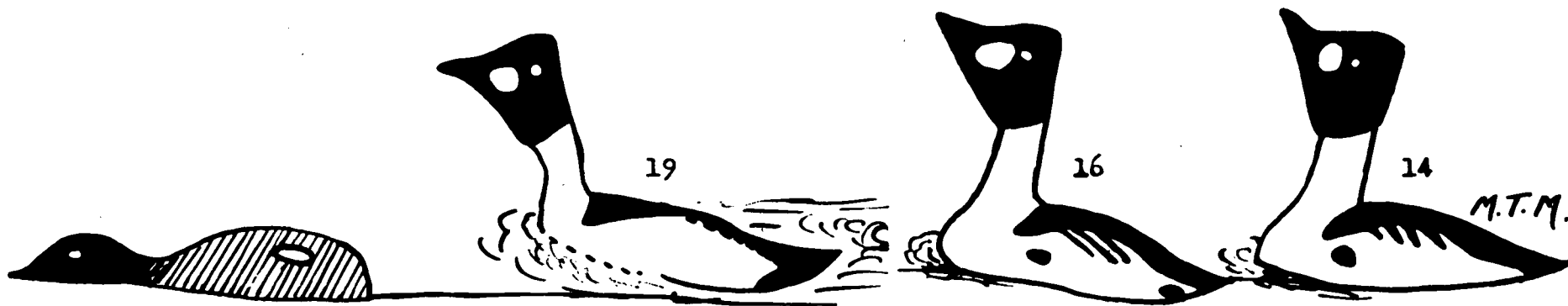


FIGURE 33

B. clangula

MOUNTING AND COITION

From a film taken by Dr. Frank McKinney at
Slimbridge, England

Read from right to left. This sequence is a continuation
of the one in Figure 32.

Mounting directly from behind, the male presses the female
down into the water, with the weight of his body and, by
treading with his, before seizing the feathers of the female's
crest. Frame 35 shows the spread tail during intromission.

16 frames/second. Shutter Speed 1/32nd second.

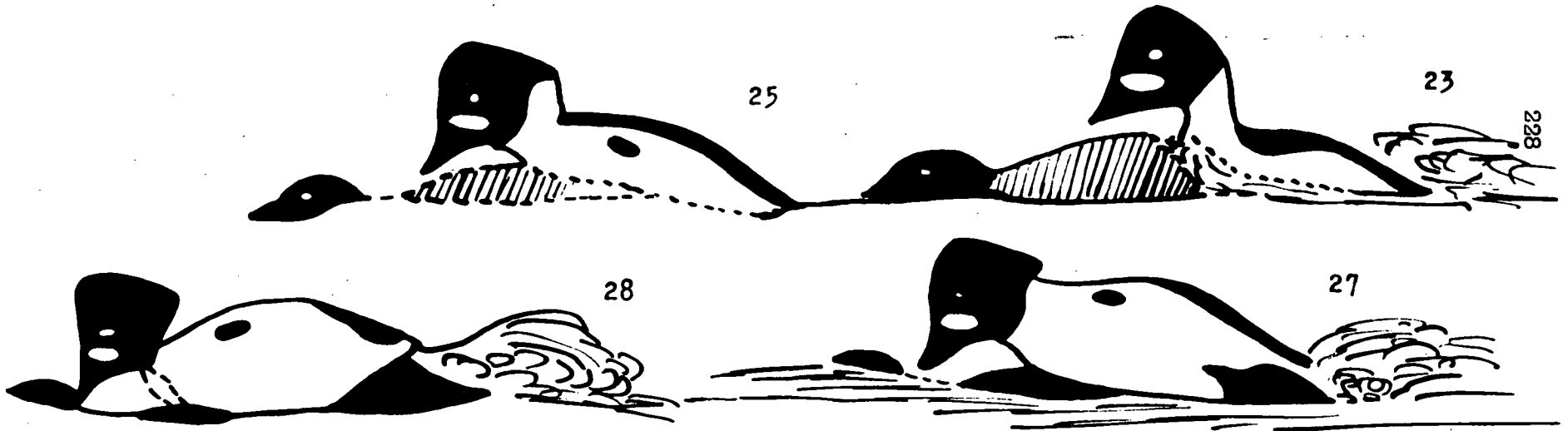


FIGURE 34

B. clangula

POST-COITION ROTATIONS

From a film taken by Dr. Frank McKinney at Slimbridge,
England

Read from right to left. This sequence is a continuation of the ones in Figures 32 and 33.

During coition a break occurs from Frame 35 to Frame 138. The male slips off sideways and begins moving forward so that his hold on the female's head draws his own head backwards (Frame 147). In Frame 149 the paddling of the feet is seen to produce some spray as the male accelerates. This continues until Frame 200.

Frame 149. At start of Rotation

Frame 200. End of first turn (male's head is raised more upright, but rotated a greater angle posteriorly than it was in Frame 149)

Frame 214. After $1\frac{1}{2}$ turns the male lets go the head of the female, leaving a projecting tuft of feathers (Frame 215).

16 frames/second. Shutter Speed $1/32$ nd second.



145



141



138



165



149



147

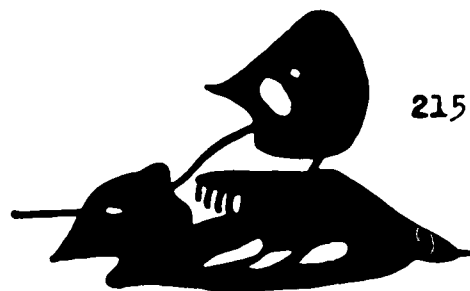
230



189



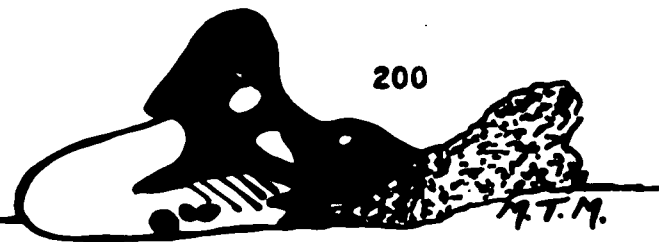
172



215



214



200

T.T.M.

FIGURE 35

B. clangula

POST-COITION STEAMING

From a film taken by Dr. Frank McKinney at Slimbridge,
England

Read from right to left. This sequence is a continuation of the ones in Figures 32, 33 and 34

The head is raised, beak horizontal, and the male swims rapidly away from the female with neck raised. The view of him that is seen by the female is that of Frame 226. Although he is Head-Turning she probably does not see the white face-patches. In the example illustrated, the male gets smaller and smaller as he swims away on the film. He never did any Splash-Bathing in this instance.

16 frames/second. Shutter Speed 1/32nd second.

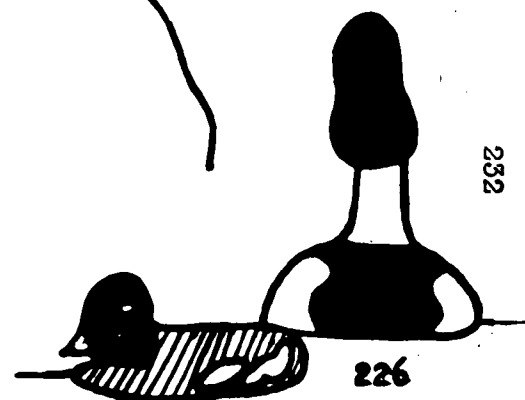
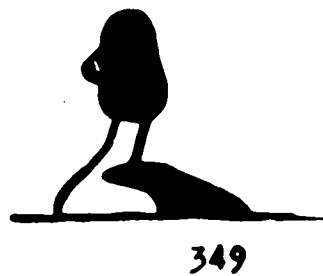
B. islandica

POST-COITION STEAMING

From a film by M.T. Myres

In the right hand picture the male is still holding onto the female. He then splashes as he paddles away. The Post-Coition Steaming pose was held in this case for 245 frames (speed of shutter?), before the bird began to Splash-Bathe. It is not known yet if the wing is always held up as shown. Compare with Figure 35.

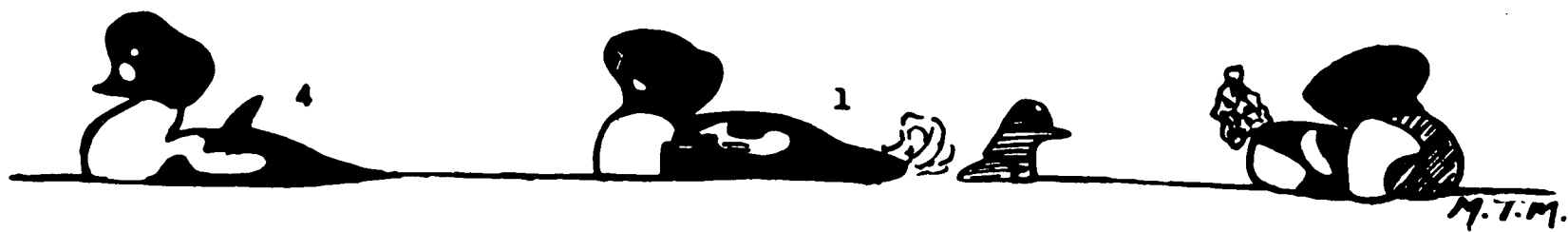
? frames/second (either 24 or 48)



232



217



THE BROOD

Leaving the NestField Description of B.islandica

At midnight on July 11, 1955 I took a nesting box off the tree to which it was attached, blocked the entrance and transported it to camp. The female was inside and the six eggs had hatched in the previous 24 hours. I cut the primaries of one wing of the female and returned her to the box. At 1000 hours on July 12, I placed the box on the ground in an enclosure a foot or two from the edge of the lake and removed the plug from the hole. Nothing happened for the first $2\frac{1}{2}$ hours, during which time there was scuffling inside the box and pecking noises as though the young were pecking at the walls. Occasionally there were low grunts from the female.

After $2\frac{1}{2}$ hours the female appeared. "The female came out first and the first young only a moment later and the rest in a rapid succession and all were out within two minutes, but I had no watch to time it." The young of course have sharp toe-nails and these are probably a special adaptation for the tree-nesting habit, since holes from which they must escape may be as much as, or more than, three feet deep. In captivity their climbing ability both against a rough wood vertical surface and against string net fencing is remarkable, and there is evidently great flexor power in the legs which, when roughly horizontal, can yet maintain the body of the duckling in a vertical posture. "I noticed that the young perched on the edge of the hole with their heads held quite high and then gave a goodly-springy-jump (? with both legs together) down at 45

degrees to the ground." Where a nest hole is at its normal height of 5-40 or more feet above the ground this jump would result in the downies landing 3-10 feet from the base of the tree.

When calling the young off the nest (nest-box in enclosure) the female gave a rapidly repeated, continuous, series of calls. This was a short note cuc, repeated over and over again. I heard it 15 minutes later used to call the young to her. They would rush after her when they heard it, leaving off whatever they were doing, to do so. The cuc-cuc-cuc call sometimes broke into the more normal following grunt. By the next day four of the six downies had developed much independence and did not always respond to the cuc-cuc call if given in a low tone. When she later called it louder and more urgently these four joined the two which were following her. The female was still giving this call, when alarmed, on the second day after the young left the nest box.

Literature of B.islandica

There are two literature descriptions of this event, both with particular interest because of their setting. The first is found in Munro (1945) who quotes Mr. Sam Sorensen's description of young leaving the nest, close to my campsite of 1955, at Westwick Lake, B.C. In the 35 years that he lived there (prior to 1945) Mr. Sorensen often saw the young fledge. The nest was 16-20 feet from the ground and about 50 yards from the edge of the lake. The young ducks "tumble out from the entrance and run to water....While the young were coming out the female kept flying back and forth between the lake and the tree. She would be seen on the water with one young, then with two and so on until finally all the brood was there."

Munro suggests that this habit of flying from the nest tree to the water may be the basis of the oft-quoted myth that the female carried her young. Presumably the female does not behave in this way when the nest hole is actually over water. Nor does it seem to occur when the distance to be travelled by the downies is some way, for I have seen a female leading her young on foot across the range from a nest 400 yards from the water's edge. However, it may be the usual, or a common practice, when the young have only a short distance to walk, for the female to keep in the air, and fly to and fro over the heads of the downies, rather than for her to land on the ground and lead them. Doubtless they are guided by seeing her in flight and by the direction from which she is heard calling. One wonders, however, whether the young do not in addition have some other means of detecting the direction of water.

The second description, appropriately comes from Iceland, where the nests are not in trees. It was made by Millais (1913) himself, at Myvatn. He describes how he came to the edge of a high bank overlooking the Skalfandi River. On the water below him, and not 15 yards away, there was a female in a great state of excitement. She kept swimming up and down uttering an oft-repeated kra-kra. As he was about to leave he observed a small black and white spot on the edge of a hole in the farther bank of the river. It disappeared and was replaced by two similar objects: —

A moment afterwards I saw the head and neck of a baby Golden-Eye peering over the edge of the hole. Immediately another chick seemed to leap upon its head in less time than it takes to tell it. Eight little Golden-Eyes literally poured out of the nesting-hole one after the other, and fell into the water close to the mother...

The distance they had to jump was, in this case, only 10 feet, but there

is little doubt that a considerably greater height would have not been any more hazardous.

Literature of *B. clangula*.

Tales of the mother goldeneye carrying the downies from the nesting hole to the ground, either on her back or in her beak run back far in the folk literature of Europe. They are apparently still told by northern countrymen in Iceland, Scandinavia and Germany, and are actually reported by such writers as Seeborn, Dresser, and Naumann (Millais, 1913). Lloyd (1854) reports a description in the Proceedings of the Academy of Sciences at Stockholm. Whilst a Pastor Bjorkman was out with his servant hunting ducks, they hid in ambush near a lake. They saw a female goldeneye alight among some willows, and then fly up again. They noticed a newly-hatched downy there. Shortly afterwards the female rejoined it "and after depositing a second duckling, flew off hurriedly as before...On her third visit they remarked her head to be inclined in a very peculiar manner; and on the following they very clearly perceived that in a sort of Olga, or hollow, formed by the head and the bill resting on the breast, she conveyed them under her throat." While it is generally accepted that such accounts are fabrications, it would be unwise to exclude them totally. It is possible that under certain conditions of distance and country an alternative behavioural pattern is invoked.

Phillips (1925) evidently quoting from Brewster (1900), says that downies "easily climb up any sort of material, smooth or wet wood, or cloth, by a series of jumps." A good account of *B. clangula* downies leaving the nest is that by R. A. Gilbert (in Brewster, 1900). He describes how

the female spent much time at the nest entrance peering outwards, and finally flew down to the water, and swam around the tree stub three times, "clucking and calling". Finally she stopped directly under the hole "and gave a single loud cluck or call, when the ducklings began scrambling up to the entrance and dropping down to the water in such quick succession as to fall on top of one another..."

They literally poured out of the nest much as shot would fall from one's hand. One or two hesitated or paused for an instant on reaching the mouth of the hole, but the greater number toppled out over the edge as soon as they appeared.... They did not seem to strike the water with much force.

While the downies were emerging the female sat motionless. When all were out she swam off ahead of the brood and quickly disappeared. The tree described in this account is illustrated, with other nesting sites, in Brewster (1900), from the Lake Umbagog, Maine, region.

In a similar account from Quebec, Macartney (1918) describes how he saw the female standing on the ground at the bottom of the tree. "She gave several low quacks or calls, and out of the hole in the tree overhead promptly tumbled about a baker's dozen of fledgling ducks"...The old bird gathered them in a bunch and led them to the water.

Phillips (1925) summarises this behaviour by saying that various reliable observers described it as a veritable "pouring out" or "boiling over" of downies. The little birds land eight or ten feet from the base of the tree. He cites an M.S. of Harper's and Merrikallis (quoted in the Bulletin of the British Ornithologist's Club 40:151-152), as well as Gilbert's account (above). Phillips writes "swims around it, clucking for a few turns, and then, stopping directly under the hole, gives a single

loud chuk which is immediately responded to by the appearance of the little ones". This may simply be an adaptation of Gilbert's account. Saunders (1916) writes of a house-site, such as is sometimes used by goldeneye: "the duck then sits on the top of the chimney and waits for the youngsters to climb up and project themselves over the edge, to roll down the roof and bang on the ground, which never seems to hurt them at all".

Bernhardt (1940) and his helpers saw the downies leave the nest. The young appeared at the entrance to the hole (which was almost 2 m. deep) fell to the lawn below, hurried to the fence and tumbled down the $3\frac{1}{2}$ m. high wall into the water where the mother awaited them. In another place the nest was 8 m. high "the old bird sat under the tree and called korr korr until the last young had jumped out of the nest hole."

There are only two more recent accounts. The first was one by Miss Jessie MacDonald in 1948 (in Carter, 1952), in New Brunswick. The other is that of Siren (1952). He was particularly interested in the distances travelled by broods of B. clangula after they had left the nest, both over-land (1500 m. in 3 hours) and across bodies of water (2140 m. in 67 minutes). The female made flights, for periods of $\frac{1}{4}$ hour each, in the direction that she subsequently led the young from the nest. Finally she sat at the nest opening (once as long as 51 minutes), and then alighted on the ground or the water beneath the nest. It is at this moment that "a special sound never registered on other occasions" was heard. When this was uttered the young "jumped one after the other from the nest to the ground or water. In the five cases observed the departure of the young took 40, 86, 95, 106, and 150 seconds-- i.e. an average of 1 minute and 35 seconds only. "The

female still waited for some time...45 seconds, to 5 minutes, 25 seconds... then she started leading the brood away".

Discussion

These accounts all agree in a number of points, First, that the female is on the water or the ground when the young emerge. Second, that there is a special call used at this time, which has an immediate and powerful effect upon the behaviour of the downies inside the nest cavity (very often in considerable darkness). Third, that the young all react quickly, by clambering up the sides of the cavity, and with little hesitation springing out into space.

It seems that in some accounts the female calls for some short time before the young appear, at others that they appear as soon as she starts to call. Perhaps the early clucking is her natural expression of nervousness, such as she uses as an alarm signal, apparently, when a brood is pursued on a lake by a boat, or is disturbed from the edge of a lake by a pedestrian. It may be that when this period is over the releasing call is uttered, but that the human observer does not necessarily distinguish the two calls. It cannot be known until we have recordings of both whether the call is exactly the same in the two species.

There is a certain agreement that the downies do use their wings during the descent. Gilbert (loc.cit) wrote: "All used their tiny wings freely, beating them continuously as they descended.", while Macartney (loc.cit) wrote: "They were unable to fly, but were sufficiently grown to be able to ease their fall to the earth, and not unlike a flock of butterflies, they came down pell-mell, fluttering and tumbling, some of

them heels over head, until they reached the ground, unharmed."

Macartney (loc.cit) entitled his paper "Golden-eye Duck carrying young", which might imply a persistence of the old tradition. But what he meant is indicated in the remark: "The old duck then sank low in the water and the ducklings gathered over her back in a compact clump. She took them across the bay..". From this it is clear that he thought that the downies were actually being carried on the back of the parent. This is extremely doubtful, and must be very unusual, if it occurs. It must be mentioned however since there are references in the literature to such a carrying-of-the-young by parent mergansers on the water and goldeneyes are thought to have relationships with the mergansers.

Thus the main ethological problems needing clarification are

- 1). whether only one call (the specific "calling-off" note) is given at fledging, or whether the anxiety call may also be given (the problem is whether the "calling-off" call always has an immediate effect or not),
- and 2). what the physiological changes (end of incubation) and motivational changes are in the female in the few hours before fledging. In the "dry-ing-off" period of the hatched downies her incubation rhythm must be reduced, and her exploratory tendencies in the direction the downies will be led, must be developed. Finally comes the period of hours, or even minutes, when she comes to visit the nest for the last time. When she is "satisfied" about the route to be taken, and the preparedness of the young to leave (it is presumably necessary for her to go into the nest so that their dry and restless condition may act as a stimulus to her on this score) she must leave the nest, give the releasing call from below and then wait for the young to come to her. But the timing must fit not

only into her own preparedness but into the stage of growing strength and activity of the young themselves. They must be made to leave the nest, before any individual might do so on his own account, for if this were to happen the period of time between each downy leaving the nest might (for the early ones at least) be considerable, and the brood would never be united on the lake. There would possibly be total loss of young from nests back in the forest. On ecological grounds alone therefore such a special stimulus is a necessity for survival of the race, although I have suspicions that downy B.islandica may have a tendency to walk downhill rather than uphill - this presumably leading them to water.

Interesting experimental work remains to be done using recordings of the "calling-off" call. For example if the female could be caught about 24 hours after the first young hatched (or could be held in the nest for another 12 hours) the penultimate, and sometimes the last egg laid might be enabled to hatch, which is often not the case in the wild. The "life" of receptivity of the young to this call could be investigated, and how long they may remain in the nest if they are deprived of it. To what extent is the response to the call a case of imprinting learning?

Hostility in the Female

If disturbed while she is on the nest the female may fling herself from the hole and fly away. Very often however she sits tight, and does not try and escape. One may suppose that predation of the eggs by small mammals may sometimes take place when the female is absent. When the female remains on the nest she will hiss like a snake if an arm is inserted into the nest cavity. I do not know if this Hissing is found only in the hole-nesting species of duck, but coming from the inside of a dark deep cavity, it may be suggested that it has survival value.

Aggressive activities (e.g. defence of the mating territory) are generally the province of the male during the early part of the breeding season, though occasionally the female may threaten an intruder. However at the time of the brood territory the female alone must defend the area involved, and females are very easily stimulated into aggressive gestures when another female approaches too closely to a brood she is guarding. Whether such motivation is reduced after the young have outgrown Stage 1, I do not know, but since only a proportion of the females with broods are in company with their own offspring by the time the downies are three weeks old (Stage 2 of Aythya, Gollop and Marshall, 1954), it is probable that rights of sole possession are less important then. Multiple broods with a number of females in company are a frequent feature of scaup brood aggregations, and this feature is also found in goldeneye. Probably the individual distance of the female declines so that only when another (accompanying) female gets very close will she be chased off. There

will be a change in behaviour therefore from the Crouch and Laying Neck on Water postures, to a quick assumption of Threat followed by a rush across the water (with the beak open and jabbing at the other bird), such as might lead into a fight in males, but in females seldom does, for the attacked bird usually escapes.

The Threat posture resembles that of the male, but in the female it can easily be confused with the Invitation to Coitus pose. The female does not appear to open the beak and "klik" in this pose. There may be a signal difference in the time it takes to assume the Laying Neck on Water and Invitation to Coitus postures, the latter being assumed more gradually. Once assumed, there is no movement except slight swimming or re-orientation to keep up with the mate, while the Threat posture is generally being constantly re-oriented in relation to another bird, at some distance in the visual field.

It happens on occasions that as two females go towards each other (especially if one has a brood) both will perform Rotary Pumping. This is often followed by the female with the brood assuming the Crouch or Threat posture. The other female then retreats or is driven off.

Searching for, and Leading the Young (B.islandica)

The call cuc which occurs at the time of fledging has already been discussed. It was noted that it also occurred when the female wished to call the brood together suddenly while on the water. It seems probable that it is a derivative of the normal leading call, mwek, but with an altered pitch.

On one occasion upon returning to her brood a female twice uttered a nasal grunting call, while on another occasion a female (with 9 downies) was disturbed by another bird, and took her brood slowly across the lake opening and closing her beak. Later I heard the nasal grunt, and later still she swam along the lake in front of me, up and down, uttering the same call as a consequence of my presence.

A female searching for her young assumes the Expectancy Look (as described earlier) and utters a nasal grunting call. This same call mwek-mwek was also used when I observed a female leading her brood of six young downies across the range to Westwick Lake on June 20th, 1955. She uttered the single note again and again at equal intervals apart as she walked ahead of them with her head held high and far back.

"

"Greeting" behaviour in females and downies (B. islandica)

Females who have brought their broods to the water often lose them to other females, and sometimes very soon after they come to water. Some females take an interest in broods of downies that they see (particularly early ones). The females direct the Rotary Pumping movement towards other females, and towards their own young or those of other females, at this period. I only saw it used occasionally by females before the males left the lakes. It is almost entirely confined (in the female) to use in the Triumph Greeting Ceremony before the drakes leave. The Rotary Pumping movement is also seen being used by Stage 2 downies. They use it when the female returns to the brood after a hostile encounter, or when

two parts of the brood come together after a separation caused by some disturbance.

Often approaching females do Rotary Pumping movements and the female with the brood does the same and then goes into the Crouch or Threat position. On one occasion a female which had 12 young a little distance away did rapid up and down (pumping) movements followed by the Threat position with neck held forwards making a clucking noise towards a single downy. She then did Jiving movements directed at it. It dove and the female did so a few minutes later. After an encounter on one occasion the female did 3-4 Jiving movements facing the intruder (but ? directed at the downies).

In Stage 1a downies the Rotary Greeting movement is a much more up and down bobbing movement (like the Head-Bobbing of drake B.albeola) than it is like Rotary Pumping. The greeting movements are performed when a disturbance has excited the brood, or when the female returns to the brood after driving off an intruder, and herself performs the Rotary Pumping movement towards them (however, it is not necessary that she should perform it for them to start doing it).

I described the activity as follows on July 7th, 1955 when the female returned to her brood, after diving: "The six young (which were seen for the first time today and were probably experiencing their first or second day on the lake) all or nearly all, began to indulge individually in a fast head up and down movement (pumping) exactly comparable to the courtship nods of Buffleheads. This went on for about two minutes, after the adult joined them and as they swam after her across the pond. The nods

were interspersed with Wing-Flappings and Upwards-Stretch movements". Eleven days later there were 22 downies (between Stage 1c and 2a) with one female at the same place. Four of these were apart from the rest and I noticed that as they returned they greeted her from some distance "not by nodding but by the male courtship up and down movements with its antero-posterior rotary component". Next day the same group were inactive on the water except for three who were rejoining the group "doing the slow courting movements, and their brothers and their guard adult also did it, but the group of eighteen had split into two parts and it may have been due in this case (instead) to the fusion of the two parts".

On one occasion Stage 2 downies did the nodding (as of B.albeola) for three or four minutes after (and perhaps during) violent attacks by the parent on a young Coot. On turning to her young she did one Rotary Pumping movement.

It seems clear that Rotary Pumping is derived from the normal Greeting displays used to maintain broken brood cohesion both by downies and their parent.

SUMMARY OF SIMILARITIES AND DIFFERENCES

BETWEEN B.islandica and B.clangula

In their locomotory, comfort and (probably) agonistic behaviour these two related species do not appear to differ. In their courtship displays there has been considerable specific differentiation from the basic pattern: —

(1) Head-Up Complex: This display hardly differs in the two species (Figures 9 and 11). Its derivation is uncertain, though it greatly resembles the "alarmed" pose. Whether this is intention flight is doubtful. The context in which the display occurs is not clearly understood.

(2) Kick Complex: These displays (two in each species) are basically similar (Figures 13 and 17; 14, 20 and 21), but have become considerably differentiated. They are more clearly distinguishable from each other in B.clangula in which the movements are also more extreme (the head for example is thrown much farther back, and retained there longer). These displays would indicate that B.islandica was closer to the ancestral stock, but the "pumping" displays seem to indicate otherwise.

(3) Pumping Complex: While the Head-Throw (Kick Complex) is the most frequent display in courting parties of B.clangula, Rotary Pumping is the most common display in B.islandica. Thus both form and frequency have been altered as the species have differentiated. Rotary Pumping (B.islandica) is a more striking movement than Bowsprit Pumping (Figure 26), but it is less differentiated than in B.clangula in which the Bowsprit pose is assumed in three possible ways.

(4) The Masthead and Backwards Swimming have not been seen in B.islandica.

(5) The displays of the Coition Sequence (especially Water-Flip, Wing-and Leg-Stretch, and the steaming movements) do not appear to differ much in the two species. Two at least of them are derived from comfort movements.

APPENDIX 1

The Illustrations of B.islandica displays in Sawyer (1928)

The captions of Plates 2 and 3 in Sawyer (1928) should be transposed. Of the displays named in this thesis the following are illustrated by Sawyer.

Plate 3. "Attitudes during rivalry"

Fig. 2	Kick
Fig. 7	Threat
Figs. 10-11	Head-Up---Neck-Withdrawn
Figs. 12-18	Fight
Figs. 19 & 21-23	Jiving
Fig. 20	Invitation to Coitus

Plate 2. "Attitudes during mating"

Fig. 1	Water-Flick
Figs. 2-3	Wing- and Leg-Stretch
Fig. 4	Wing Preen
Figs. 5-7	Invitation to Coitus
Figs. 8-11 & 13-16	Coition
Figs. 12 & 17	Post-Coition Rotations
Fig. 18	Post-Coition Steaming

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