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THE UNIVERSITY OF ALBERTA

SPACING BEHAVIOUR OF BREEDING BUFFLEHEADS (*BUCEPHALA ALBEOLA*) ON PONDS IN THE SOUTHERN BOREAL FOREST

by

© RICHARD HALLAM DONAGHEY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Spacing behaviour of breeding buffleheads (*Bucephala albeola*) on ponds in the southern boreal forest" submitted by Richard Hallam Donaghey in partial fulfilment of the requirements for the degree of Master of Science.

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Date . . May 29, 1970. .

ABSTRACT

Spacing behaviour of buffleheads was studied for three field seasons to determine the nature of the spacing system(s) and its (their) adaptive significance. Breeding pairs and females with broods were observed intensively from elevated blinds at a bog pond and less intensively at a cattail and a lily pond.

Buffleheads were caught and individually colour-marked with nasal saddles. Unmarked paired males and their marked mates were watched daily at the bog pond and their social interactions recorded during all phases of the breeding cycle. Colour-marked female buffleheads with broods were observed intensively at a bog pond over a 23-day period and less intensively at the other ponds.

Agonistic behaviour patterns of buffleheads were described and quantified in terms of encounters. Spatial relationships among buffleheads were recorded by plotting the positions of individuals engaged in agonistic encounters.

Paired males established and defended pair-spaces largely by fighting and evicting conspecifics, but also by threat encounters, during the prelaying period. Most agonistic encounters involving paired males occurred within boundary zones that were relatively stable on any given day but shifted with time in relation to the reproductive state of their mates. Space was maintained mostly by threat encounters but also by fighting during the laying and incubation periods. Paired males defended their mates within their own space and even within their neighbour's space.

At high densities paired males totally divided the open water area of a bog pond among themselves, and excluded unpaired males. At

intermediate and lower densities on a lily pond and a cattail pond, respectively, paired males maintained an exclusive shoreline, boundary zones were less distinct away from the shoreline and unpaired males were not expelled from the central parts of these ponds.

Frequency and intensity of agonistic encounters involving males, and size of pair-spaces varied according to the reproductive state of females and the density of breeding pairs.

Colour-marked females with broods established and maintained a brood-space by fighting and threat encounters. In one situation a female gradually expanded her brood-space as that of another female contracted, until she was evicted from the pond, while the space of a third female remained relatively stable. The spacing system of females with broods was similar to that of pairs in terms of agonistic boundary encounters, expulsion of intruders and exclusive occupation of an area.

Females with broods that held larger brood-spaces were more aggressive in terms of the frequency, outcome and initiation of agonistic encounters. Size of brood-space was positively correlated with size of brood. Females with the largest broods were more aggressive suggesting that brood size determined level of aggression which in turn determined size of brood-space. Females with younger broods tended to be more aggressive than those with older broods of the same size. Females with larger, older broods were more aggressive and held larger brood-spaces than females with smaller, younger broods. Brood size appeared to be a much more important determinant of aggression than age of brood.

The concepts of home range and territory and the problems associated with studying them, particularly in ducks, are discussed. The nature of the spacing system in bufflehead is evaluated in terms of the

behavioural manifestations of territoriality. The adaptive significance of spacing behaviour is discussed.

It is concluded that breeding pairs and female buffleheads with broods defend a territory with boundary zones on ponds within their home range. Thus buffleheads exhibit a territorial system on ponds in a southern boreal forest region.

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INTRODUCTION

Members of a population of birds distribute themselves in space and time. The resulting dispersion pattern reflects both the ecology and the behaviour of the species. Ecological aspects of spacing involve the response of individuals to resources in the environment, while behavioural aspects involve habitat selection and establishment and maintenance of space through social interactions. The significance of spacing is that "it has important effects on the population dynamics, population genetics, and evolution of species" (Brown and Orians, 1970).

The spaces occupied by individuals, pairs, or groups are referred to as either a home range, a territory, an individual space, or a colony (Brown and Orians, 1970). Territoriality has received most attention because most birds are territorial and they have been studied more than most other groups of animals.

There has been substantial research on territorial behaviour in birds, particularly passerines, since Howard (1920) first emphasized the importance of this phenomenon in birds. Howard's concept of territory was applied to ducks by Hochbaum (1944) in his study of canvasback (*Aythya valisineria*) and other species of breeding ducks on Delta Marsh in southern Manitoba. Hochbaum claimed that a number of species of ducks were territorial in that they "defended an area" by "territorial defense flights".

In subsequent research Sowls (1955:48) introduced the concept of home range for ducks as the "area within which a bird spends its period of isolation between the break-up of spring gregariousness following spring arrival and the reformation of fall gregariousness". Sowls (1955) and Dzubin (1955) adopted the concept of home range for ducks because

they both found that territorial behaviour varied markedly from that proposed by Hochbaum for the same dabbler species of the genus *Anas* and for canvasbacks in that: a) paired males used and defended several areas not just one; b) definite boundaries to defended areas were not always established by pairs; c) home ranges of neighbouring pairs often overlapped in space; d) resources were temporally shared between pairs. Thus Dzubin (1955:293) suggested that territory be restricted to the "defended portion of the home range from which a drake attacks another pair, drake or female, of his own species".

In a review of this subject, McKinney (1965) stated that "much attention has been given to inquiring whether and how ducks 'defend areas' and how chasing behaviour (especially aerial pursuit) is related to such areas". He stressed the need for investigating in ducks the "broader biological problems of pair-spacing - the pattern of pair distribution on the breeding grounds, the [behavioural] mechanisms by which this is achieved, and the survival value of the different patterns found in different species".

I decided to investigate this problem in buffleheads (*Bucephala albeola*), a species of diving duck, because: 1) they are one of the most abundant breeding ducks on wetlands in the boreal forest based on a survey near Utikuma Lake, Alberta (Donaghey, 1974); and 2) buffleheads apparently space themselves on ponds and lakeshores (Erskine, 1972:57) but opinions differ on the nature of the spacing.

Erskine (1972) implied that, in general, only the concepts of home range and mated-female distance (Conder, 1949; Koskimies and Routamo, 1953) applied to buffleheads. However, Munro (1942) stated, without evidence, that in buffleheads "a breeding pair establishes a definite

territory which the male vigorously defends from encroachment by other males". Stansell (1909) observed that "when two or more pairs occupy a single pond, the males are usually very pugnacious, often quarreling and trying to drive each other off the pond for hours at a time".

These observations by Munro (1942) and Stansell (1909) suggest that aggressive behaviour of males serves to space breeding pairs. Therefore I decided to thoroughly investigate spacing behaviour in buffleheads, and to concentrate on social interactions between and within breeding pairs in relation to space and time. I chose to watch buffleheads only on small ponds, rather than lakeshores, because ponds have a higher ratio of shoreline to open water area, thus density of buffleheads and their frequency of interactions are more likely to be greater on ponds.

Buffleheads seem particularly well suited for a study of spacing behaviour because breeding pairs appear to restrict their activities to part of a pond and to use mostly the open water. From elevated blinds buffleheads were visible almost continuously and spacing behaviour could be accurately described and quantified.

The purpose of this study then was to determine: 1) the exact nature of any spacing system(s) of breeding buffleheads on ponds, and 2) the adaptive significance of any spacing behaviour observed.

STUDY PONDS

The study ponds are situated north of Atikameg (55° 54'N, 115° 39'W) in the Utikuma - Lesser Slave Lakes region of north-central Alberta. This area, in the Mixedwood Section of the southern Boreal Forest (Rowe, 1959), is mostly covered with upland forests of young trembling aspen (*Populus tremuloides*), mainly regeneration after fire, interspersed with patches of mature aspen, white spruce (*Picea glauca*) and white birch (*Betula papyrifera*). The lower, wetter upland sites are characterised by balsam poplar (*Populus balsamifera*), while the lowland sites have black spruce (*Picea mariana*) and tamarack (*Larix laricina*) trees, and willow (*Salix* spp.), alder (*Alnus* spp.) and labrador tea (*Ledum groenlandicum*) shrubs.

The terrain is gently undulating with an average elevation of about 670 m. Summers are short and cool. Mean summer precipitation is 20 cm, with June and July being the wettest months. Mean July temperature is around 16°C (Hardy, 1967).

Four study ponds were chosen. To record possible changing behavioural relationships in breeding pairs of buffleheads I considered three ponds the maximum that could be studied satisfactorily. To document social interactions between pairs relative to the environment, three ponds (H, J and K) were chosen that had more than one resident pair of buffleheads and had different shoreline vegetation. An additional pond (L) was selected to study behaviour of female buffleheads with broods.

Some features of the bufflehead's environment were described by classifying each pond as a habitat type depending on its wetland vegetation, and further described according to aspects of limnology and

the presence of other aquatic birds (other ducks, grebes and rails). Wetland vegetation of a pond refers here to the submersed vegetation of the open water, and the emergent and other vegetation in a zone 10 to 20 m from the shoreline.

To aid in waterfowl research and management a detailed classification of prairie wetlands has been developed based on the pattern of vegetation zones and water permanence (Stewart and Kantrud, 1971). Comparable classifications of forest wetlands are few, some exceptions being those of Gilmer (1971) and Cowardin and Johnson (1973) in north-central Minnesota, and Jeglum's (1972) survey of boreal forest wetlands in Saskatchewan. Jeglum (1972) quantified vegetation stands on the basis of their physiognomy and dominance, and Cowardin and Johnson (1973) grouped stands into plant communities with or without permanent water on the basis of species abundance. I made no attempt to quantify vegetation stands. Instead each pond was classified broadly on the basis of its shoreline vegetation, irrespective of whether the shoreline was composed of several plant communities or a single species of emergent plant, or whether some combination of physical and botanical characteristics was used. The main vegetative characteristics of each study pond are described first, then their limnological features and aquatic birds are briefly described and compared.

POND J. Bog pond (1.5 ha) Figure 1a

In the zone of permanent open water submersed vegetation was sparse. Most of the shoreline was relatively solid and was composed of several bog communities with patches of marshy and/or spongy emergent vegetation in the bays. Some shoreline was characteristic of sedge fen (Jeglum, 1972) with *Calamagrostis* spp. and a fine-leaved sedge (*Carex*

Figure 1a. Pond J with a shoreline of bog plants.

Aerial photograph taken July 1973 from south-west facing north-east. An elevated blind is on south side to right of centre. Small peripheral ponds occur around J. Part of cattail Pond C is in middle top of photograph.

Figure 1b. Pond H with a shoreline of cattail.

The lighter areas peripheral to the dark cattail represent a narrow zone of sedges and grasses, and extensive open meadows. Aerial photograph taken July 1972 from north-west facing south-east. A blind is left of centre at edge of far shoreline in front of a clearing.

aquatilis) the dominants. Other sections of shoreline, better classified as bog, consisted of an association of *Ledum groenlandicum* - *Sphagnum* spp. - *Vaccinium vitis-idaea*. Farther away from the shoreline were shrubs such as tall willows (*Salix* spp.), and dwarf birch (*Betula glandulifera*) and stands of muskeg (black spruce trees associated with *Ledum groenlandicum* - *Sphagnum* - *Vaccinium vitis-idaea*). Marshy emergent vegetation such as coarse-leaved sedges and *Eleocharis palustris* formed patches of shoreline in the bays. Common bladderwort (*Utricularia vulgaris*) and marsh cinquefoil (*Potentilla palustris*) were the dominant vegetation of the small, peripheral bog ponds to the south. Nesting habitat of buffleheads included poplar stubs among stands of mature and young aspen to the north and west.

POND H. Cattail pond (3.8 ha) Figure 1b

In the zone of permanent open water *Chara* spp. was the dominant submersed vegetation. The shoreline was composed entirely of a deep marsh zone of cattail (*Typha latifolia*). Peripheral to the cattail was a shallow marsh zone of coarse-leaved sedges (the dominant species was *Carex rostrata*) associated with whitetop (*Scolochloa festucacea*). Surrounding the shallow marsh zone were extensive open areas of wet meadow and prairie species of plants grazed by cattle in spring and mowed at the end of summer. Nesting habitat of buffleheads included poplar stubs among stands of mature and young poplar to the south.

PONDS K and L. Floating-mat - pond-lily ponds (3.7 ha and 3.3 ha, respectively) Figure 2a, b

Yellow pond-lily (*Nuphar variegatum*), the dominant aquatic plant with floating leaves, covered nearly half of the open water on Pond L

Figure 2a. Pond K with a floating-mat shoreline of mainly cattail and sedges, and pond-lilies on the open water.

Aerial photograph taken July 1972 from west facing east. Blind is to lower right of photograph.

Figure 2b. Pond L with a floating-mat shoreline of mainly cattail and sedges, and pond-lilies on the open water.

Aerial photograph taken July 1973 from south-east facing north-west. An elevated blind is to lower left of photograph.

and about one fifth on Pond K. Nearer the shoreline clasping leaf pondweed [illegible] was the dominant species of submersed vegetation. The shoreline zone consisted of a floating spongy mat of cattail and sedges, mainly [illegible]. At the water's edge was a band of tall willow and alder shrubs and mostly dead white birch with an undercover of ericaceous bog shrubs in places. A forest of young aspen and stands of mature white spruce trees closely surrounded the ponds. Hereafter this habitat type is simply referred to as lily pond.

Other characteristics of the study ponds are now briefly described and compared. The four study ponds were all small (1.5 to 3.8 ha of open water area), shallow (mostly less than 2 m), fresh (conductance less than 500 micromhos), alkaline (ph 7.6 to 8.6), with permanent and relatively stable water levels.

Characteristics of water chemistry (Table 1) were determined from analysis of a surface sample of open water taken near the shoreline and preserved with chloroform. Cattail Pond H appeared to be more eutrophic in terms of nutrients (as measured by conductance, and total dissolved solids) than the other ponds.

Aquatic invertebrates from each pond were sampled 1 to 2 m from the shoreline with a dip net and preserved in 10 to 20 percent formalin. Composition of aquatic invertebrates was similar for the bog and lily ponds, but more diverse on cattail Pond H. For example, in addition to groups common to both Pond H and the other ponds, cladocerans, mayfly nymphs and some families of aquatic beetles were present in Pond H but not the other ponds. Aquatic insects were more abundant in Pond H, especially Corixidae, Diptera (mostly Chironomidae), Ephemeroptera and

Table 1. Characteristics of water chemistry on the study ponds.

Habitat type	Pond	Date sampled (1973)	Colour	Turbidity (Hach kit)	Conductance (micromhos)	Milligrams per litre											
						pH before alkalinity	Phenlphthallen alkalinity as $CaCO_3$	Total alkalinity as $CaCO_3$	Phosphate (ortho)	Silica	Nitrate-N	Total dissolved solids	Iron	Hardness as $CaCO_3$ Calcium	Hardness as $CaCO_3$ Total	Chloride	Sulphate
Cattail	H	Aug. 25	115	30	400	8.42	5.7	131.0	0.04	4.45	0.04	373.0	0.07	116	208	3.30	88
Bog	J	Aug. 27	162	37	240	8.[illegible]	5.7	101.0	0.10	4.90	0.05	180.4	0.02	102	128	2.84	30
Lily	K	Aug. 27	300	58	190	7.82	0	87.2	0.17	4.00	0.07	176.1	0.08	74	108	1.88	7
Lily	L	Aug. 27	280	49	180	7.60	0	84.1	0.10	5.40	0.07	173.2	0.07	74	108	1.42	11

Odonata (especially Zygoptera nymphs). In the bog and lily ponds Amphipoda and Diptera (mostly *Chaoborus*) were the most common invertebrates taken in the samples.

Waterfowl and other aquatic birds (Podicipedidae, Rallidae) were censused on the study ponds (Donaghey, 1974). Fourteen species of ducks, including buffleheads, and five species of other aquatic birds occurred on the study ponds. More resident species of dabbling and diving ducks and other water birds occurred on cattail Pond H in a species ratio (6:8:5) respectively, than on lily Ponds K and L combined (5:4:3), with the least number of species on bog Pond J (4:2:2) (Donaghey, 1974).

Four species of dabblers - mallard (*Anas platyrhynchos*), American wigeon (*Anas americana*), blue-winged teal (*Anas discors*), and American green-winged teal (*Anas crecca*); two species of divers - lesser scaup (*Aythya affinis*) and bufflehead; and two species of other aquatic birds - red-necked grebe (*Podiceps grisegena*) and sora (*Porzana carolina*) were resident on all study ponds. Common goldeneye (*Bucephala clangula*) and ring-necked duck (*Aythya collaris*) were resident on Ponds K, L and H. On Pond J they were transient species, although the latter species may have attempted to breed there.

There were a greater number of diving ducks than dabblers on all ponds. Greater numbers of divers occurred on Pond H than on any other pond. Lesser scaups were the most abundant diving ducks on all ponds, but were most numerous on Pond H.

METHODS

Field work was conducted over three summers, May to August 1972, April to August 1973, and the end of April to mid-June and two weeks in July in 1974.

No attempt was made to catch buffleheads in 1972, the first field season. However, to study spacing behaviour, it became apparent that ducks would have to be individually colour-marked. In 1973 almost all potential capture methods were tried. To minimize disturbance and possible disruption of the breeding cycle of the few pairs on the study ponds, I tested the techniques first on other ponds. Trapping on the study ponds began only when most pairs were well established. I caught adult females at their nest cavity (Fig. 3, technique modified from Erskine, 1959). Most buffleheads were caught in rectangular, welded wire traps with mirrors (Fig. 4b). I designed these traps with two funnel entrances, one at each end, leading into a double-sided mirror so as to stimulate birds toward their image (basic trap design modified from Schierbaum and Talmage, 1954; Addy, 1956:sect. 1610 and 1620; Rogers, 1964). Buffleheads were also caught by night-lighting from a boat (technique and equipment modified from that used by Lindmeier and Jessen, 1961; Bishop and Barratt, 1969), in floating ball traps (Thornsberry and Cowardin, 1971) and in mist-nets. In 1974 traps were set out at Pond J before pairs arrived.

Flying adults and yearlings, and class III flightless juveniles (Gollop and Marshall, 1954), when trapped, were leg-banded and colour-marked with nasal saddles (Sugden and Poston, 1968) (Fig: 4a). These markers were made of either plasticized polyvinyl chloride or nylon, and attached with a nylon pin. Saddles were made of one colour (red,

Figure 3. Opening up female red's nest cavity 9.5 m (31 ft) above ground.

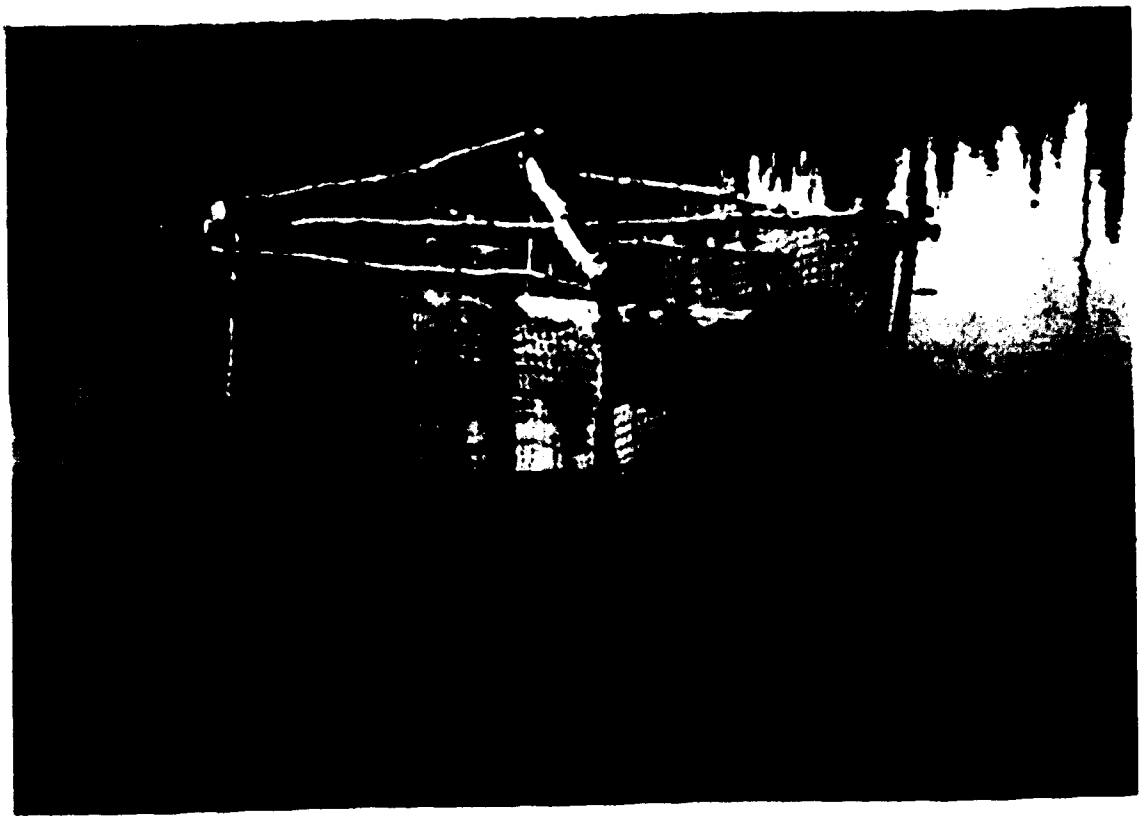
Ropes hold a 9.1 m (30 ft) aluminum ladder upright away from rotten stub. By lashing spruce poles to the base of ladder the same technique was used to open up female white's cavity 11.6 m (38 ft) above ground in a nearby stub.

Figure 4a. A female bufflehead individually colour-marked with a yellow nasal saddle.

U.S. Fish and Wildlife aluminum band is on the right leg.

Figure 4b. Welded wire trap with two funnel entrances leading into a double-sided mirror.

Sides of trap are constructed of one inch welded wire mesh, with plastic netting on top.



yellow, green, blue or white) and combinations of two colours in contrasting broad stripes a) orange, yellow, blue or white with black; b) red or green with white; c) yellow or red with blue. These saddles were ideal for consistently recognizing individuals interacting vigorously. To specify the sex of individuals I use the letter F for females, and M for males. To denote females individually colour-marked with nasal saddles I use letters, for example F B is the female with a blue saddle, and F Or-Bk is the female with an orange and black saddle. The only colour-marked male will be designated M B(K), K indicating the pond where he was resident.

Unmarked individual paired males were recognized with reference to the space they occupied and their behaviour toward conspecifics, especially their relationship with their mate, either marked or unmarked. Unmarked females of a pair were recognized individually by their flight path to a specific nest site. Unmarked females with broods were individually recognized by the size and age of their brood and their spatial relationships with other females with broods. To denote unmarked individual females resident on a particular pond I use a combination of letters and numbers, for example, F 1(J) is female one on Pond J. In 1974 at Pond J none of the resident paired males were individually colour-marked, yet they were all mated to marked females. Every day for 6 weeks I watched the behavioural responses of these males to their mates and neighbouring pairs. Thus I felt confident that the same individual males were mated to the same colour-marked females throughout the breeding cycle. I use letters to refer to these individual males, for example M W or pair W, means an individual unmarked male mated to F W.

From blinds placed on the ground buffleheads were not visible continuously in 1972. In 1973 elevated blinds (Fig. 5) were constructed facing north where possible to have the best light conditions for observing, and at a position where most shoreline was visible. During April four towers were erected at three ponds (J, K and H) before the arrival of buffleheads. An additional elevated blind was built in mid-July at another pond (L) for watching female buffleheads with broods.

I observed buffleheads from blinds for a total of about 500 hours during all three field seasons with emphasis throughout on recording social interactions. Throughout May to early June breeding pairs were watched at Pond J in 1972, Ponds H, J, and K in 1973 and Pond J in 1974. In 1972 pairs were observed only during their incubation period, while in 1973 at any one pond the interval between observation days varied. Thus all pairs were not watched during all stages of the breeding cycle. In 1974 I intensively watched breeding pairs for 30 days from their arrival through incubation. In 1972 buffleheads were observed at all times of day. Interactions were few but seemed to peak about mid-morning. Therefore in 1973 on any particular day interactions were recorded for ten hours from 0800 to 1800 D.S.T., and for five hours from 0800 to 1300 in 1974.

Throughout July 1973 colour-marked female buffleheads with broods were watched intensively at Pond J for a total of 100 hours, usually from 0800 to 1800 on any given day, except from 1200 to 2200 (July 7) and 1100 to 2100 (July 9). Other females with broods were watched for shorter periods at Ponds H and J in 1972, Ponds H and L in 1973 and Pond J in 1974. Walking to the blind by myself alarmed females with broods, especially near the blind, much more than pairs. Therefore

Figure 5. Elevated blind with 360° vision at Pond J.

Four similar blinds were erected at Ponds H, K and L in [redacted].

during the brood period a person went with me to the blind, soon left and then these females quickly resumed their activity near the blind.

All agonistic interactions seen between buffleheads and conspecifics were recorded, mostly on tape. For each intraspecific encounter I tried to record: time of day, individuals involved, main behaviour patterns, initiator and outcome. With evenly matched unmarked males it was difficult to determine the outcome of most encounters. Interactions seen between buffleheads and other species were often incomplete and recorded in less detail.

To record spatial relationships between interacting individuals, their positions were located on Pond J with reference to colour-marked stakes along the shoreline, and plotted on field maps. The error in locating a bird's position near the shoreline and plotting it was estimated to be ± 3 m. A bird's position out on the open water was more difficult to plot because no stakes were placed there, but errors were probably no greater than ± 10 m, mostly ± 5 m.

At the larger study ponds there were much greater errors in plotting positions of birds so these data have not been used to determine details of spatial relationships.

The location of supplanting attacks and fights, and the mid-point between individuals engaged in threat and approach - withdrawal encounters, were plotted on overlay maps drawn to scale. Boundaries were plotted primarily from the positions of threat and fighting encounters. Pair and brood-spaces were measured with a planimeter and expressed to the nearest 0.05 ha.

We searched for nest cavities of breeding female buffleheads for two main reasons. Firstly, to catch and mark the occupant, and

secondly, to open up the cavity (Erskine, 1954) to determine stage of the breeding cycle, clutch size and hatching success. Any nest cavity in a stub visible from the blind was easily found by watching the female fly directly to it. Nest sites of particular females nesting in the forest well away from the pond were more difficult to find. We located these cavities by progressively following the female in flight from the pond above the forest canopy, until she descended or was lost to sight, then a localized ground search was made for likely nest stubs.

Stages in the breeding cycle (the week of laying and incubation) of individual female buffleheads breeding in 1972 and 1973 were estimated by backdating from the date of arrival at a pond of class Ia (downy) broods. I crudely estimated date of clutch-initiation of three females breeding in 1973 by making several assumptions regards date of hatching, incubation period, clutch size and rates of egg-laying. Firstly, young buffleheads leave the nest cavity 24 to 36 hours after hatching (Erskine, 1972:92), therefore newly hatched broods (class Ia) were considered to be two days old on the day they arrived at a pond. In one instance, where a female deserted her clutch, I estimated age of the embryos on the basis of characteristics used in determining the age of embryos in other species of waterfowl (Cooper and Batt, 1972; Caldwell and Snart, 1974). Secondly, Erskine (1972:89) found that "incubation periods ranged from 28 to 33 days, with most clutches hatching 29 to 31 days after the last egg was laid", therefore I assumed incubation period to be 30 days. Thirdly, clutch size was known for two of the three females whose date of clutch-initiation was estimated. In estimating clutch size of the third female I considered two factors, the number of eggs that fail to hatch, and early mortality

of young, which refers here to losses of young in the first week, including those that fail to leave the cavity, and losses that occur while young are travelling on land to water, or after they have reached it. The contents of the cavity were determined by opening it up after the brood had left. I assumed that one of her young was lost on land, because they travelled about 300 m to water and I counted the number of young in her brood only a few hours after they arrived at a pond (see Erskine 1972:112-113 for further details regarding this assumption). Finally, based on laying rates of three females in this study, I assumed that eggs were laid at 2-day intervals, although as Erskine (1972:80) pointed out some individual females may lay eggs at a faster rate.

In 1974 the precise stage of the breeding cycle was determined for three colour-marked females. For one female dates of laying were determined by daily inspection of her nest cavity during the laying period. For the other two females I determined the days they laid from their daily activity patterns (flights toward the nest site and the periods of time away from the pond) together with known clutch size of one female, and a good estimate of clutch size of the other female based on her class Ia brood of seven. For two females incubation probably started the day the last egg was laid, but for convenience I assumed it began next day. For the female whose clutch size was estimated, incubation probably started two days after the estimated date of laying of egg seven, thus allowing for a clutch of eight eggs and the possibility that one of her young was lost because they travelled at least 600 m to Pond J.

The availability of nest sites was increased at Pond K, in an attempt to raise the density of breeding pairs and subsequent broods,

and hence the frequency of interactions. In early May 1973 at Pond K, three nest-boxes (measuring 41 cm deep, 15 cm square bottom) and three artificial cavities were erected on dead stubs and poles around the shoreline for this purpose.

To determine the habitat used by female buffleheads with broods in relation to other species of water birds I censused 20 ponds between July 8 and 19, 1974, the optimal period for censusing bufflehead broods.

Data were analyzed statistically using Chi-square tests, and Spearman's rank correlation (Siegel, 1956). A probability value of 0.05 or less was considered significant.

RESULTS

LIFE HISTORY CHARACTERISTICS IN SPACE AND TIME

Annual Cycle

Buffleheads reared on the study area, or resident there as subadults or adults, most likely winter on the Pacific coast as indicated by two recoveries of birds banded on the study area and other birds banded in the Peace River - Lesser Slave Lake region (Erskine, 1972:123-124). One bufflehead banded at Pond H as a juvenile on August 9, 1973 was recovered in Washington State on November 9, 1973; and another bird banded and colour-marked at Pond M as a subadult female on May 30, 1973 and last seen at Pond H on June 16, 1973 was recovered in Oregon State on October 15, 1974. Both sexes tend to return to wintering grounds used in previous years (Erskine, 1961).

Pair formation apparently can occur on the wintering grounds, but also during spring migration and on the breeding grounds because Erskine (1961) suggests that many male buffleheads start migration unpaired.

Most adult females are paired on arrival at the breeding grounds where there is a surplus of unpaired males in each season. Breeding pairs settle on ponds and lakeshores, the female tending to return to nest in the same area as in previous years (Erskine, 1961).

Tree-cavities, usually those excavated by common flickers (*Colaptes auratus*), are used for nesting. While the female is occupied with laying, her mate waits on a nearby pond or lakeshore. The pair bond breaks up at about the onset of incubation (Drury *et al.*, MS; Erskine, 1972:88, 90). While the female incubates, post-breeding males gather for moulting on lakes used in previous years (Trauger, pers. comm.).

The female alone cares for the brood, but usually leaves them before they are fledged and able to fly, and homes to moulting areas (Erskine, 1961). Fall migration in October to the wintering grounds completes the cycle.

Spring Arrival

Arrival of buffleheads was studied at three ponds (H, J and K) in 1973, and two ponds (H and J) in 1974. Buffleheads were among the earliest ducks to arrive on the study area. In 1973 I saw the first bufflehead, a lone male, on April 22, 4 days after the first mallards were seen.

Early arriving buffleheads settle on ponds partially ice-free or temporarily disperse to smaller peripheral ponds with open water. For instance, on April 26, 1973 a pair flushed from the open water of a small, peripheral pond near Pond J, the latter being still fully ice-covered on that date. However, by May 2, 1973, though Pond J was still almost fully ice-covered two breeding pairs had settled there on the only available ice-free water, a strip along the north shoreline.

Breeding pairs settled a few days later on Pond H than Pond J. Pond H was more than half ice-free on May 1, 1973 and had one pair and a lone male bufflehead. A second pair settled between May 5 and 7, 3 to 5 days after the pond was probably ice-free.

Pond K was fully ice-covered on April 30, 1973 but completely ice-free by May 3. It was not known if any buffleheads settled on May 1 or 2 but by May 3 one lone male bufflehead was present. By the afternoon of May 4 two pairs of buffleheads were present on Pond K. Thus by May 3, 1973 all three ponds (H, J and K) were ice-free and each occupied by at least one pair of buffleheads.

In 1974 on April 27 I saw the first bufflehead, a lone male, on partially ice-free Pond J. This pond was ice-free by April 29, 4 days earlier than in 1973. Three colour-marked females, all paired upon arrival, returned to Pond J in 1974. I saw the first of these females (F B) on April 28 at Pond M, then at Pond J the next morning. The two other colour-marked females with their mates were first seen at Pond J on May 3 and May 4.

On ice-free Pond H I saw one unmarked pair on April 30, 1974 and two pairs on May 14 (a colour-marked female and her mate and an unmarked pair).

In summary the break-up period of the study ponds occurred from the last 2 to 3 days of April to the first 2 to 3 days of May. In both years breeding pairs of buffleheads settled on ponds partially ice-free and/or within a few days after ponds were fully ice-free. Breeding pairs settled a few days earlier on bog Pond J, than either cattail Pond H or lily Pond K.

Migrational Homing

The degree of migrational homing by adult females to the study ponds was determined from the return of colour-marked birds. Six adult females (four from Pond J and two from Pond H) were individually colour-marked in 1973. Four of these females returned to the study ponds the next year.

All three marked females that returned to Pond J in 1974 occupied this pond while nesting and/or with a brood the previous year. The only marked female that returned to Pond H was resident there throughout the nesting and brood periods the previous year. These returns of adult female buffleheads provide evidence of a high degree of precise homing

to the same small ponds used the previous year. Evidence from a much larger sample (Erskine, 1961) indicates a strong tendency for adult female buffleheads to return to the same lake where they nested at the previous year. Thus females appear to exhibit a strong homing tendency to both lakes and ponds.

Migrational homing among other species of female ducks has been well documented, for example, in species of ground-nesting dabblers of the genus *Anas* (Sowls, 1955), the lesser scaup, a ground-nesting diver (Trauger, 1971) and the cavity-nesting wood duck (*Aix sponsa*) (Grice and Rogers, 1965).

The return of individual male buffleheads to a specific breeding site used in previous years has not been documented. During this study only one adult male bufflehead was colour-marked. This paired male, B(K), but not his mate, was caught and marked at his breeding Pond K on June 12, 1973. On May 30, 1974 I saw M B(K) with an unmarked female on the same part of the pond it occupied the previous year. This pair was not seen on visits to Pond K on May 10 and 14 but was seen on two subsequent visits on June 3 and 5.

These observations of the only paired male marked suggest that male buffleheads also may tend to return to the same breeding pond used previously. Observations were too infrequent to determine if M B(K) was paired on arrival, or homed to the breeding grounds and acquired a mate there. For several reasons M B(K) may have been paired to the same female as in the previous year, and was paired on arrival, and thus merely followed his mate home. Evidence presented later suggests that females select the breeding pond and the pair-space at that pond. Also pair bonds of buffleheads could be renewed either on the wintering

grounds, because Erskine (1961) provided evidence that both sexes tend to return to the same areas in successive winters, or during spring migration, if they use the same stopover points, because Erskine (1961) suggested that many male buffleheads start migration unpaired. Finally, if males home to the breeding grounds separately from females then pair bonds could be renewed there. The return of male buffleheads to wintering, moulting and breeding areas in successive years suggests that their homing tendency is well developed.

Poston (1974) provided evidence of migrational homing by unpaired male northern shovelers (*Anas clypeata*). The only marked male shovelers (two adults and one juvenile) to home to his study area were all unpaired on arrival. Grice and Rogers (1965) found that among cavity-nesting wood ducks only ten percent of adult males returned to their natal and/or breeding areas. It was not stated if these males were paired or unpaired on arrival. Recoveries elsewhere led Grice and Rogers (1965) to conclude that male wood ducks, because they apparently form pairs on the wintering grounds with females from other populations, tend to follow a female to her natal area rather than his own.

Survival of Adult Females

Adult female buffleheads appear to have a high survival rate, based on small samples. In this study, of six adult marked females, four returned to the study ponds, a survival rate of 67 percent. An even higher survival rate was found among the first eight female buffleheads recaptured at their nest sites in interior British Columbia (Erskine, 1972:179). From mortality rates given by Erskine (1972:179) I calculated the average annual survival rate for these eight females to be 76 percent for the first five years, or 72 percent over a 7-year

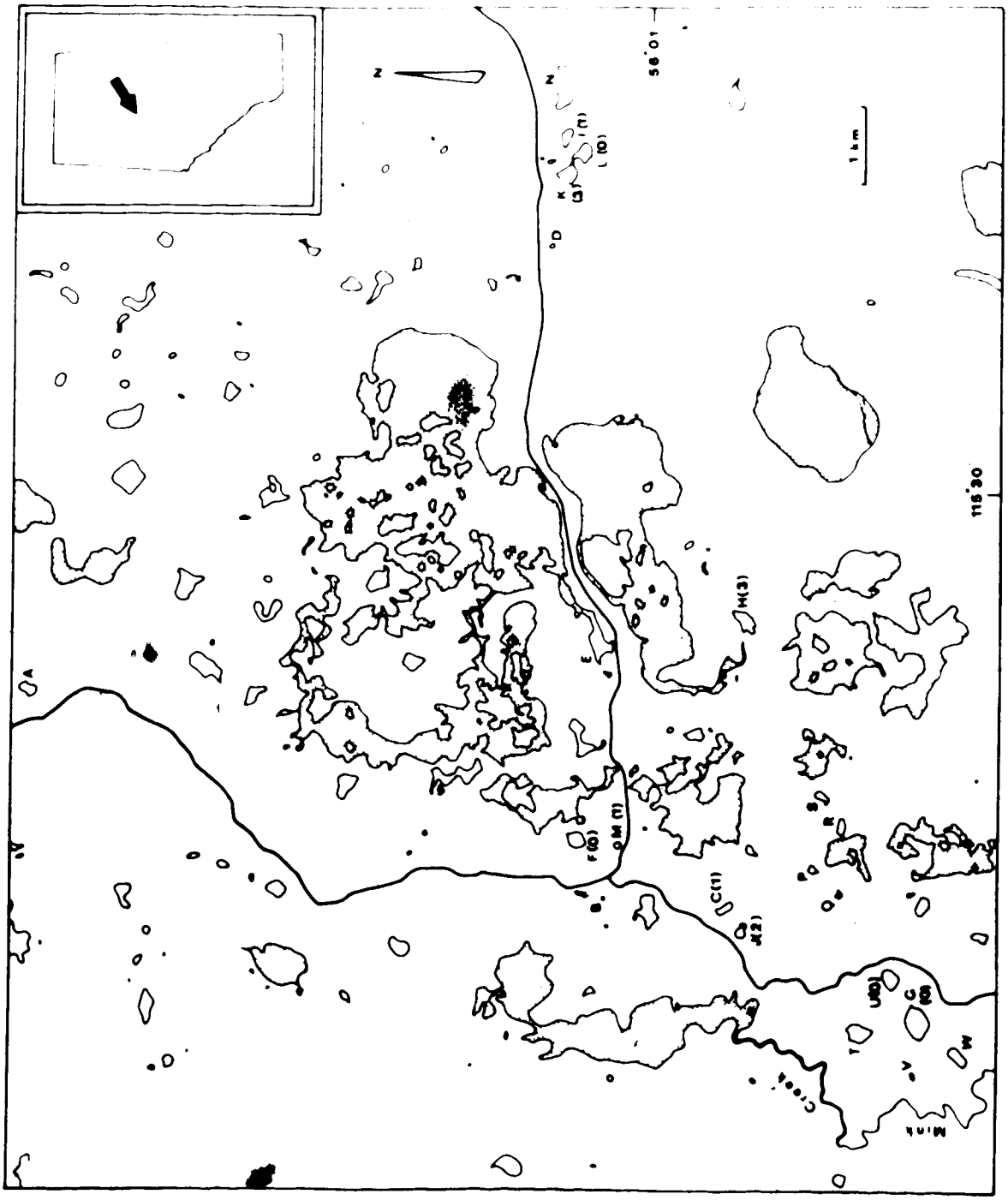
period. On the basis of all recaptures of adult female buffleheads at the nest site Erskine (1972:177) calculated their annual survival rate to be 50 percent, only slightly higher than that obtained from recoveries of banded birds. Erskine (1972:180) pointed out that the numbers of a breeding population of buffleheads in British Columbia could not be maintained "unless the survival rates of first-year birds or of mature females or both were higher than those here obtained from banding recoveries and recaptures". Female buffleheads first breed at the age of two years (Erskine, 1972:84). Ricklefs (1973) showed that among birds in general the greater the age at first breeding the higher the annual adult survival rate. In birds first breeding at the age of two years, such as swifts, herons, geese, owls and shorebirds, the annual average survival rate ranged from 60 to 80 percent (Ricklefs, 1973). This general relationship between age at first breeding and average annual survival rate, and the survival rate of adult female buffleheads based on small samples suggests that a 50 percent average annual survival rate of adult female buffleheads is an underestimate. Thus the survival rate observed in this study (67 percent) is probably more realistic.

Distribution of Breeding Pairs on Ponds

Pattern of pair-spacing was determined in May 1972 by censusing breeding buffleheads on ponds along 13 km (8 miles) of road. Of the ten ponds, six had breeding buffleheads (three ponds each with one pair, and three ponds each with two to three pairs). This distribution gave a clumped spatial pattern of breeding pairs (Fig. 6). This pattern reflects the distribution and availability of ponds and nesting habitat suitable for buffleheads.

Figure 6. Distribution of breeding pairs of buffleheads on ponds on the study area in 1972.

Letters refer to individual ponds visited and numbers in parentheses to the number of pairs of buffleheads on each pond. Zero indicates ponds with no pairs. No ponds are denoted with letter O. Stippled areas represent open water of lakes, but not ponds. Thicker lines are roads.


N
56°01
1 km
115°30
H(3)
F(0)
M(1)
C(1)
J(2)
Creek
Mink

Numbers and Densities of Breeding Pairs on Ponds

The [redacted] densities of breeding pairs resident on the study ponds va[redacted] ponds for each year, but was relatively constant for the [redacted] tween years (Table 2).

[redacted] that maintained a pair-space on a study pond th[redacted] out[redacted] and early June, and were known to have nested or most lik[redacted], are termed residents. Colour-marking of individual fema[redacted] that a sample of birds in the Pond J area definitely consi[redacted] two groups of breeding pairs: 1) the resident breeding pairs, [redacted] 2) breeding pairs that failed to establish a pair-space on Pond J, [redacted] occupied nearby peripheral ponds and nested nearby. Because [redacted] latter group were resident in the Pond J area, but not on Pond J, I [redacted]opose to call them peripheral breeders, rather than non-residents.

Both [redacted]ent and peripheral breeding pairs occurred in the Pond J area in [redacted] 1974. In 1973 both the two resident females on Pond J and two p[redacted]ipheral females were colour-marked. One peripheral pair occupied small ponds around Pond J (Fig. 1a) and the female of this pair (F Y) nested in a cavity within 50 m of Pond J. The other peripheral female (F B) was first individually recognized with her brood on a small pond adjacent to J, and then on Pond J.

In 1974 the three paired females resident on Pond J were all colour-marked. A peripheral female (F Or) nested nearby, and settled on Pond J with her brood. A second female may have been a peripheral breeder, because Pond C north of J was not occupied by any resident breeding pairs, but an unmarked female with a brood arrived there. Therefore on Pond J there were two and three resident breeding pairs in

Table 2. Numbers and densities of resident breeding pairs of buffleheads on the four study ponds from 1972 to 1974.

Pond Size (ha)	H 3.8		J 1.5		K 3.7		L 3.3	
	No. Pairs[a]	Pairs/ha	No. Pairs	Pairs/ha	No. Pairs	Pairs/ha	No. Pairs	Pairs/ha
1972	3[b]	0.8	2	1.3	3[c]	0.8	0[d]	0
1973	2	0.5	2	1.3	3	0.8	1[c]	0.3
1974	2[c]	0.5	3	2.0	3[c]	0.8	0[e]	0

[a]Based on at least eight censuses in May unless otherwise indicated.

[b]Based on maximum number of breeding pairs seen at any one time during six hours of observation on May 22 and May 23, and all day observations on June 5.

[c]Based on 3-5 censuses from May 10 to June 8.

[d]Based on one census on May 5.

[e]Based on one census on May 10.

1973 and 1974 respectively. In addition there was at least one and probably two peripheral breeding pairs in both years in the Pond J area.

The sample of breeding pairs in the Pond H area includes resident breeding pairs on Pond H, in addition to other females that settled on Pond H with their broods. With unmarked individuals it was not clear whether this latter group were resident pairs that settled on Pond H later than the known resident pairs, or were peripheral breeding pairs that occupied nearby lakes, rather than ponds (see Fig. 6). In 1972 there were an estimated three breeding pairs, and four broods on Pond H. However, it was not known whether these broods were with females of resident or peripheral breeding pairs.

In 1973 there were definitely two resident breeding pairs on Pond H, with one of the females colour-marked (F R-W). Female R-W arrived with her brood at Pond H, then another female with a brood arrived but left soon after. A third female with a brood arrived between July 19 and 21. This latter female had no pair-space on Pond H at the time she would have been laying, so she must have been a peripheral breeder that brought her brood to Pond H.

The sample of breeding pairs seen in the Pond K area included resident pairs that presumably nested, and late arriving pairs that settled on Pond K then dispersed. In 1973 three resident pairs settled, then two other pairs arrived later, but subsequently left. Without marked individuals it was not possible to know the exact status of breeding pairs. However, the number of resident pairs on Ponds K, L, and I (Fig. 6) always exceeded the subsequent number of broods on these ponds, suggesting that few if any peripheral breeding pairs nested nearby.

SPACING BEHAVIOUR OF BREEDING PAIRS

Introduction

Spacing behaviour of breeding pairs is defined here as any behaviour that distributes pairs among different habitats and spaces out pairs within a given habitat. Spacing behaviour of breeding pairs of buffleheads on ponds involves two main elements: 1) the selection of a pond and nesting habitat, and 2) agonistic behaviour that may serve to disperse pairs to different ponds, or to space pairs on a single pond. Sexual behaviour on the breeding grounds, such as pair-maintenance display and copulatory behaviour, is included here as spacing behaviour because it is space-related. This section emphasizes agonistic and sexual behaviour of buffleheads on ponds in relation to space and time. For the present it seems preferable to use the term space (for example, pair-space or brood-space), rather than territory, to denote that part of a study pond held by a pair or individual. The territory concept has generated much controversy when applied to ducks, so use of this concept in relation to my findings will be evaluated later. The time referred to here is the nesting period from the arrival of pairs to the hatching of young.

Fighting between male buffleheads at more or less fixed positions in space, when their mates were both present and absent, was first recorded at one pond in 1972. At this pond (J) the two resident pairs were observed only during the incubation period. Most fights were recorded during the first two weeks of incubation, but fighting persisted into the third week, when the pair bond of one of the males apparently broke. These observations of use of the pair-space by paired females and fighting between their mates along a boundary zone

suggested that males maintain an exclusive pair-space for their mates for almost the entire nesting period.

Observations of bufflehead in 1973 at three ponds confirmed the above general nature of their agonistic behaviour patterns in relation to space, but showed that at different ponds the resident pairs maintained pair-spaces for varying periods relative to the breeding cycle.

In both years no individuals were marked during the nesting period while the pair-bond was intact and observations were incomplete at any one pond for all stages of the breeding cycle. Thus the exact nature of the spacing mechanism over time remained unclear.

In 1974, however, the spatial-temporal relationships between and within pairs were determined at one pond by daily recording the social interactions of marked individuals during all stages of the breeding cycle. The rest of this section consists of three parts. Part I describes the sexual and agonistic behaviour of breeding pairs, Part II describes and quantifies agonistic behaviour in space and time, and Part III deals with sexual behaviour in space and time.

Part I. Description of Sexual and Agonistic Behaviour

Sexual Behaviour

Sexual behaviour in buffleheads is space-related as it assists to maintain the pair-bond and the male's attachment to a space for the duration of that bond.

In describing sexual behaviour of buffleheads I have used the terminology of Myres (1959a; 1959b) and Johnsgard (1965), and have followed the ethological convention of capitalizing ritualized behaviour patterns which are considered to be displays.

Sexual behaviour of buffleheads has been described in detail (Myres, 1959a; 1959b) and summarized (Johnsgard, 1965; Erskine, 1972; Drury *et al.*, MS) so brief mention of their terms and display sequences supplemented by my own observations should suffice. Although pair-forming displays and sequences, such as Fly-over and Landing, Alternating and Cutting-out (Myres, 1959a), do occur on the breeding grounds they are not considered here as adult females were paired on arrival at the study ponds.

1. Pair-maintaining Displays

   a. Female

The two most common female displays are Head Display and Following (Myres, 1959a). Head Display is similar to Crest-erection of males. Following is the female's main response to male display. In response to Leading by a particular male the female rushes after, and follows him, gives a loud, gutteral call, and alternately extends and withdraws her neck (Myres, 1959a).

Drury *et al.*, (MS) describe two other female patterns of behaviour, the Side-to-Side and Sweep, both of which express

aggressive and sexual elements and occur when the pair are close together, either in the absence (Side-to-Side) or in the presence of another male (Sweep). In the Side-to-Side, Drury *et al.*, (MS) describe the female posture as intermediate between a crouch and Head-forward (Myres, 1959a) of the male, and that in the Sweep a female threatens a rival male. I observed an individual (F Y) with similar behaviour to the above patterns. This female adopted a crouched posture while fairly stationary and close to her mate engaged in a threat encounter with a neighbouring male. As her mate dove she called and stretched her neck in response to the approach of a rival male in the Head-forward posture. I did not distinguish between the Side-to-Side and Sweep.

b. Male

The most common male display is Head-bobbing (Myres, 1959a), perhaps more correctly termed Oblique-pumping (Johnsgard, 1965).

Three sequences of display, that apparently function to maintain the pair bond, occur on the breeding grounds. The first is an approach flight and/or approach swim - Head-bobbing - Leading (Myres, 1959a) with or without Lateral Head-turning and Bill-pointing (Johnsgard, 1965) by the male to the female, and Following by the female. Bill-pointing, the rapid bill movements by a Leading male back towards the female Following, has been termed Pecking (Myres, 1959a) or Ticking (Drury *et al.*, MS). I observed this sequence throughout the breeding cycle more often than those below.

The second sequence by a male is the Display Flight (Fly-over-Landing) - Headshake-forwards - Wing-lifting - Head-bobbing

(Myres, 1959a). Myres (1959a) states that Wing-lifting is sometimes not performed in the sequence but it always precedes high intensity Head-bobbing. Johnsgard (1965) reports that the Folded-wings-lifted posture (Wing-lifting) sometimes briefly interrupts Oblique-pumping, and then the latter display is usually resumed. He does not link Wing-lifting in the Display Flight sequence, instead he describes Short Flights ending in Wing-flaps (my sequence three). On a few occasions I saw Head-bobbing punctuated by Wing-lifting, but my observations agree more with those of Myres' since Wing-lifting was mostly seen in the Display Flight sequence preceding Head-bobbing, rather than following it. My 1974 observations of paired colour-marked females suggest that the Display Flight sequence with Wing-lifting mostly occurs during the prelaying and laying periods, and that the first sequence above is the more frequent one during the incubation period.

Johnsgard (1965) described a third sequence by a male as ritualized Short Flights followed by Wing-flaps as he lands near a female. I frequently observed this sequence especially after intra- and interspecific aggressive encounters. A male also performs this sequence of behaviour patterns in the absence of his mate, suggesting that the first two sequences have a more specific function in pair maintenance, whereas the third sequence has a more general function, perhaps in maintenance of space.

Other pair-maintaining displays are Crest-erection (Myres, 1959a) by males, and Diving-as-a-pair (Erskine, 1972). The latter display was seen more often during prelaying than during any other stage of the breeding cycle. Finally, evidence that copulatory

behaviour functions to maintain the pair bond is presented later.

Analysis of the frequency of these displays in various situations and in relation to the breeding cycle is needed to clarify their function in regards to maintenance of the pair bond.

2. Copulatory Behaviour

The female assumes a Prone posture while the male performs two precopulatory displays: the Water-twitch and Preen-dorsally. Then the male mounts the female, waggles the tail from side to side during copulation and may give a Wing-flick (Flick-of-the-wings) about the time of intromission. The sequence of post-copulatory behaviour is Rotations by the pair, then male Plunge and/or Splash-bathe, Upward-stretch, Wing-flap and Tail-wag, while the female bathes, and gives upward-stretch, wing-flap and tail-wag (Myres, 1959a; 1959b).

My observations agree with Myres (1959a; 1959b) and Johnsgard (1965) that Water-twitch is more frequent than Preen-dorsally. The sequence of copulatory behaviour I saw in June 1974 contradicts Erskine's (1972:33) statement that the two pre-copulatory displays "are each repeated several times, in no particular sequence". I observed that Water-twitch initiated the sequence and was followed either by Preen-dorsally, or mostly by one or more Water-twitches, then Preen-dorsally, and this sequence may be repeated one or more times. Water-twitch preceded and followed each Preen-dorsally. Mounting was preceded by the Water-twitch. Wing-flick was not seen. Post-copulatory behaviour varied among individuals. Pair Y performed faster Rotations than either pair W or pair B. The mate of F Y usually Splash-bathed with no Plunge, whereas M W and M B mostly Plunged.

Myres (1959a; 1959b) mentions that first attempts at mounting

on 2 of 12 occasions and apparently successive attempts were unsuccessful as Rotations and male Plunge were not seen. I observed many copulations in which the first attempt was unsuccessful, but most of these were followed by a successful copulation. When a male slipped off the back of a female with no Rotation or Plunge, he usually quickly gave either a Water-twitch, or Water-twitch - Preen-dorsally - Water-twitch followed by a successful mounting and post-copulatory behaviour. Copulatory behaviour in relation to space and time is dealt with later.

Intraspecific Agonistic Behaviour

In describing the agonistic behaviour of male buffleheads I have again capitalized ritualized behaviour patterns, such as the Head-forward posture, which are distinguished as displays by Myres (1959a) and Johnsgard (1965). I have not considered as displays any agonistic behaviour patterns that involved movement toward or away from an opponent (such as in an approach - withdrawal encounter) or behaviour patterns involving pure attack and escape elements (such as supplanting attacks, retreats, fighting, flap-paddle chasing on the water surface, and aerial pursuits). Therefore these behaviour patterns have not been capitalized.

With the exception of the Head-forward posture (Myres, 1959a), descriptions of agonistic behaviour have been brief, incomplete and mostly associated with pair-formation (Myres, 1959a; Erskine, 1972; Drury *et al.*, MS).

Agonistic behaviour patterns in relation to space will be described in terms of encounters between males. An encounter involving two paired males refers here to a continuous sequence of agonistic behaviour that ends when one male engages in other activity such as Wing-flap Display,

preening, swimming or flying away from his opponent. Encounters involving males were classified into five categories according to their intensity and sequence of behaviour patterns, and further subdivided according to the number and sex of other individuals involved. Agonistic behaviour is described below in order of increasing intensity.

1. Approach - Withdrawal

a. Male - male encounters

These encounters, either between paired males or a paired and an unpaired male, occur mostly within or near a boundary zone when the approach of one male results in prompt withdrawal or avoidance by another male. The most common form of approach - withdrawal is swimming and diving. Only the approaching male may assume a Head-forward posture unlike threat encounters where it is performed by both males.

Approach flights were distinguished when one bird flew toward and landed short of its opponent or its position, before the latter escaped, usually by a retreat flight or retreat swim underwater. When an unpaired male flew over the pair-space of a paired male the latter often made a short approach flight and landed as the intruder flew out of his pair-space.

b. Pair - male encounters

i. Paired male - pair boundary encounter

When a paired male swims and dives toward a neighbouring female or pair within or near a boundary zone, the male with the female withdraws by rapid Leading with his mate Following.

ii. Unpaired male - pair encounter inside the pair-space of the pair

This encounter occurs when an unpaired male performs the Display Flight sequence close to a paired female with her mate. The paired male responds by Leading his mate away and she responds by Following. The paired male may then attack the unpaired male.

2. Threat

Reciprocal threat encounters occur mostly between two paired neighbouring males along a boundary zone, but sometimes involve an unpaired male or three males. A male approaching a boundary zone by either swimming and diving and alternately surfacing in the Head-forward posture, or especially by an approach flight, provides a visual stimulus for a neighbouring male to respond with a similar approach and then a threat encounter ensues. Opponents then face each other in the Head-forward posture and maintain an individual distance of 20 to 30 m by diving attacks and escapes back and forth along a boundary zone. If the attacker C in the Head-forward posture turns and dives toward its opponent, the attacked D usually responds by an escape dive and retreat swim underwater either laterally or directly away from C. Both birds usually surface in the Head-forward posture. C usually responds in one of three ways: 1) C dives in escape in response to D's attack dive; 2) C turns and/or swims away from D and C responds by approach swimming and diving; or 3) when D escapes laterally C may dive in attack. In this way attack and escape movements may continue from 1 to 5 minutes, sometimes longer.

One bird usually ends an encounter by an avoidance flight or by swimming away and preening for a minute or more. Threat display along a boundary zone may be interrupted by momentary preening or wing-flick for

a few seconds and then be resumed.

During threat encounters I confirmed that interacting males capture invertebrates during diving because on many occasions they surfaced with green animals, presumably Chironomidae larvae, in their bills and mouthed them on turning away from their opponent. Feeding was especially noticeable when individual distance was maintained at 30 m or more. Presumably this feeding was displacement activity, but the possibility that it was functional cannot be excluded. Sometimes in encounters between paired males, one male remains close to his mate while she feeds and either performs quick shallow dives or remains in the Head-forward posture or crouched in response to his opponent's diving.

3. Attack - Retreat

This encounter is initiated when the attacker makes a supplanting attack directly at an intruder. The bird attacked retreats and the aggressor occupies its vacated or a nearby position a moment later. One attack is often sufficient to expel the intruder, but if it only retreats a short distance, the attacker makes repeated attacks until the trespasser flees from the pair-space. Retreat by the attacked ends the encounter. There is no aerial pursuit.

Three types of supplanting attacks can be distinguished, the attack underwater, attack rush and aerial attack, which increase in intensity from low to high, respectively. The bird attacked responds by escape dive and retreat swim underwater, retreat rush or retreat flight. All these responses were recorded for each intensity of attack. For example attack flight by the attacker usually elicited retreat flight by the attacked but sometimes the latter made an escape dive or retreat

rush to avoid an attack flight. Attack flights varied in length from 10 m to 100 m.

Most supplanting attacks were by paired males directed at unpaired males that intruded well within the pair-space of the former. Established paired males rarely intruded into their neighbour's pair-space much beyond the boundary zone. A supplanting attack by a male at a female is described later.

4. Fighting

Hinde (1952) and Marler (1956) used the term fighting to include both supplanting attacks (with no contact between individuals) and combats (with contact). Raveling (1970) and Ridpath (1972a) used fights to refer to situations where only contact occurs. An intermediate situation to the above is fighting in blue-winged ducks which McKinney (1970) describes as mainly posturing and attack lunges with little contact. Similarly in male buffleheads I use fighting to refer to reciprocal attacks at close quarters whether contact is seen or not. Contact is not conspicuous in underwater fighting, but is clearly seen during fights on the surface of the water when one bird sometimes seizes another.

Munro (1942) and Erskine (1972) each saw one fight, apparently associated with pair-formation. Myres (1959a) reports that threat may lead to fights but gives no description. Thus fighting has been rarely seen, and has not been described in any detail nor in relation to space.

Fighting between neighbouring males occurred in four situations according to their position in relation to boundary zones, and involvement of females.

a. Male - male encounters

i. Boundary fights

These fights, mainly between paired males, but also between a paired and an unpaired male, were seen often but much less frequently than threat. Most fights follow threat encounters and occur within a boundary zone when individual distance is reduced rapidly to 10 m or less. Opposing birds dive in attack and a fight erupts underwater accompanied by vigorous splashing and wing thrashing with the birds mostly submerged. Presumably contact often occurs underwater. When the combatants surface, one bird sometimes has hold of the tail, back or a wing of its opponent which vigorously flaps away to get free. When the attacked bird breaks free it may continue fighting or flap-paddle in retreat prompting its opponent to initiate a flap-paddle chase (described later). Males fighting on the surface of the water constantly change positions and repeatedly miss contact as they lunge at each other and jab down with open bills. During flap-paddle chases the pursuer sometimes grabs the pursued by the tail or back. Fights usually last less than a minute. Fighting encounters usually end with both males side by side giving an appeasement display then the Wing-flap Display (both described later).

ii. Fights inside a neighbour's space

A male, chasing an unpaired male out of his pair-space or attacking other species of ducks, may suddenly land within his neighbour's pair-space or within the boundary zone. In [redacted]e, the occupant promptly launches an aerial attack

directly at the intruder and fighting follows if the latter does not flee.

b. Pair - male encounters

i. Pair attacked inside their own space by male intruder

When a rival male directs an attack flight at a neighbouring female inside her pair-space, one response by her mate is to fly over in defence, intercept his opponent's attacks and fight with the intruding male.

ii. Intruding pair attacked inside their neighbour's space by resident male

A female intruder inside her neighbour's pair-space releases an attack flight by the resident male. The mate of the attacked female, if not by her side, flies over to defend her, and a fight between the males may break out.

c. Flap-paddle chasing

These chases between two males can be included as fighting because they often interrupt or terminate boundary fights and three-bird encounters within a pair-space. A flap-paddle chase refers to two males, one in pursuit of the other, rushing and flap-paddling with their wings over the water for a short distance. When the attacker makes a rush or lunges with open bill at an opponent, the attacked may flap-paddle in escape prompting the attacker to initiate a flap-paddle chase.

5. Aerial Pursuit Between Two Males

a. Paired male - unpaired male

In most aerial pursuits a paired male chases an unpaired male. When an unpaired male flies low with intent to land, or

lands within the pair-space of a paired male, the latter usually launches an immediate aerial attack and aerial pursuit of the intruder in retreat flight. The pursuing male breaks off the chase and lands near his boundary zone as the trespasser flees from his pair-space.

b. Paired males

Aerial pursuit is infrequent between established paired males. In contrast, aerial pursuits are frequent, energetic and long lasting when one male is re-establishing a pair-space after a temporary absence of several days because of disturbance or exclusion. In vigorous aerial pursuits the pursuer opens its bill and occasionally grabs the tail of the pursued in flight and they often plunge into the water.

6. Three-bird Attack and Pursuit Encounters

a. Pair - paired male neighbours

When an intruding paired male attacks a neighbouring female of a pair her mate flies over to defend her. Tactics preceding attack are as follows. During threat encounters between two paired neighbouring males C and D, male C swims and dives away from pair D and male D follows without his mate. Then male C dives toward female D, so that male C surfaces closer to female D than male D. When male D dives, male C (instead of diving in response) directs an aerial attack at female D while her mate is underwater. Counter-acting tactics by the male of a pair are to stay close to his mate during threat encounters and to dive shallowly and surface quickly, so that he can fly to his mate and intercept any attacks by his opponent before the female takes flight. The attacked female dives

or flashes to escape, but also flies to retreat especially when her mate is slow to defend her. A three-bird pursuit-flight occurs when the female takes flight pursued by the attacking male with her mate following. During high intensity pursuit-flights the attacking male lunges at the female of a pair in the air, and when her mate catches up to them he buffers the attacks by constantly positioning himself between his mate and the attacker. Females appeared to be much more manoeuvrable in the air than males, so the attacking male rarely succeeded in grasping a female. The attacked pair may be temporarily forced off the pond but a tenacious female soon returns.

In high intensity three-bird encounters on the water, the attacker (male C), after making an aerial attack, repeatedly lunges at female D while her mate (male D) continually tries to intercept the attacks. Fighting often erupts between the two males. At the end of a fight the mate of the attacked female flies over to her, performs rapid Leading and she responds by Following. If the three birds land together after a pursuit-flight, the defender (male D) also performs rapid Leading with his mate Following. If the attacker still remains near the pair after Leading and Following, either at the end of a three-bird flight or a three-bird encounter on the water, the mate of the female usually dives in attack underwater. Male C usually responds with a retreat flight, but may flap-paddle in retreat prompting male D to initiate a short flap-paddle chase before male C flies in retreat to his pair-space.

Low intensity three-bird encounters occur on the water between established pairs. Male attacks at a paired female are not

persistent or vigorous and are inhibited when her mate flies over to defend her, and performs Leading with his mate Following. The sequences of behaviour patterns in high and low intensity three-bird attack and pursuit encounters are shown in Figure 7.

Three-bird pursuit-flights may also occur shortly before a resident pair flies toward the nest site. When the pair take flight and circle the pond, a neighbouring male flies up in attack and sometimes forces the pair to land again.

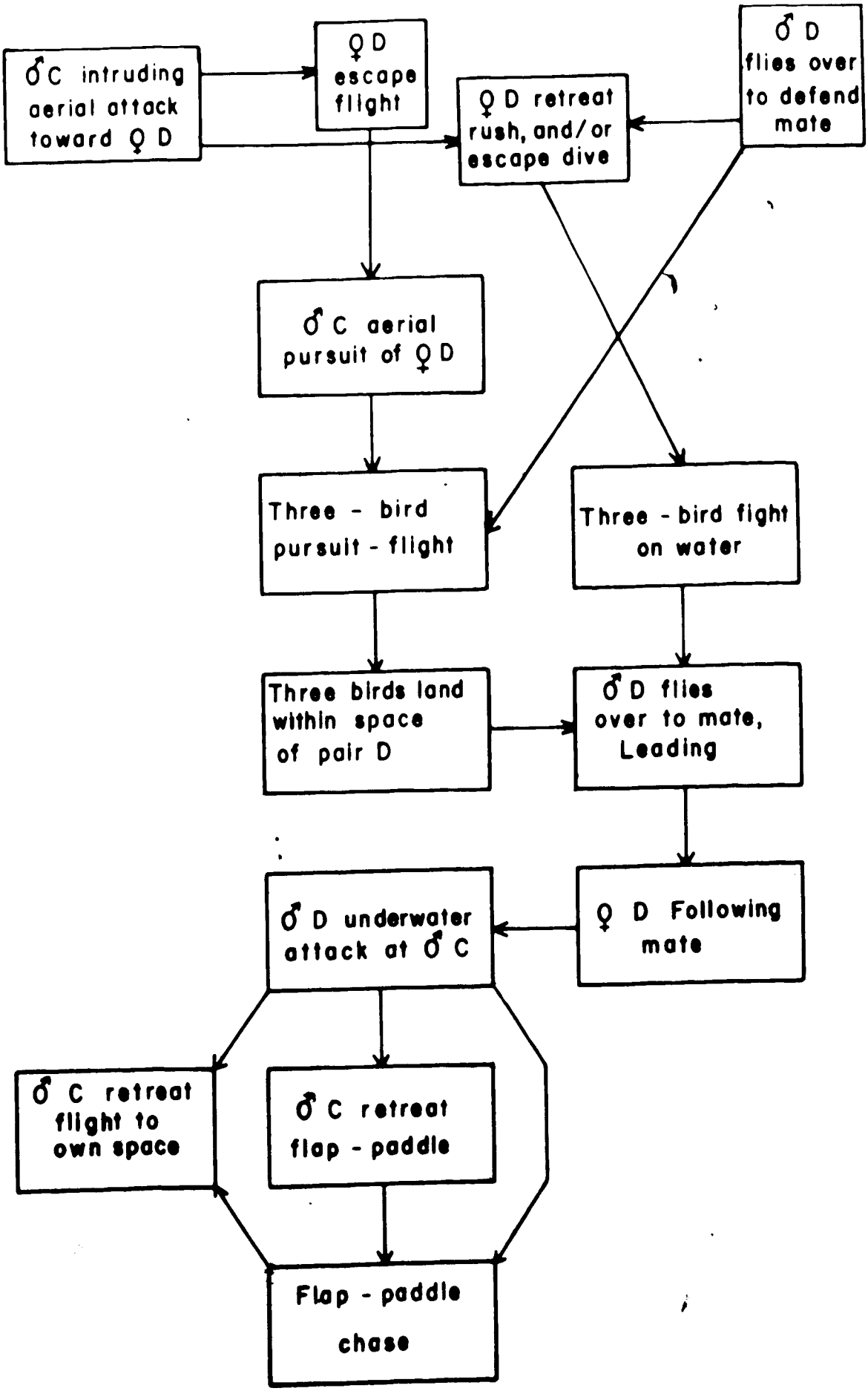
b. Strange pair - neighbouring male

A three-bird pursuit-flight occurs when a strange pair attempts to settle on a pond already occupied by resident conspecifics. As a strange pair flies over a pond and attempts to land in a pair-space, one resident male after another repeatedly chase the strange pair from their pair-spaces until eventually the strange pair leaves the pond.

7. Appeasement Display

Males give an appeasement display during fighting on the water. Two males cease attacking and orient themselves alongside each other in a parallel posture with the head forward, wings flicking and tail elevated. One bird, usually the loser of an encounter, turns his head away and they both swim apart. This appeasement display which I shall term Facing Away (after Tinbergen, 1959) serves to conceal the bill (fighting weapon) and inhibit attack (Cullen, 1957). The bird that initiated Facing Away swims away and may glance back at its opponent, who sometimes makes an attack rush. Another short fight or flap-paddle chase may occur, or the attacked male dives and retreat swims underwater before both birds swim apart and end the encounter. Similarly in the

Figure 7. Sequence of behaviour patterns in attack and pursuit encounters among a paired male and a neighbouring pair.


♂C intruding aerial attack toward ♀D
♀D escape flight
♂D flies over to defend mate
♀D retreat rush, and/or escape dive
♂C aerial pursuit of ♀D
Three - bird pursuit - flight
Three - bird fight on water
Three birds land within space of pair D
♂D flies over to mate, Leading
♂D underwater attack at ♂C
♀D Following mate
♂C retreat flight to own space
♂C retreat flap - paddle
Flap - paddle chase

kittiwake (*Rissa tridactyla*) Cullen (1957) observed that attack is not appeased completely and may continue on an opponent or be redirected at a mate.

The Facing Away appeasement posture is widespread among gulls (Moynihan, 1958; Tinbergen, 1959), but, except for Myres (1959a), appeasement display has not been described for ducks (Lorenz, 1951, 1952, 1953; McKinney, 1961, 1970; Johnsgard, 1965). In Canada geese (*Branta canadensis*) Raveling (1970) describes a Submissive posture which "serves the functions of identifying single geese, allowing approach, habituation, and ultimately pair formation" and "also serves to prevent violent attacks".

In bufflehead the Upward-stretch and Wing-flap following fighting and occurring during pair-formation were considered by Myres (1959a:186) to be an appeasement display. After fighting male bufflehead Face Away and do not perform the Wing-flap until they are well apart from each other. Thus it is unlikely that the Wing-flap Display would serve to inhibit attack at close quarters and therefore should not be considered an appeasement display.

8. Wing-flap Display

This display usually, but not always, terminates fighting, attack and pursuit encounters. The sequence of display components is Splash-bathing (Head-dipping - Wing-ruffling) - Upward-stretch - Wing-flap - Tail-wag. In male - male encounters Wing-flap seems to be usually initiated by the loser, then performed by the winner. In some situations, regardless of whether an apparent loser flies to his mate or stays near his opponent, the winner Wing-flaps first. Thus initiation of the Wing-flap is not a reliable indicator of the outcome of an

encounter. Further study of the context of the Wing-flap is needed before it can be used in predicting outcome.

Part II. Agonistic Behaviour in Space and Time

Introduction

These results deal firstly with selection of a particular part of a study pond by bufflehead and then emphasize the spatial-temporal relationships between and within pairs on these ponds.

The space occupied by four colour-marked adult females in successive years suggests that selection of a particular part of a pond may be initiated by the female of a pair. Three marked paired females returned to Pond J in 1974. Only one of these (F W) occupied the pond as a resident nesting female in 1973. The other two females (F B and F Y) were first resident on Pond J in 1973 as females with broods. In 1974 pair B arrived first and settled on the same space (east-end bay) selected by F B with a brood in 1973 (compare Fig. 10 - Map 1 and Fig. 20 - Maps 1 to 9). Pair W arrived next and settled nearest pair B's space, rather than in the north-west bay occupied apparently by two transient pairs (Fig. 10 - Map 1), perhaps because F W preferred to settle nearest the east-end bay which she occupied as a nesting female the previous year. On arrival F W repeatedly trespassed into the east-end bay strongly suggesting she preferred this space. Pair Y arrived last and settled in the north-west bay, the core area of the space occupied by F Y with a brood in 1973 (compare Fig. 10 - Map 2 and Fig. 20 - Maps 1 to 9). On Pond H in May 1974 a paired female (F R-W) settled on the same space she occupied while nesting and with a brood in the previous year. Thus the most important factor in selection of a particular pair-space appears to be the female's previous familiarity with it either while nesting or with a brood. Moreover, a female that successfully raises a brood on a particular pond or space may have a

stronger tendency, than a female that is unsuccessful, to return there as a nesting female the following year. Of the four marked females that returned to the study ponds in 1974, only F W failed to rear a brood in 1973. However, the nest cavity used by F W in 1973 was occupied the previous year by an unmarked female which arrived at Pond J with a brood of 12, nine of which apparently survived to fledging. Adult female buffleheads show a strong tendency to use the same nest cavity at least in two successive years (Erskine, 1961; 1972) and to return to the same ponds used previously (see above). Although F W deserted her clutch in 1973, it seems highly likely that this unmarked female that successfully reared a brood in 1972 and used the same nest cavity as F W did in 1973, was in fact F W. Therefore all marked females that apparently selected a pair-space on the study ponds in 1974 probably successfully reared broods there in previous years.

Selection of a particular pair-space appears to be modified by environmental stimuli at the time of settling. The most important of these stimuli probably is the density and location of other bufflehead pairs in relation to the suitable bays of the pond. Other pond characteristics such as the shoreline vegetation and availability of food and loafing sites are possible additional cues that birds use in selecting a space.

On the evidence presented, the female initiates selection of the pair-space. However, it is possible that at times paired male bufflehead select the space, for example, M B(K) occupied the same space in successive years but may have merely followed his mate to the space that she had selected.

For a detailed quantitative analysis of spatial-temporal

relationships between and within pairs at least one member of each pair should be colour-marked, the precise stage of the breeding cycle known for each pair and for statistical purposes there should be a large number of interactions recorded. Only the 1974 data for Pond J met these conditions. Analysis of these data first should provide a framework for comparing data for other years and habitat types. Unless otherwise mentioned all data refers to that for Pond J in 1974. The 1973 data revealed variations in the nature of spacing systems and differences in social behaviour in relation to the environment. These data are included where appropriate.

Establishment of Space - Pond J 1974

1. Introduction

Early arriving pairs that acquire a space on a pond by settling do not always remain to breed (Table 3). None of the early arriving unmarked pairs became residents, even though one unmarked pair occupied the pond on April 29 (ice-free date) and at least two unmarked pairs settled there before F W arrived about 4 days later. Also on May 4, the day before F Y settled on the pond, three unmarked pairs were present but none of these became residents. Thus arriving first does not ensure that a pair will establish a space on the pond.

Next, only previously marked paired females became residents (Table 3). In 1973 F B and F Y each reared a brood at Pond J, while F W was resident on Pond J during the nesting period. So only those males mated to females with breeding experience on Pond J the previous year succeeded in establishing a space there in 1974. The unmarked pairs that left the pond may have been transients or were evicted by the resident males. Thus these unmarked pairs may have dispersed to

Table 3. Numbers of pairs of bufflehead on Pond J during the period of establishment from April 28 to May 8, 1974.

Date	Number of pairs observed	Colour-marked paired females present
April 28[a]	0	-
29[b]	2	B
30	2	B
May 1	3	B
2	2	B
3	4	B, W
4[c]	5	B, W
5[d]	4	B, W, Y
6	4	B, W, Y
7	3	B, W, Y
8	3	B, W, Y

[a]Pond J partially ice-free. Female B and mate seen at 2000 at bog Pond M.

[b]Ice-free date for Pond J.

[c]Female Y and mate seen at peripheral pond near J at 1830.

[d]0800 1 red-necked grebe, 2 bufflehead pairs (B, Y) on pond
0930 1 unmarked bufflehead pair arrived
1015 Pair W arrived

other ponds or remained in the Pond J area as the peripheral pairs.

How then do pairs establish and maintain a space? The behavioural mechanisms involved appear to be complex so these should be most clearly identified by a detailed analysis of changes in agonistic behaviour between individuals in relation to space, time and the breeding cycle.

Agonistic encounters were classified into five categories described earlier: 1) approach - withdrawal, 2) threat, 3) attack - retreat, 4) fighting, and 5) aerial pursuit. These encounters were further subdivided mainly into male - male and male - pair encounters. The number and category of these agonistic encounters between individuals over time for different combinations of members of pairs are given in Figures 8 and 9.

The location of agonistic encounters between individuals changed over time, sometimes daily, resulting in changes in boundary zones and size of pair-spaces of the residents (Fig. 10 - Maps 1 to 11). In 1974 inaccuracies were greater in plotting the location of encounters between M W and M Y than those between M W and M B. To check the location of encounters involving M Y, on one afternoon I determined the positions of M Y from the west side of Pond J, and these were in general agreement to those I plotted from the blind on the south side. Thus despite the above inaccuracies in plotting positions of birds, I believe the maps accurately reflect changing spatial relationships between individuals.

To determine how space is established these daily changes, especially from May 4 to 7, are analyzed in more detail, with emphasis on the frequency, intensity and locations of agonistic encounters

Figure 8. Frequency and intensity of agonistic encounters among two males and their colour-marked mates on Pond J during May and early June, 1974.

The numbers 1 to 5 correspond to the following 5 categories of male - male and male - pair agonistic encounters described in the text.

1. Approach - withdrawal
2. Threat
3. Attack - retreat
4. Fight
5. Aerial pursuit

The relative stage in the breeding cycle of each of the two marked females is presented parallel to the abscissa and indicated by the following letters.

P - prelaying period

L - laying period

I - incubation period

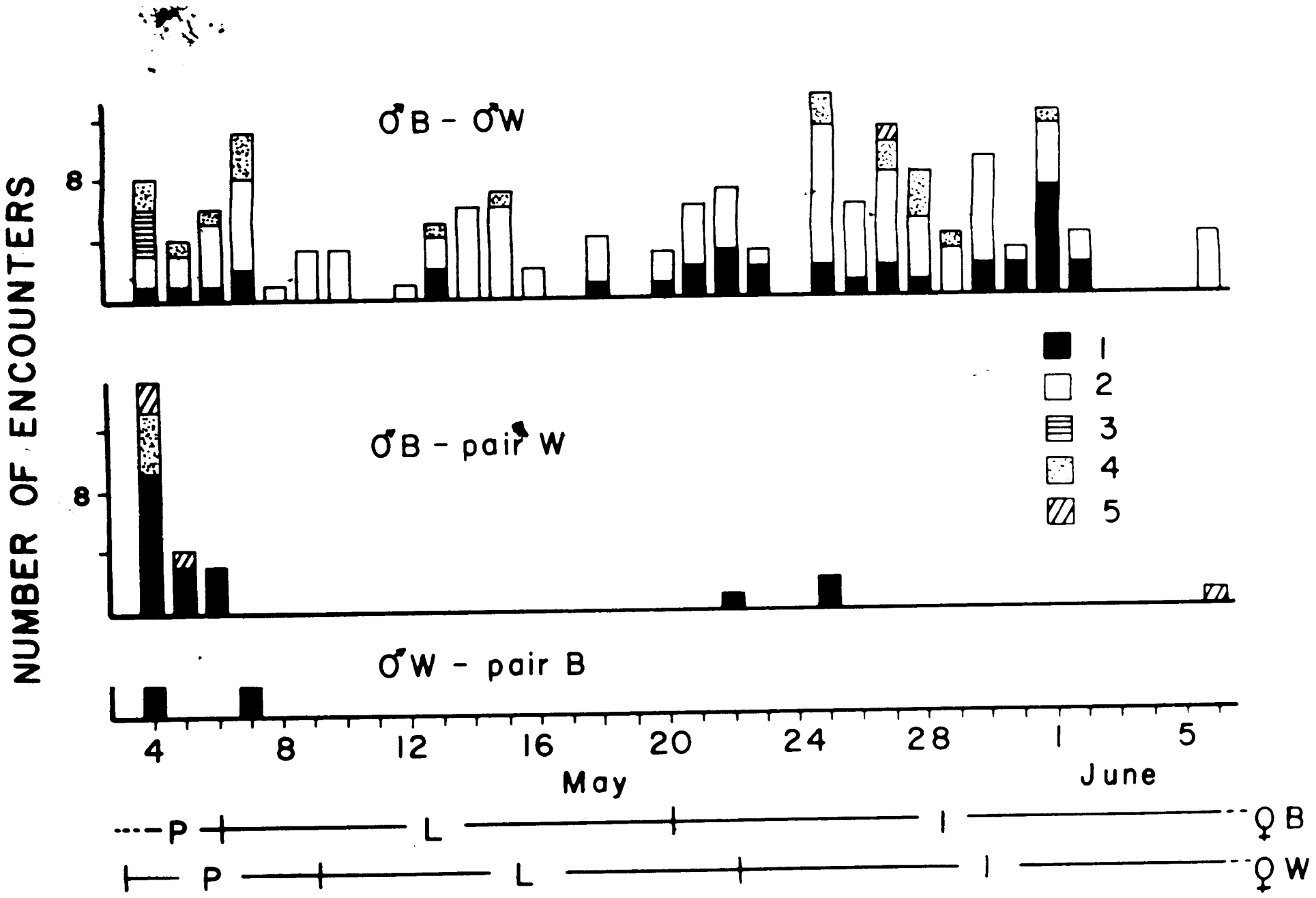

NUMBER OF ENCOUNTERS
♂B - ♂W
8
♂B - pair W
8
1
2
3
4
5
♂W - pair B
4
8
12
16
20
24
28
1
5
May
June
P
L
I
♀B
P
L
I
♀W

Figure 9. Frequency and intensity of agonistic encounters among two males and their colour-marked mates on Pond J during May and early June, 1974.

The numbers 1 to 5 correspond to the following 5 categories of male - male and male - pair agonistic encounters described in the text.

1. Approach - withdrawal
2. Threat
3. Attack - retreat
4. Fight
5. Aerial pursuit

The relative stage of the breeding cycle of each of the two marked females is presented parallel to the abscissa and indicated by the following letters.

P - prelaying period

L - laying period

I - incubation period

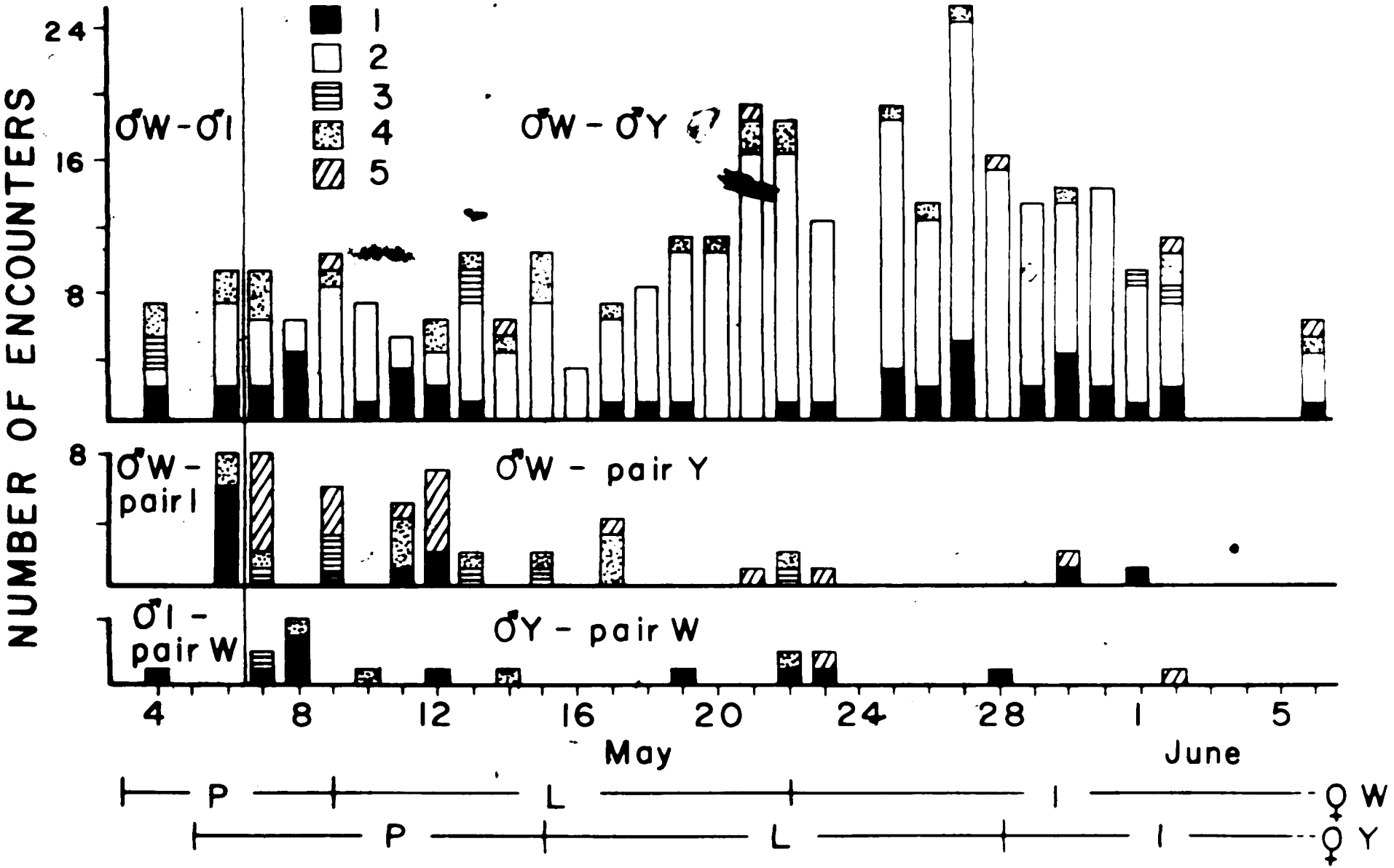

NUMBER OF ENCOUNTERS
24
16
8
8
1
2
3
4
5
♂W-♂1
♂W-♂Y
♂W - pair 1
♂W - pair Y
♂1 - pair W
♂Y - pair W
4
8
12
16
20
24
28
1
5
May
June
P
L
1
♀W
P
L
1
♀Y

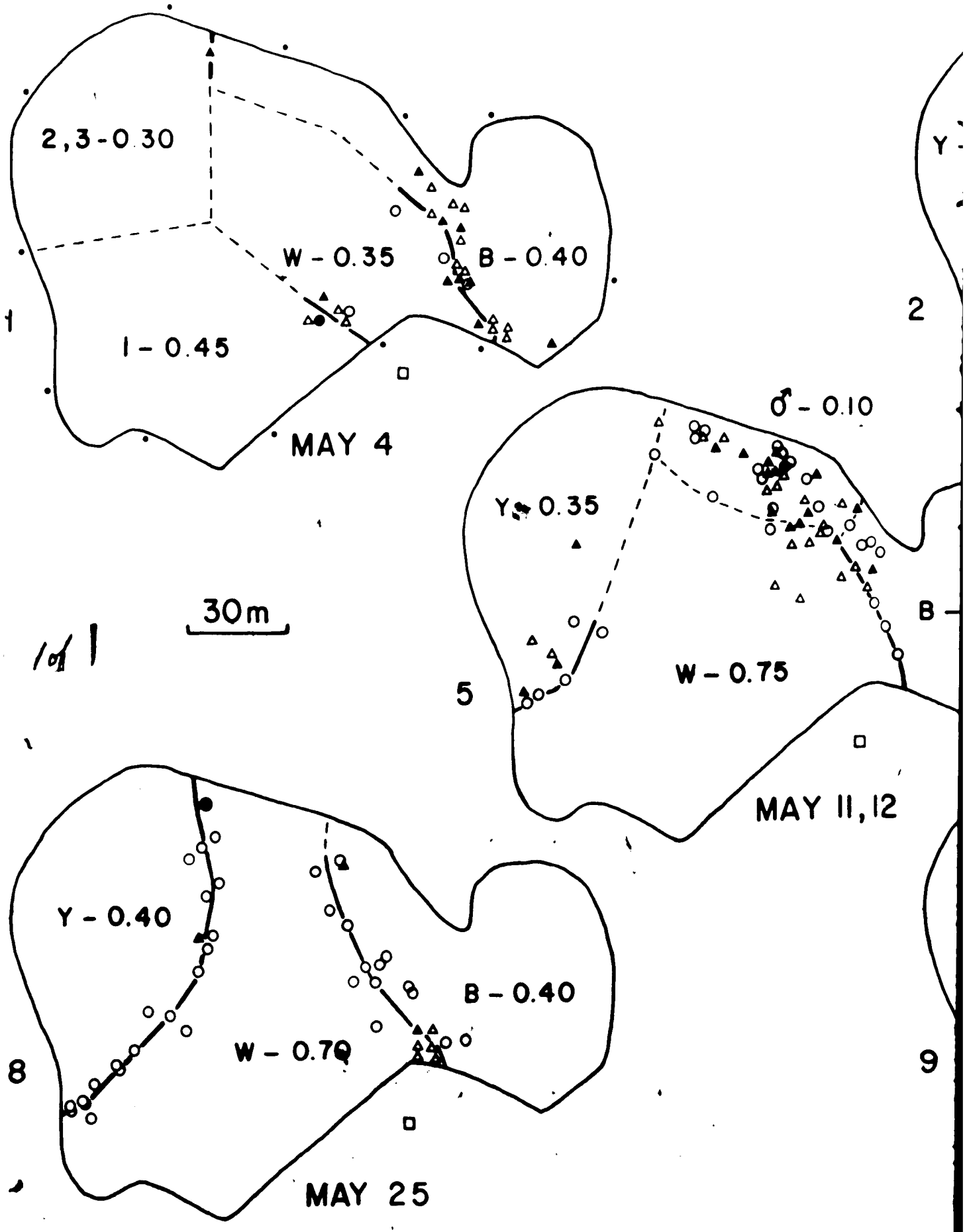
Figure 10. Spatial relationships among three resident males and their colour-marked mates on Pond J between May 4 and June 6, 1974.

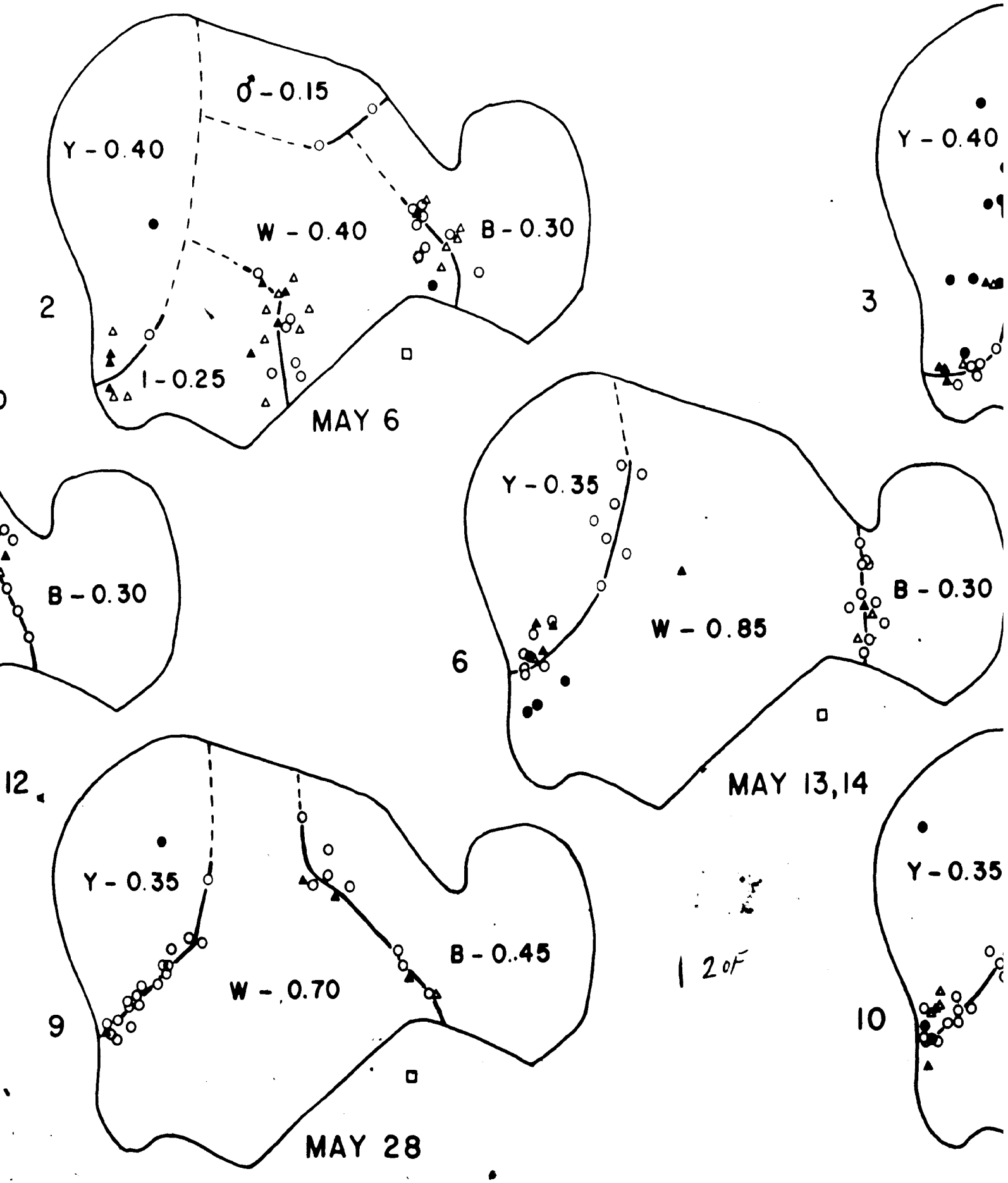
A male symbol, numbers or letters preceding decimal fractions and placed in each space on given days denotes the following individuals:

♂	unmarked unpaired male
1, 2 or 3	unmarked pairs
B, W or Y	females individually colour-marked with nasal saddles and their respective mates
B	female blue and her mate
W	female white and her mate
Y	female yellow and her mate

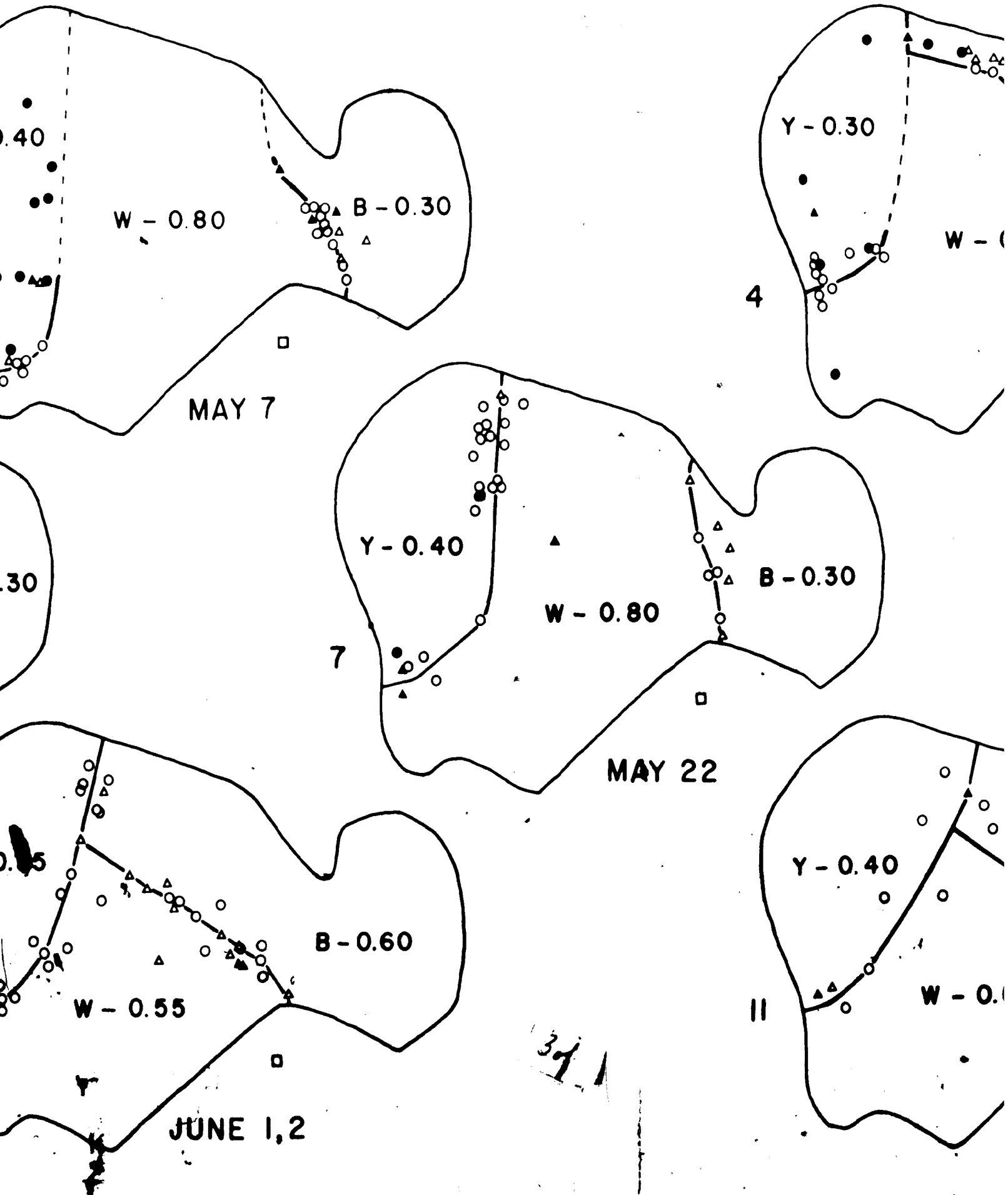
Decimal fractions following the above prefix represent the area of space expressed to the nearest 0.05 hectare (ha), held by each pair or individual on given days. For example, B-0.40, indicates a space of 0.40 ha held by pair B.

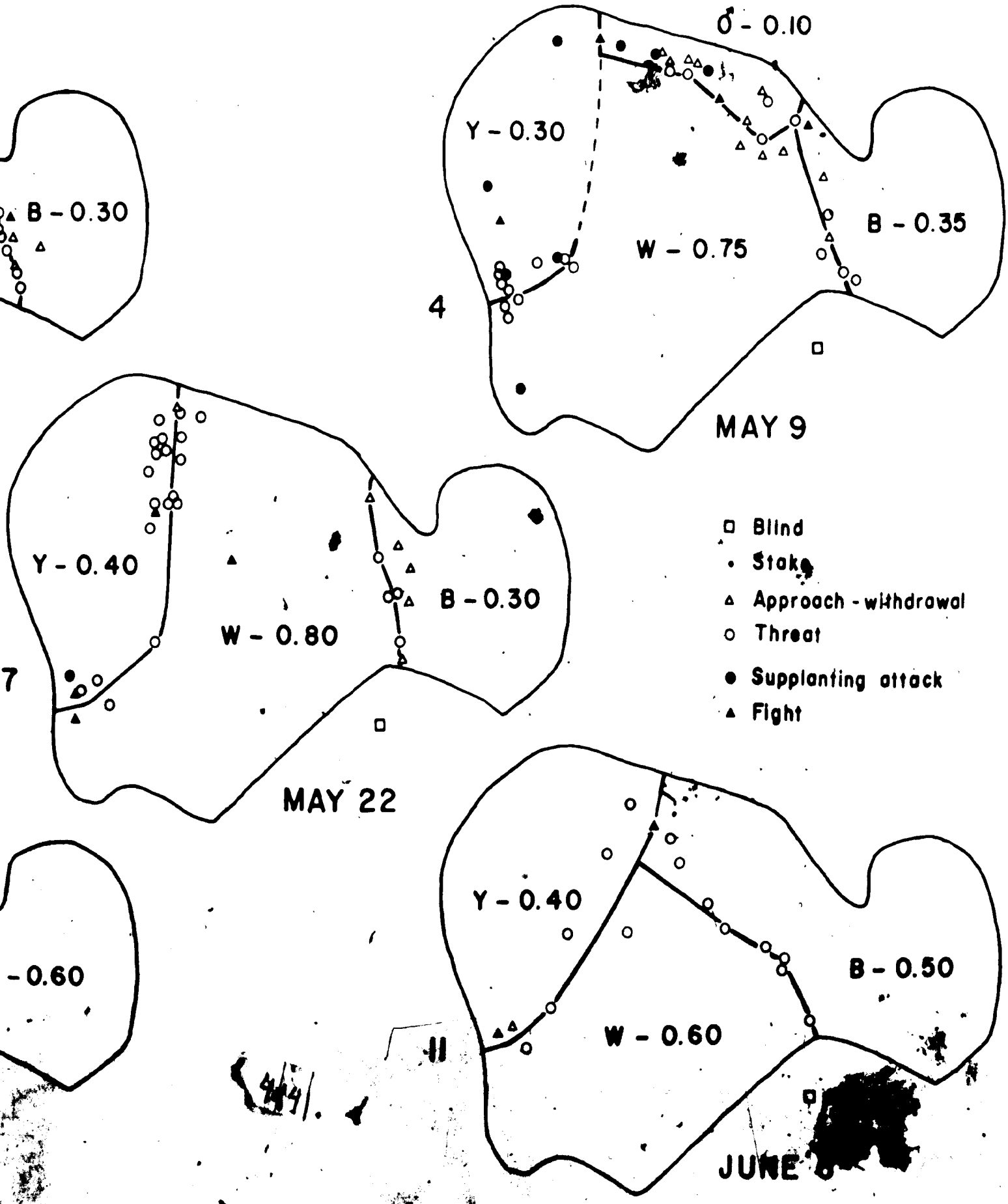
Solid lines are boundaries based on locations of interacting males engaged in threats and fights especially, and other agonistic encounters. Dashed lines are boundaries estimated from movements of individuals.


2,3 - 0.30
W - 0.35
B - 0.40
1 - 0.45
1
MAY 4
♂ - 0.10
Y - 0.35
30m
1 of 1
5
W - 0.75
MAY 11, 12
Y - 0.40
B - 0.40
W - 0.70
8
MAY 25
2
9


♂ - 0.15
Y - 0.40
W - 0.40
B - 0.30
I - 0.25
2
MAY 6
3
Y - 0.40
B - 0.30
Y - 0.35
W - 0.85
B - 0.30
6
MAY 13,14
12
Y - 0.35
B - 0.45
W - 0.70
9
MAY 28
Y - 0.35
10

1 2 of


W - 0.80
B - 0.30
MAY 7
Y - 0.30
4
Y - 0.40
W - 0.80
B - 0.30
7
MAY 22
B - 0.60
W - 0.55
JUNE 1,2
Y - 0.40
11


♂ - 0.10
Y - 0.30
B - 0.35
W - 0.75
4
MAY 9
B - 0.30
Y - 0.40
B - 0.30
W - 0.80
7
MAY 22
Blind
Stake
Approach - withdrawal
Threat
Supplanting attack
Fight
- 0.60
Y - 0.40
B - 0.50
W - 0.60
11
JUNE

between individuals. Changes in size of space and agonistic behaviour in relation to the stages of the breeding cycle are emphasized later.

The establishment period was recognized as that interval from the arrival of breeding pairs to the establishment of stable boundary zones and the division of the open water area of the pond among the pairs. These conditions appear to be satisfied by May 7 (Fig. 10 - compare Maps 2 and 3), but from May 8 to 12 an unpaired male was again resident on the pond (Fig. 10 - Maps 4 and 5). Thus the pond was not totally divided up among the pairs until May 13 (Fig. 10 - Map 6) when the unpaired male was no longer resident. Therefore from April 29 to May 12 was chosen as the establishment period.

2. Interactions Among Paired Males

From pair B's arrival on April 29 to May 3, when pair W probably arrived, there was little aggression between the pairs. On May 4 hostility between pairs rose steeply as the newly arrived pair W challenged mostly pair B. There were ten fights involving M W, eight with M B and two with an unmarked paired male (M 1), more than any other day (Figs. 8 and 9). On May 4 F W repeatedly intruded into pair B's space resulting in more M B - pair W encounters than any other day (Fig. 8). Of eight M B - M W fights, six were caused by F W's position in space and two of these ended in a three-bird pursuit-flight. Even though pair W usurped some shoreline from pair B (Fig. 10 - Map 1), M B resisted the intrusion of pair W.

On May 5 the lull in interactions probably reflects the arrival of a red-necked grebe on the pond and the absence of pair W for nearly half the observation period. This grebe was gone from the pond by May 6.

On May 6 M W diverted aggression away from pair B to pair 1. Male W was involved in almost twice as many encounters with M 1 than with M B. There was only one fight between M W and M B, but four fights between M W and M 1. Male Y had three fights with M 1, so increased pressure from both neighbouring males was applied against M 1 (Fig. 10 - Map 2, Figs. 8 and 9). Pair 1 left the pond sometime between 1800 on May 6 and 0800 on May 7. Their departure probably resulted from increased encroachment and aggression toward them at both their boundary zones with neighbouring pairs, particularly the boundary zone with pair W, because pair 1's space and shoreline was about halved from May 4 to May 6. Thus pair W's strategy to expand their shoreline was first to encroach and exert pressure on pair B's boundary zone, and when this met with resistance, to apply pressure on their other neighbours.

On May 7, with the departure of pair 1, not only did M W interact more with M Y (19 encounters) than with M B (13 encounters), but the category of encounters differed markedly (Fig. 10 - Map 3, Figs. 8 and 9). Of the 13 encounters involving M B nearly all (11) were male - male, mostly threat. However, of 19 encounters involving M Y nearly half (9) were male - male. Only two of the 13 encounters involving M B were male - pair (M W - pair B), whereas more than half of the encounters involving M Y (10) were male - pair. Male W initiated all eight M W - pair Y encounters, by intruding aerial attacks at F Y. Six of these aerial attacks resulted in three-[illegible] pursuit-flights, because M Y was too slow to defend his mate nevertheless each time F Y returned to her space. Pair Y was forced off the pond once but soon returned. Female Y's strong tenacity to her pair-space probably

resulted largely from her previous experience with it. A female without previous breeding experience on the pond may have been less tenacious and more easily driven off the pond.

From May 8 to 12 (Fig. 10 - Maps 4 and 5) the increased hostility against the resident unpaired male by the paired males is described later. Among the paired males from May 8 to 12 (Figs. 8 and 9) there were few M B - M W encounters. Male W continued a high level of aggression toward F Y up to May 12, when I believe F Y entered a suitable nest cavity for the first time since her arrival. It is noteworthy that M W initiated attacks at F Y on May 9 and 11 when M W's mate was away from the pond, but not on May 8 and 10 when M W remained close to his mate on the days before she laid eggs. The fewer three-bird pursuit-flights reflects M Y's defence of his mate on the water. The high number of pursuit flights on May 12 are of a different nature. These were all initiated by M W while pair Y engaged in nest-searching flights and were not initiated by aerial attacks at F Y on the water. On May 10 M Y first made an intruding aerial attack at F W.

3. Locations of Paired Male Encounters

Paired males established wide boundary zones within which they interacted mostly by threat and fighting encounters. These zones were not fixed in space over time but sometimes changed from day to day. However, for any given day boundary zones were relatively stable because the locations of almost all male encounters were clustered along a definite boundary zone; most encounters occurred near the shoreline (Fig. 10 - Maps 1 to 6). The width of the zone was determined by the location of encounters which varied according to the position of the encroaching individual and the response of and distance to its opponent.

Paired males initiate aerial attacks at the female of a neighbouring pair, whereupon the mate of the attacked female flies over to defend her. The approach of a neighbouring paired female or pair may elicit attack by a neighbouring male. Thus even within boundary zones the position of agonistic encounters could result from defence of a mate or defence of a space. One way to distinguish between these two types of defence is to know the position in space of paired females in relation to their interacting mates, and to know the position in space of the birds that release aggression. Three examples were chosen to illustrate clearly the position of paired females in relation to their interacting mates and the boundary zones (Fig. 11). These examples occurred on May 4 when pair W actively challenged pair B both by deep intrusion and encroachment at the boundary zone. In all three cases it was the challenger's behaviour and position in space in relation to a boundary zone that released aggression by a paired male opponent. The approach flight of a challenging pair (pair W) to a boundary zone was a prime stimulus for the neighbouring male (M B) to respond with an approach flight (Fig. 11 - Map 1). Likewise the position of a neighbouring male (M W) at a boundary zone and his behaviour (swimming and diving in threat) elicited approach swimming and diving in threat by his opponent (Fig. 11 - Map 2). In the third case the position of the intruding pair W elicited a prompt direct aerial attack by the resident M B (Fig. 11 - Map 3). In all cases the male occupant initiating the encounters responded to the challenger's position in relation to a boundary zone and not to the latter's proximity to the former's mate. Thus M B excluded conspecifics from an area, and was not just defending the personal space around his mate from the approach and attacks of

Figure 11. Release of agonistic behaviour in response to positions in space and behaviour patterns of neighbouring males with respect to positions of their mates, boundary zones and area of space held by each pair.

Solid lines indicate the movements of male B. Dashed lines indicate the movements of pair W. Numbers inside each map of Pond J refer to the sequential positions, movements and behaviour patterns of opposing individuals during agonistic encounters on May 4, 1974 as follows:

Map 1.

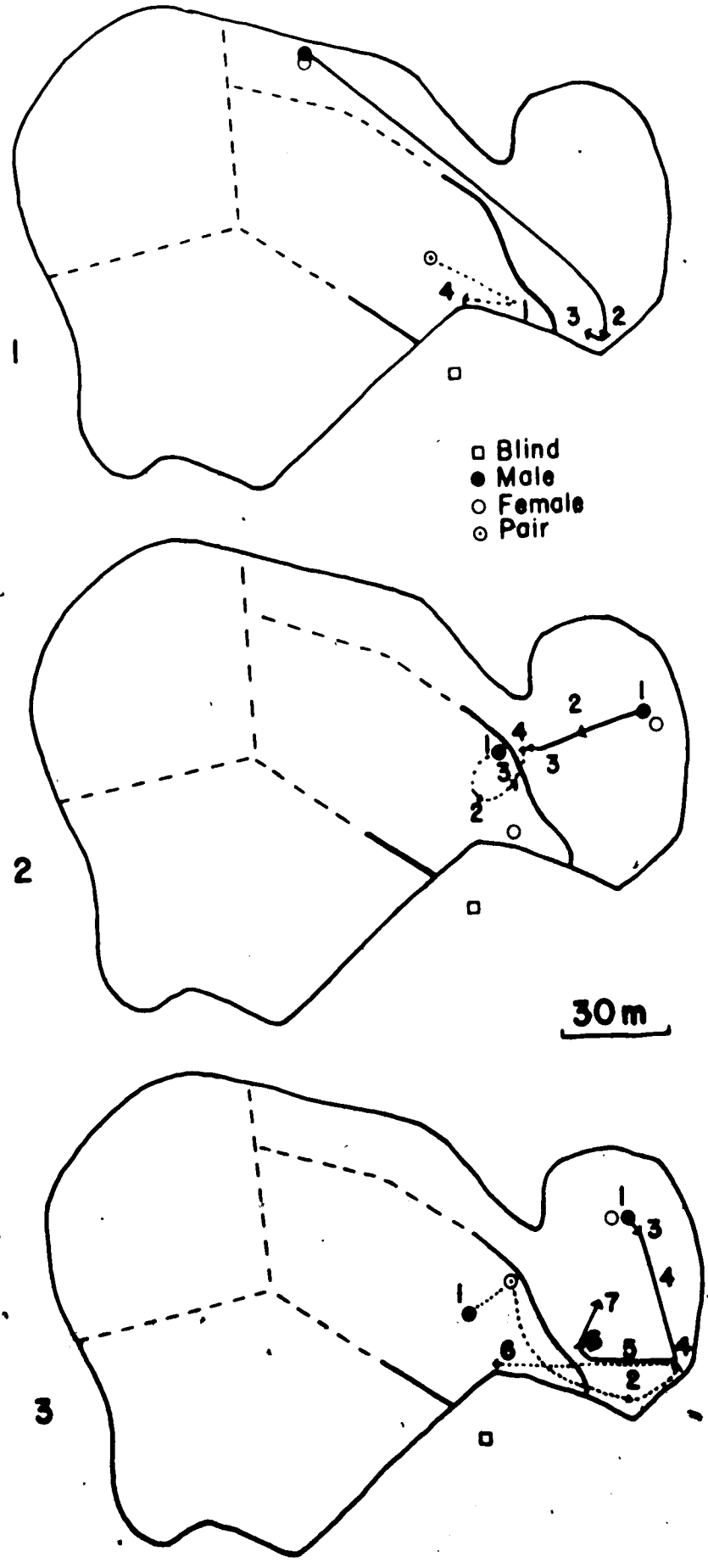
1 Pair W land at position 1 after being away from the pond.
2 Male B leaves mate and initiates an encounter by making an approach flight and landing at position 2.
3 Male B approach swims toward pair W.
4 Pair W withdraw with male W Leading and female W Following.

Map 2.

1 Male W at boundary away from his mate. Male B with his mate.
2 Male B initiates threat encounter by approach swimming and diving toward male W. Male W retreats, swimming and diving.
3 Male B continues approach swimming and diving. Male W approaches, swimming and diving.
4 Fight between male W and male B.

Map 3.

1 Pair B resting. Male W swims toward female W.
2 Pair W (female leading) swim toward and intrude along shoreline into pair B's space while pair B resting.
3 Male B alert, detects intruders. Male B swims a short distance towards trespassers.
4 Male B aerial attack at pair W. Brief fight between male W and male B, with male W intercepting male B's lunges at female W.
5 Three-bird pursuit-flight with male B the pursuer.
6 Male B breaks off pursuit and lands near the boundary zone as pair W flee into their own space.
7 Male B swims toward mate.


1
2
3
Blind
Male
Female
Pair
30m

neighbours. However, when a trespassing paired male attacks the female of a neighbouring pair, the mate of the attacked female defends her within their own space. Paired males even defend their mates within the space of a neighbouring pair. Thus defence of a mate occurs in certain contexts. Excluding conspecifics from an area and defence of a mate are not mutually exclusive; both occur.

4. Interactions Among Unpaired and Paired Males

Two unmated males were present on Pond J on April 30 and May 1, and one unpaired male from May 2 to 12, except for May 7. On May 4 and 5 a lone male was not attached to any particular area of the pond, rather it intruded within the pair-spaces and approached near the females of paired males, and was continuously attacked and chased by the latter (Fig. 10 - Map 1). By May 6 a lone male was localized on a space that presumably became vacant by the withdrawal of M B (Fig. 10 - Map 2). On May 7 there was no unpaired male on the pond. From May 8 to 12 an unmated male, presumably the same individual, occupied more or less the same space as that of a lone male on May 6 (Fig. 10 - Maps 4 and 5). This unpaired male engaged in threats and fights with paired males and initially excluded them from his space. This unmated male also continued to intrude into the space of paired males by approach and Display Flights to their mates. Once the unpaired male made an aerial attack and then pursued a strange pair attempting to settle within his space.

The hostility of all the paired males toward the unpaired male resident on his own space increased from May 8 to 12 (Fig. 10 - Maps 4 and 5). In the three days from May 8 to 10 there were a total of seven fights between the unpaired male and the paired males, whereas in the two days of May 11 and 12 there were 11 fights.

The unpaired male resisted eviction from the pond until May 12. Then there was a dramatic change in the intensity of hostility of the paired males and the response of the unpaired male. On May 13 at 0800 there was no unpaired male on the pond. On four occasions a lone male flew over the pond but quickly left after being attacked and pursued by the paired males. At 1000 an unpaired male flew over the pond and for the next 18 minutes before it left it continually retreated from the repeated aerial attacks and pursuit flights by one paired male after another, mostly M W and M B, whenever the unpaired male flew over or landed within their pair-space. From then on no unmated males established a space on the pond as they were always promptly attacked and pursued and forced off the pond by the paired males.

5. Locations of Paired Male - Unpaired Male Encounters

The boundary zone of the unpaired male's space was more distinct and the space more exclusive from May 8 to 10 than from May 11 to 12 (Fig. 10 - Maps 4 and 5). There was no distinct boundary zone on May 11 and 12 as most encounters were concentrated in a disputed area occupied by the unpaired male, and M W and M Y (Fig. 10 - Map 5).

Maintenance of Space - Pond J 1974

1. Interactions Among Paired Males

The period of maintenance of space refers here to that interval from May 13 to June 6. Two phases can be distinguished: phase I when boundary zones were fairly stable, and phase II when boundary zones were changing. Phase I corresponds to the eight days from May 13 to 20 from about mid-laying to about the start of incubation for two of the three paired females. Thus phase I could be called the late laying phase.

26746

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SPACING BEHAVIOUR OF BREEDING BUFFLEHEADS (*BUCEPHALA ALBEOLA*) ON PONDS IN THE SOUTHERN BOREAL FOREST

by

© RICHARD HALLAM DONAGHEY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1975

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Spacing behaviour of breeding buffleheads (*Bucephala albeola*) on ponds in the southern boreal forest" submitted by Richard Hallam Donaghey in partial fulfilment of the requirements for the degree of Master of Science.

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Supervisor

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Date . . May 29, 1970. .

ABSTRACT

Spacing behaviour of buffleheads was studied for three field seasons to determine the nature of the spacing system(s) and its (their) adaptive significance. Breeding pairs and females with broods were observed intensively from elevated blinds at a bog pond and less intensively at a cattail and a lily pond.

Buffleheads were caught and individually colour-marked with nasal saddles. Unmarked paired males and their marked mates were watched daily at the bog pond and their social interactions recorded during all phases of the breeding cycle. Colour-marked female buffleheads with broods were observed intensively at a bog pond over a 23-day period and less intensively at the other ponds.

Agonistic behaviour patterns of buffleheads were described and quantified in terms of encounters. Spatial relationships among buffleheads were recorded by plotting the positions of individuals engaged in agonistic encounters.

Paired males established and defended pair-spaces largely by fighting and evicting conspecifics, but also by threat encounters, during the prelaying period. Most agonistic encounters involving paired males occurred within boundary zones that were relatively stable on any given day but shifted with time in relation to the reproductive state of their mates. Space was maintained mostly by threat encounters but also by fighting during the laying and incubation periods. Paired males defended their mates within their own space and even within their neighbour's space.

At high densities paired males totally divided the open water area of a bog pond among themselves, and excluded unpaired males. At

intermediate and lower densities on a lily pond and a cattail pond, respectively, paired males maintained an exclusive shoreline, boundary zones were less distinct away from the shoreline and unpaired males were not expelled from the central parts of these ponds.

Frequency and intensity of agonistic encounters involving males, and size of pair-spaces varied according to the reproductive state of females and the density of breeding pairs.

Colour-marked females with broods established and maintained a brood-space by fighting and threat encounters. In one situation a female gradually expanded her brood-space as that of another female contracted, until she was evicted from the pond, while the space of a third female remained relatively stable. The spacing system of females with broods was similar to that of pairs in terms of agonistic boundary encounters, expulsion of intruders and exclusive occupation of an area.

Females with broods that held larger brood-spaces were more aggressive in terms of the frequency, outcome and initiation of agonistic encounters. Size of brood-space was positively correlated with size of brood. Females with the largest broods were more aggressive suggesting that brood size determined level of aggression which in turn determined size of brood-space. Females with younger broods tended to be more aggressive than those with older broods of the same size. Females with larger, older broods were more aggressive and held larger brood-spaces than females with smaller, younger broods. Brood size appeared to be a much more important determinant of aggression than age of brood.

The concepts of home range and territory and the problems associated with studying them, particularly in ducks, are discussed. The nature of the spacing system in bufflehead is evaluated in terms of the

behavioural manifestations of territoriality. The adaptive significance of spacing behaviour is discussed.

It is concluded that breeding pairs and female buffleheads with broods defend a territory with boundary zones on ponds within their home range. Thus buffleheads exhibit a territorial system on ponds in a southern boreal forest region.

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INTRODUCTION

Members of a population of birds distribute themselves in space and time. The resulting dispersion pattern reflects both the ecology and the behaviour of the species. Ecological aspects of spacing involve the response of individuals to resources in the environment, while behavioural aspects involve habitat selection and establishment and maintenance of space through social interactions. The significance of spacing is that "it has important effects on the population dynamics, population genetics, and evolution of species" (Brown and Orians, 1970).

The spaces occupied by individuals, pairs, or groups are referred to as either a home range, a territory, an individual space, or a colony (Brown and Orians, 1970). Territoriality has received most attention because most birds are territorial and they have been studied more than most other groups of animals.

There has been substantial research on territorial behaviour in birds, particularly passerines, since Howard (1920) first emphasized the importance of this phenomenon in birds. Howard's concept of territory was applied to ducks by Hochbaum (1944) in his study of canvasback (*Aythya valisineria*) and other species of breeding ducks on Delta Marsh in southern Manitoba. Hochbaum claimed that a number of species of ducks were territorial in that they "defended an area" by "territorial defense flights".

In subsequent research Sowls (1955:48) introduced the concept of home range for ducks as the "area within which a bird spends its period of isolation between the break-up of spring gregariousness following spring arrival and the reformation of fall gregariousness". Sowls (1955) and Dzubin (1955) adopted the concept of home range for ducks because

they both found that territorial behaviour varied markedly from that proposed by Hochbaum for the same dabbler species of the genus *Anas* and for canvasbacks in that: a) paired males used and defended several areas not just one; b) definite boundaries to defended areas were not always established by pairs; c) home ranges of neighbouring pairs often overlapped in space; d) resources were temporally shared between pairs. Thus Dzubin (1955:293) suggested that territory be restricted to the "defended portion of the home range from which a drake attacks another pair, drake or female, of his own species".

In a review of this subject, McKinney (1965) stated that "much attention has been given to inquiring whether and how ducks 'defend areas' and how chasing behaviour (especially aerial pursuit) is related to such areas". He stressed the need for investigating in ducks the "broader biological problems of pair-spacing - the pattern of pair distribution on the breeding grounds, the [behavioural] mechanisms by which this is achieved, and the survival value of the different patterns found in different species".

I decided to investigate this problem in bufflehead (*Bucephala albeola*), a species of diving duck, because: 1) they are one of the most abundant breeding ducks on wetlands in the boreal forest based on a survey near Utikuma Lake, Alberta (Donaghey, 1974); and 2) bufflehead apparently space themselves on ponds and lakeshores (Erskine, 1972:57) but opinions differ on the nature of the spacing.

Erskine (1972) implied that, in general, only the concepts of home range and mated-female distance (Conder, 1949; Koskimies and Routamo, 1953) applied to bufflehead. However, Munro (1942) stated, without evidence, that in bufflehead "a breeding pair establishes a definite

territory which the male vigorously defends from encroachment by other males". Stansell (1909) observed that "when two or more pairs occupy a single pond, the males are usually very pugnacious, often quarreling and trying to drive each other off the pond for hours at a time".

These observations by Munro (1942) and Stansell (1909) suggest that aggressive behaviour of males serves to space breeding pairs. Therefore I decided to thoroughly investigate spacing behaviour in buffleheads, and to concentrate on social interactions between and within breeding pairs in relation to space and time. I chose to watch buffleheads only on small ponds, rather than lakeshores, because ponds have a higher ratio of shoreline to open water area, thus density of buffleheads and their frequency of interactions are more likely to be greater on ponds.

Buffleheads seem particularly well suited for a study of spacing behaviour because breeding pairs appear to restrict their activities to part of a pond and to use mostly the open water. From elevated blinds buffleheads were visible almost continuously and spacing behaviour could be accurately described and quantified.

The purpose of this study then was to determine: 1) the exact nature of any spacing system(s) of breeding buffleheads on ponds, and 2) the adaptive significance of any spacing behaviour observed.

STUDY PONDS

The study ponds are situated north of Atikameg (55° 54'N, 115° 39'W) in the Utikuma - Lesser Slave Lakes region of north-central Alberta. This area, in the Mixedwood Section of the southern Boreal Forest (Rowe, 1959), is mostly covered with upland forests of young trembling aspen (*Populus tremuloides*), mainly regeneration after fire, interspersed with patches of mature aspen, white spruce (*Picea glauca*) and white birch (*Betula papyrifera*). The lower, wetter upland sites are characterised by balsam poplar (*Populus balsamifera*), while the lowland sites have black spruce (*Picea mariana*) and tamarack (*Larix laricina*) trees, and willow (*Salix* spp.), alder (*Alnus* spp.) and labrador tea (*Ledum groenlandicum*) shrubs.

The terrain is gently undulating with an average elevation of about 670 m. Summers are short and cool. Mean summer precipitation is 20 cm, with June and July being the wettest months. Mean July temperature is around 16°C (Hardy, 1967).

Four study ponds were chosen. To record possible changing behavioural relationships in breeding pairs of buffleheads I considered three ponds the maximum that could be studied satisfactorily. To document social interactions between pairs relative to the environment, three ponds (H, J and K) were chosen that had more than one resident pair of buffleheads and had different shoreline vegetation. An additional pond (L) was selected to study behaviour of female buffleheads with broods.

Some features of the bufflehead's environment were described by classifying each pond as a habitat type depending on its wetland vegetation, and further described according to aspects of limnology and

the presence of other aquatic birds (other ducks, grebes and rails). Wetland vegetation of a pond refers here to the submersed vegetation of the open water, and the emergent and other vegetation in a zone 10 to 20 m from the shoreline.

To aid in waterfowl research and management a detailed classification of prairie wetlands has been developed based on the pattern of vegetation zones and water permanence (Stewart and Kantrud, 1971). Comparable classifications of forest wetlands are few, some exceptions being those of Gilmer (1971) and Cowardin and Johnson (1973) in north-central Minnesota, and Jeglum's (1972) survey of boreal forest wetlands in Saskatchewan. Jeglum (1972) quantified vegetation stands on the basis of their physiognomy and dominance, and Cowardin and Johnson (1973) grouped stands into plant communities with or without permanent water on the basis of species abundance. I made no attempt to quantify vegetation stands. Instead each pond was classified broadly on the basis of its shoreline vegetation, irrespective of whether the shoreline was composed of several plant communities or a single species of emergent plant, or whether some combination of physical and botanical characteristics was used. The main vegetative characteristics of each study pond are described first, then their limnological features and aquatic birds are briefly described and compared.

POND J. Bog pond (1.5 ha) Figure 1a

In the zone of permanent open water submersed vegetation was sparse. Most of the shoreline was relatively solid and was composed of several bog communities with patches of marshy and/or spongy emergent vegetation in the bays. Some shoreline was characteristic of sedge fen (Jeglum, 1972) with *Calamagrostis* spp. and a fine-leaved sedge (*Carex*

Figure 1a. Pond J with a shoreline of bog plants.

Aerial photograph taken July 1973 from south-west facing north-east. An elevated blind is on south side to right of centre. Small peripheral ponds occur around J. Part of cattail Pond C is in middle top of photograph.

Figure 1b. Pond H with a shoreline of cattail.

The lighter areas peripheral to the dark cattail represent a narrow zone of sedges and grasses, and extensive open meadows. Aerial photograph taken July 1972 from north-west facing south-east. A blind is left of centre at edge of far shoreline in front of a clearing.

aquatilis) the dominants. Other sections of shoreline, better classified as bog, consisted of an association of *Ledum groenlandicum* - *Sphagnum* spp. - *Vaccinium vitis-idaea*. Farther away from the shoreline were shrubs such as tall willows (*Salix* spp.), and dwarf birch (*Betula glandulifera*) and stands of muskeg (black spruce trees associated with *Ledum groenlandicum* - *Sphagnum* - *Vaccinium vitis-idaea*). Marshy emergent vegetation such as coarse-leaved sedges and *Eleocharis palustris* formed patches of shoreline in the bays. Common bladderwort (*Utricularia vulgaris*) and marsh cinquefoil (*Potentilla palustris*) were the dominant vegetation of the small, peripheral bog ponds to the south. Nesting habitat of buffleheads included poplar stubs among stands of mature and young aspen to the north and west.

POND H. Cattail pond (3.8 ha) Figure 1b

In the zone of permanent open water *Chara* spp. was the dominant submersed vegetation. The shoreline was composed entirely of a deep marsh zone of cattail (*Typha latifolia*). Peripheral to the cattail was a shallow marsh zone of coarse-leaved sedges (the dominant species was *Carex rostrata*) associated with whitetop (*Scolochloa festucacea*). Surrounding the shallow marsh zone were extensive open areas of wet meadow and prairie species of plants grazed by cattle in spring and mowed at the end of summer. Nesting habitat of buffleheads included poplar stubs among stands of mature and young poplar to the south.

PONDS K and L. Floating-mat - pond-lily ponds (3.7 ha and 3.3 ha, respectively) Figure 2a, b

Yellow pond-lily (*Nuphar variegatum*), the dominant aquatic plant with floating leaves, covered nearly half of the open water on Pond L

Figure 2a. Pond K with a floating-mat shoreline of mainly cattail and sedges, and pond-lilies on the open water.

Aerial photograph taken July 1972 from west facing east. Blind is to lower right of photograph.

Figure 2b. Pond L with a floating-mat shoreline of mainly cattail and sedges, and pond-lilies on the open water.

Aerial photograph taken July 1973 from south-east facing north-west. An elevated blind is to lower left of photograph.

and about one fifth on Pond K. Nearer the shoreline clasping leaf pondweed [illegible] was the dominant species of submersed vegetation. The shoreline zone consisted of a floating spongy mat of cattail and sedges, mainly [illegible]. At the water's edge was a band of tall willow and alder shrubs and mostly dead white birch with an undercover of ericaceous bog shrubs in places. A forest of young aspen and stands of mature white spruce trees closely surrounded the ponds. Hereafter this habitat type is simply referred to as lily pond.

Other characteristics of the study ponds are now briefly described and compared. The four study ponds were all small (1.5 to 3.8 ha of open water area), shallow (mostly less than 2 m), fresh (conductance less than 500 micromhos), alkaline (ph 7.6 to 8.6), with permanent and relatively stable water levels.

Characteristics of water chemistry (Table 1) were determined from analysis of a surface sample of open water taken near the shoreline and preserved with chloroform. Cattail Pond H appeared to be more eutrophic in terms of nutrients (as measured by conductance, and total dissolved solids) than the other ponds.

Aquatic invertebrates from each pond were sampled 1 to 2 m from the shoreline with a dip net and preserved in 10 to 20 percent formalin. Composition of aquatic invertebrates was similar for the bog and lily ponds, but more diverse on cattail Pond H. For example, in addition to groups common to both Pond H and the other ponds, cladocerans, mayfly nymphs and some families of aquatic beetles were present in Pond H but not the other ponds. Aquatic insects were more abundant in Pond H, especially Corixidae, Diptera (mostly Chironomidae), Ephemeroptera and

Table 1. Characteristics of water chemistry on the study ponds.

Habitat type	Pond	Date sampled (1973)	Colour	Turbidity (Hach kit)	Conductance (micromhos)	Milligrams per litre											
						pH before alkalinity	Phenlphthallen alkalinity as $CaCO_3$	Total alkallnity as $CaCO_3$	Phosphate (ortho)	Silica	Nitrate-N	Total dissolved solids	Iron	Calcium Hardness as $CaCO_3$	Total	Chloride	Sulphate
Cattail	H	Aug. 25	115	30	400	8.42	5.7	131.0	0.04	4.45	0.04	373.0	0.07	116	208	3.30	88
Bog	J	Aug. 27	162	37	240	8.38	5.7	101.0	0.10	4.90	0.05	180.4	0.02	102	128	2.84	30
Lily	K	Aug. 27	300	58	190	7.82	0	87.2	0.17	4.00	0.07	176.1	0.08	74	108	1.88	7
Lily	L	Aug. 27	280	49	180	7.60	0	84.1	0.10	5.40	0.07	173.2	0.07	74	108	1.42	11

Odonata (especially Zygoptera nymphs). In the bog and lily ponds Amphipoda and Diptera (mostly *Chaoborus*) were the most common invertebrates taken in the samples.

Waterfowl and other aquatic birds (Podicipedidae, Rallidae) were censused on the study ponds (Donaghey, 1974). Fourteen species of ducks, including buffleheads, and five species of other aquatic birds occurred on the study ponds. More resident species of dabbling and diving ducks and other water birds occurred on cattail Pond H in a species ratio (6:8:5) respectively, than on lily Ponds K and L combined (5:4:3), with the least number of species on bog Pond J (4:2:2) (Donaghey, 1974).

Four species of dabblers - mallard (*Anas platyrhynchos*), American wigeon (*Anas americana*), blue-winged teal (*Anas discors*), and American green-winged teal (*Anas crecca*); two species of divers - lesser scaup (*Aythya affinis*) and bufflehead; and two species of other aquatic birds - red-necked grebe (*Podiceps grisegena*) and sora (*Porzana carolina*) were resident on all study ponds. Common goldeneye (*Bucephala clangula*) and ring-necked duck (*Aythya collaris*) were resident on Ponds K, L and H. On Pond J they were transient species, although the latter species may have attempted to breed there.

There were a greater number of diving ducks than dabblers on all ponds. Greater numbers of divers occurred on Pond H than on any other pond. Lesser scaups were the most abundant diving ducks on all ponds, but were most numerous on Pond H.

METHODS

Field work was conducted over three summers, May to August 1972, April to August 1973, and the end of April to mid-June and two weeks in July in 1974.

No attempt was made to catch buffleheads in 1972, the first field season. However, to study spacing behaviour, it became apparent that ducks would have to be individually colour-marked. In 1973 almost all potential capture methods were tried. To minimize disturbance and possible disruption of the breeding cycle of the few pairs on the study ponds, I tested the techniques first on other ponds. Trapping on the study ponds began only when most pairs were well established. I caught adult females at their nest cavity (Fig. 3, technique modified from Erskine, 1959). Most buffleheads were caught in rectangular, welded wire traps with mirrors (Fig. 4b). I designed these traps with two funnel entrances, one at each end, leading into a double-sided mirror so as to stimulate birds toward their image (basic trap design modified from Schierbaum and Talmage, 1954; Addy, 1956:sect. 1610 and 1620; Rogers, 1964). Buffleheads were also caught by night-lighting from a boat (technique and equipment modified from that used by Lindmeier and Jessen, 1961; Bishop and Barratt, 1969), in floating ball traps (Thornsberry and Cowardin, 1971) and in mist-nets. In 1974 traps were set out at Pond J before pairs arrived.

Flying adults and yearlings, and class III flightless juveniles (Gollop and Marshall, 1954), when trapped, were leg-banded and colour-marked with nasal saddles (Sugden and Poston, 1968) (Fig: 4a). These markers were made of either plasticized polyvinyl chloride or nylon, and attached with a nylon pin. Saddles were made of one colour (red,

Figure 3. Opening up female red's nest cavity 9.5 m (31 ft) above ground.

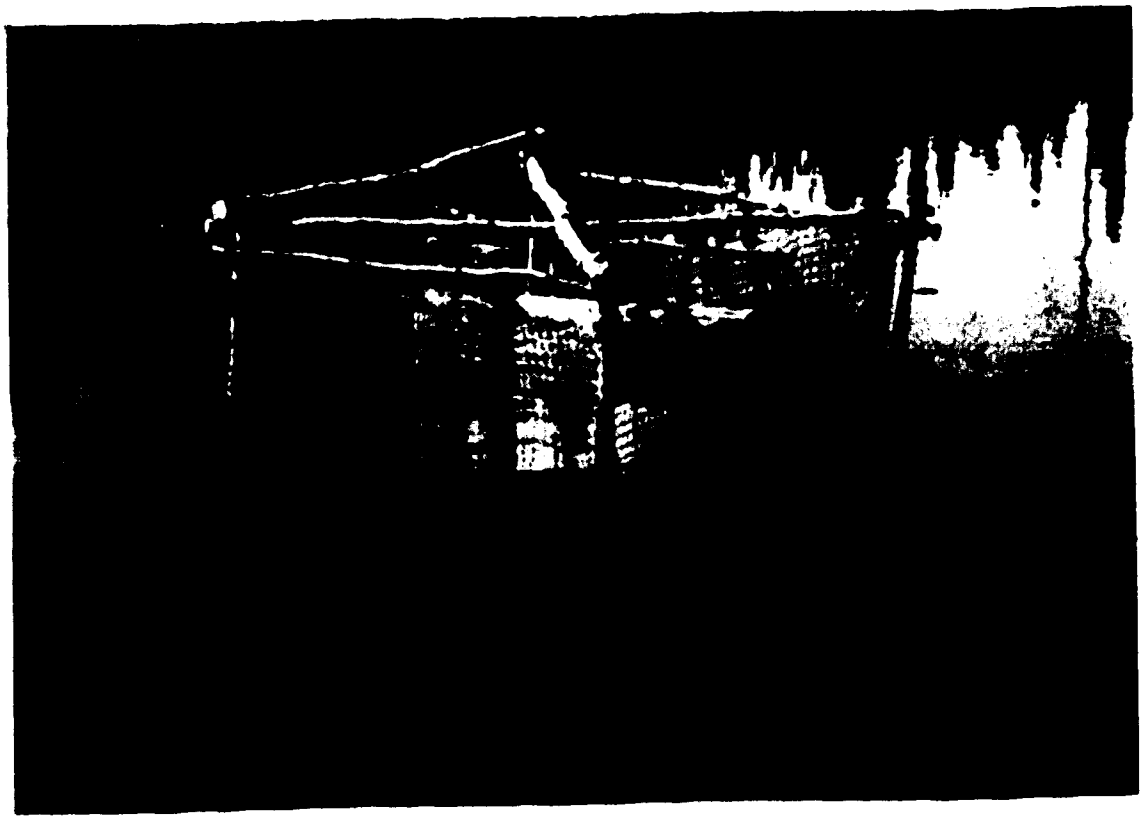
Ropes hold a 9.1 m (30 ft) aluminum ladder upright away from rotten stub. By lashing spruce poles to the base of ladder the same technique was used to open up female white's cavity 11.6 m (38 ft) above ground in a nearby stub.

Figure 4a. A female bufflehead individually colour-marked with a yellow nasal saddle.

U.S. Fish and Wildlife aluminum band is on the right leg.

Figure 4b. Welded wire trap with two funnel entrances leading into a double-sided mirror.

Sides of trap are constructed of one inch welded wire mesh, with plastic netting on top.



yellow, green, blue or white) and combinations of two colours in contrasting broad stripes a) orange, yellow, blue or white with black; b) red or green with white; c) yellow or red with blue. These saddles were ideal for consistently recognizing individuals interacting vigorously. To specify the sex of individuals I use the letter F for females, and M for males. To denote females individually colour-marked with nasal saddles I use letters, for example F B is the female with a blue saddle, and F Or-Bk is the female with an orange and black saddle. The only colour-marked male will be designated M B(K), K indicating the pond where he was resident.

Unmarked individual paired males were recognized with reference to the space they occupied and their behaviour toward conspecifics, especially their relationship with their mate, either marked or unmarked. Unmarked females of a pair were recognized individually by their flight path to a specific nest site. Unmarked females with broods were individually recognized by the size and age of their brood and their spatial relationships with other females with broods. To denote unmarked individual females resident on a particular pond I use a combination of letters and numbers, for example, F 1(J) is female one on Pond J. In 1974 at Pond J none of the resident paired males were individually colour-marked, yet they were all mated to marked females. Every day for 6 weeks I watched the behavioural responses of these males to their mates and neighbouring pairs. Thus I felt confident that the same individual males were mated to the same colour-marked females throughout the breeding cycle. I use letters to refer to these individual males, for example M W or pair W, means an individual unmarked male mated to F W.

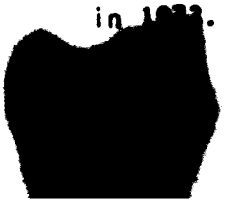
From blinds placed on the ground buffleheads were not visible continuously in 1972. In 1973 elevated blinds (Fig. 5) were constructed facing north where possible to have the best light conditions for observing, and at a position where most shoreline was visible. During April four towers were erected at three ponds (J, K and H) before the arrival of buffleheads. An additional elevated blind was built in mid-July at another pond (L) for watching female buffleheads with broods.

I observed buffleheads from blinds for a total of about 500 hours during all three field seasons with emphasis throughout on recording social interactions. Throughout May to early June breeding pairs were watched at Pond J in 1972, Ponds H, J, and K in 1973 and Pond J in 1974. In 1972 pairs were observed only during their incubation period, while in 1973 at any one pond the interval between observation days varied. Thus all pairs were not watched during all stages of the breeding cycle. In 1974 I intensively watched breeding pairs for 30 days from their arrival through incubation. In 1972 buffleheads were observed at all times of day. Interactions were few but seemed to peak about mid-morning. Therefore in 1973 on any particular day interactions were recorded for ten hours from 0800 to 1800 D.S.T., and for five hours from 0800 to 1300 in 1974.

Throughout July 1973 colour-marked female buffleheads with broods were watched intensively at Pond J for a total of 100 hours, usually from 0800 to 1800 on any given day, except from 1200 to 2200 (July 7) and 1100 to 2100 (July 9). Other females with broods were watched for shorter periods at Ponds H and J in 1972, Ponds H and L in 1973 and Pond J in 1974. Walking to the blind by myself alarmed females with broods, especially near the blind, much more than pairs. Therefore

Figure 5. Elevated blind with 360° vision at Pond J.

Four similar blinds were erected at Ponds H, K and L in 1973.



during the brood period a person went with me to the blind, soon left and then these females quickly resumed their activity near the blind.

All agonistic interactions seen between buffleheads and conspecifics were recorded, mostly on tape. For each intraspecific encounter I tried to record: time of day, individuals involved, main behaviour patterns, initiator and outcome. With evenly matched unmarked males it was difficult to determine the outcome of most encounters. Interactions seen between buffleheads and other species were often incomplete and recorded in less detail.

To record spatial relationships between interacting individuals, their positions were located on Pond J with reference to colour-marked stakes along the shoreline, and plotted on field maps. The error in locating a bird's position near the shoreline and plotting it was estimated to be ± 3 m. A bird's position out on the open water was more difficult to plot because no stakes were placed there, but errors were probably no greater than ± 10 m, mostly ± 5 m.

At the larger study ponds there were much greater errors in plotting positions of birds so these data have not been used to determine details of spatial relationships.

The location of supplanting attacks and fights, and the mid-point between individuals engaged in threat and approach - withdrawal encounters, were plotted on overlay maps drawn to scale. Boundaries were plotted primarily from the positions of threat and fighting encounters. Pair and brood-spaces were measured with a planimeter and expressed to the nearest 0.05 ha.

We searched for nest cavities of breeding female buffleheads for two main reasons. Firstly, to catch and mark the occupant, and

secondly, to open up the cavity (Erskine, 1954) to determine stage of the breeding cycle, clutch size and hatching success. Any nest cavity in a stub visible from the blind was easily found by watching the female fly directly to it. Nest sites of particular females nesting in the forest well away from the pond were more difficult to find. We located these cavities by progressively following the female in flight from the pond above the forest canopy, until she descended or was lost to sight, then a localized ground search was made for likely nest stubs.

Stages in the breeding cycle (the week of laying and incubation) of individual female buffleheads breeding in 1972 and 1973 were estimated by backdating from the date of arrival at a pond of class Ia (downy) broods. I crudely estimated date of clutch-initiation of three females breeding in 1973 by making several assumptions regards date of hatching, incubation period, clutch size and rates of egg-laying. Firstly, young buffleheads leave the nest cavity 24 to 36 hours after hatching (Erskine, 1972:92), therefore newly hatched broods (class Ia) were considered to be two days old on the day they arrived at a pond. In one instance, where a female deserted her clutch, I estimated age of the embryos on the basis of characteristics used in determining the age of embryos in other species of waterfowl (Cooper and Batt, 1972; Caldwell and Snart, 1974). Secondly, Erskine (1972:89) found that "incubation periods ranged from 28 to 33 days, with most clutches hatching 29 to 31 days after the last egg was laid", therefore I assumed incubation period to be 30 days. Thirdly, clutch size was known for two of the three females whose date of clutch-initiation was estimated. In estimating clutch size of the third female I considered two factors, the number of eggs that fail to hatch, and early mortality

of young, which refers here to losses of young in the first week, including those that fail to leave the cavity, and losses that occur while young are travelling on land to water, or after they have reached it. The contents of the cavity were determined by opening it up after the brood had left. I assumed that one of her young was lost on land, because they travelled about 300 m to water and I counted the number of young in her brood only a few hours after they arrived at a pond (see Erskine 1972:112-113 for further details regarding this assumption). Finally, based on laying rates of three females in this study, I assumed that eggs were laid at 2-day intervals, although as Erskine (1972:80) pointed out some individual females may lay eggs at a faster rate.

In 1974 the precise stage of the breeding cycle was determined for three colour-marked females. For one female dates of laying were determined by daily inspection of her nest cavity during the laying period. For the other two females I determined the days they laid from their daily activity patterns (flights toward the nest site and the periods of time away from the pond) together with known clutch size of one female, and a good estimate of clutch size of the other female based on her class Ia brood of seven. For two females incubation probably started the day the last egg was laid, but for convenience I assumed it began next day. For the female whose clutch size was estimated, incubation probably started two days after the estimated date of laying of egg seven, thus allowing for a clutch of eight eggs and the possibility that one of her young was lost because they travelled at least 600 m to Pond J.

The availability of nest sites was increased at Pond K, in an attempt to raise the density of breeding pairs and subsequent broods,

and hence the frequency of interactions. In early May 1973 at Pond K, three nest-boxes (measuring 41 cm deep, 15 cm square bottom) and three artificial cavities were erected on dead stubs and poles around the shoreline for this purpose.

To determine the habitat used by female buffleheads with broods in relation to other species of water birds I censused 20 ponds between July 8 and 19, 1974, the optimal period for censusing bufflehead broods.

Data were analyzed statistically using Chi-square tests, and Spearman's rank correlation (Siegel, 1956). A probability value of 0.05 or less was considered significant.

RESULTS

LIFE HISTORY CHARACTERISTICS IN SPACE AND TIME

Annual Cycle

Buffleheads reared on the study area, or resident there as subadults or adults, most likely winter on the Pacific coast as indicated by two recoveries of birds banded on the study area and other birds banded in the Peace River - Lesser Slave Lake region (Erskine, 1972:123-124). One bufflehead banded at Pond H as a juvenile on August 9, 1973 was recovered in Washington State on November 9, 1973; and another bird banded and colour-marked at Pond M as a subadult female on May 30, 1973 and last seen at Pond H on June 16, 1973 was recovered in Oregon State on October 15, 1974. Both sexes tend to return to wintering grounds used in previous years (Erskine, 1961).

Pair formation apparently can occur on the wintering grounds, but also during spring migration and on the breeding grounds because Erskine (1961) suggests that many male buffleheads start migration unpaired.

Most adult females are paired on arrival at the breeding grounds where there is a surplus of unpaired males in each season. Breeding pairs settle on ponds and lakeshores, the female tending to return to nest in the same area as in previous years (Erskine, 1961).

Tree-cavities, usually those excavated by common flickers (*Colaptes auratus*), are used for nesting. While the female is occupied with laying, her mate waits on a nearby pond or lakeshore. The pair bond breaks up at about the onset of incubation (Drury *et al.*, MS; Erskine, 1972:88, 90). While the female incubates, post-breeding males gather for moulting on lakes used in previous years (Trauger, pers. comm.).

The female alone cares for the brood, but usually leaves them before they are fledged and able to fly, and homes to moulting areas (Erskine, 1961). Fall migration in October to the wintering grounds completes the cycle.

Spring Arrival

Arrival of buffleheads was studied at three ponds (H, J and K) in 1973, and two ponds (H and J) in 1974. Buffleheads were among the earliest ducks to arrive on the study area. In 1973 I saw the first bufflehead, a lone male, on April 22, 4 days after the first mallards were seen.

Early arriving buffleheads settle on ponds partially ice-free or temporarily disperse to smaller peripheral ponds with open water. For instance, on April 26, 1973 a pair flushed from the open water of a small, peripheral pond near Pond J, the latter being still fully ice-covered on that date. However, by May 2, 1973, though Pond J was still almost fully ice-covered two breeding pairs had settled there on the only available ice-free water, a strip along the north shoreline.

Breeding pairs settled a few days later on Pond H than Pond J. Pond H was more than half ice-free on May 1, 1973 and had one pair and a lone male bufflehead. A second pair settled between May 5 and 7, 3 to 5 days after the pond was probably ice-free.

Pond K was fully ice-covered on April 30, 1973 but completely ice-free by May 3. It was not known if any buffleheads settled on May 1 or 2 but by May 3 one lone male bufflehead was present. By the afternoon of May 4 two pairs of buffleheads were present on Pond K. Thus by May 3, 1973 all three ponds (H, J and K) were ice-free and each occupied by at least one pair of buffleheads.

In 1974 on April 27 I saw the first bufflehead, a lone male, on partially ice-free Pond J. This pond was ice-free by April 29, 4 days earlier than in 1973. Three colour-marked females, all paired upon arrival, returned to Pond J in 1974. I saw the first of these females (F B) on April 28 at Pond M, then at Pond J the next morning. The two other colour-marked females with their mates were first seen at Pond J on May 3 and May 4.

On ice-free Pond H I saw one unmarked pair on April 30, 1974 and two pairs on May 14 (a colour-marked female and her mate and an unmarked pair).

In summary the break-up period of the study ponds occurred from the last 2 to 3 days of April to the first 2 to 3 days of May. In both years breeding pairs of buffleheads settled on ponds partially ice-free and/or within a few days after ponds were fully ice-free. Breeding pairs settled a few days earlier on bog Pond J, than either cattail Pond H or lily Pond K.

Migrational Homing

The degree of migrational homing by adult females to the study ponds was determined from the return of colour-marked birds. Six adult females (four from Pond J and two from Pond H) were individually colour-marked in 1973. Four of these females returned to the study ponds the next year.

All three marked females that returned to Pond J in 1974 occupied this pond while nesting and/or with a brood the previous year. The only marked female that returned to Pond H was resident there throughout the nesting and brood periods the previous year. These returns of adult female buffleheads provide evidence of a high degree of precise homing

to the same small ponds used the previous year. Evidence from a much larger sample (Erskine, 1961) indicates a strong tendency for adult female buffleheads to return to the same lake where they nested at the previous year. Thus females appear to exhibit a strong homing tendency to both lakes and ponds.

Migrational homing among other species of female ducks has been well documented, for example, in species of ground-nesting dabblers of the genus *Anas* (Sowls, 1955), the lesser scaup, a ground-nesting diver (Trauger, 1971) and the cavity-nesting wood duck (*Aix sponsa*) (Grice and Rogers, 1965).

The return of individual male buffleheads to a specific breeding site used in previous years has not been documented. During this study only one adult male bufflehead was colour-marked. This paired male, B(K), but not his mate, was caught and marked at his breeding Pond K on June 12, 1973. On May 30, 1974 I saw M B(K) with an unmarked female on the same part of the pond it occupied the previous year. This pair was not seen on visits to Pond K on May 10 and 14 but was seen on two subsequent visits on June 3 and 5.

These observations of the only paired male marked suggest that male buffleheads also may tend to return to the same breeding pond used previously. Observations were too infrequent to determine if M B(K) was paired on arrival, or homed to the breeding grounds and acquired a mate there. For several reasons M B(K) may have been paired to the same female as in the previous year, and was paired on arrival, and thus merely followed his mate home. Evidence presented later suggests that females select the breeding pond and the pair-space at that pond. Also pair bonds of buffleheads could be renewed either on the wintering

grounds, because Erskine (1961) provided evidence that both sexes tend to return to the same areas in successive winters, or during spring migration, if they use the same stopover points, because Erskine (1961) suggested that many male buffleheads start migration unpaired. Finally, if males home to the breeding grounds separately from females then pair bonds could be renewed there. The return of male buffleheads to wintering, moulting and breeding areas in successive years suggests that their homing tendency is well developed.

Poston (1974) provided evidence of migrational homing by unpaired male northern shovelers (*Anas clypeata*). The only marked male shovelers (two adults and one juvenile) to home to his study area were all unpaired on arrival. Grice and Rogers (1965) found that among cavity-nesting wood ducks only ten percent of adult males returned to their natal and/or breeding areas. It was not stated if these males were paired or unpaired on arrival. Recoveries elsewhere led Grice and Rogers (1965) to conclude that male wood ducks, because they apparently form pairs on the wintering grounds with females from other populations, tend to follow a female to her natal area rather than his own.

Survival of Adult Females

Adult female buffleheads appear to have a high survival rate, based on small samples. In this study, of six adult marked females, four returned to the study ponds, a survival rate of 67 percent. An even higher survival rate was found among the first eight female buffleheads recaptured at their nest sites in interior British Columbia (Erskine, 1972:179). From mortality rates given by Erskine (1972:179) I calculated the average annual survival rate for these eight females to be 76 percent for the first five years, or 72 percent over a 7-year

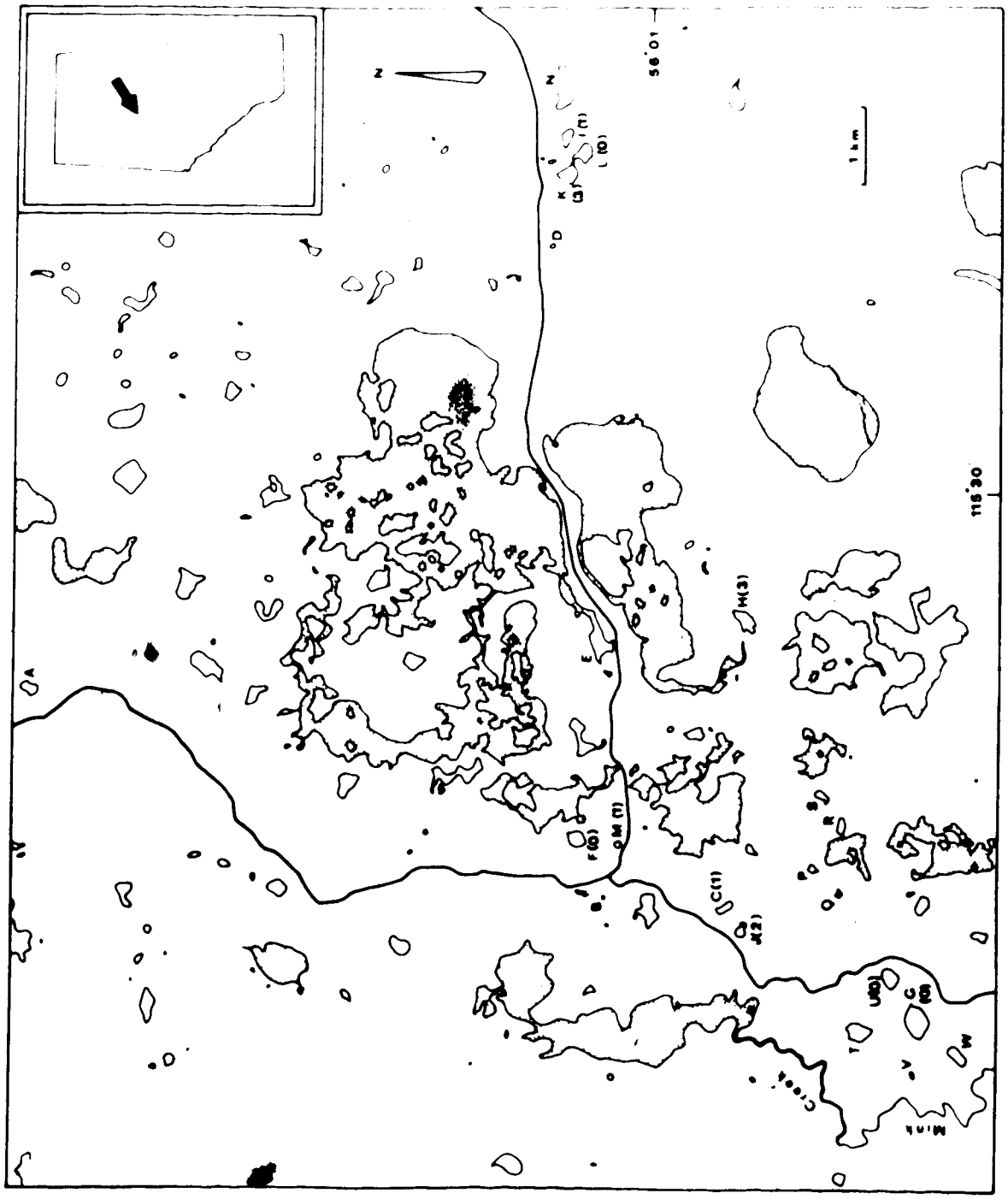
period. On the basis of all recaptures of adult female buffleheads at the nest site Erskine (1972:177) calculated their annual survival rate to be 50 percent, only slightly higher than that obtained from recoveries of banded birds. Erskine (1972:180) pointed out that the numbers of a breeding population of buffleheads in British Columbia could not be maintained "unless the survival rates of first-year birds or of mature females or both were higher than those here obtained from banding recoveries and recaptures". Female buffleheads first breed at the age of two years (Erskine, 1972:84). Ricklefs (1973) showed that among birds in general the greater the age at first breeding the higher the annual adult survival rate. In birds first breeding at the age of two years, such as swifts, herons, geese, owls and shorebirds, the annual average survival rate ranged from 60 to 80 percent (Ricklefs, 1973). This general relationship between age at first breeding and average annual survival rate, and the survival rate of adult female buffleheads based on small samples suggests that a 50 percent average annual survival rate of adult female buffleheads is an underestimate. Thus the survival rate observed in this study (67 percent) is probably more realistic.

Distribution of Breeding Pairs on Ponds

Pattern of pair-spacing was determined in May 1972 by censusing breeding buffleheads on ponds along 13 km (8 miles) of road. Of the ten ponds, six had breeding buffleheads (three ponds each with one pair, and three ponds each with two to three pairs). This distribution gave a clumped spatial pattern of breeding pairs (Fig. 6). This pattern reflects the distribution and availability of ponds and nesting habitat suitable for buffleheads.

Figure 6. Distribution of breeding pairs of buffleheads on ponds on the study area in 1972.

Letters refer to individual ponds visited and numbers in parentheses to the number of pairs of buffleheads on each pond. Zero indicates ponds with no pairs. No ponds are denoted with letter O. Stippled areas represent open water of lakes, but not ponds. Thicker lines are roads.


N
56°01
1 km
115°30
H(3)
F(0)
M(1)
C(1)
J(2)
Creek
Mink

Numbers and Densities of Breeding Pairs on Ponds

The [redacted] densities of breeding pairs resident on the study ponds va[redacted] ponds for each year, but was relatively constant for the [redacted] tween years (Table 2).

[redacted] that maintained a pair-space on a study pond th[redacted] out[redacted] and early June, and were known to have nested or most lik[redacted], are termed residents. Colour-marking of individual fema[redacted] that a sample of birds in the Pond J area definitely consi[redacted] two groups of breeding pairs: 1) the resident breeding pairs, [redacted] 2) breeding pairs that failed to establish a pair-space on Pond J, [redacted] occupied nearby peripheral ponds and nested nearby. Because [redacted] latter group were resident in the Pond J area, but not on Pond J, I [redacted]opose to call them peripheral breeders, rather than non-residents.

Both [redacted]ent and peripheral breeding pairs occurred in the Pond J area in [redacted] 1974. In 1973 both the two resident females on Pond J and two [redacted]ipheral females were colour-marked. One peripheral pair occupied small ponds around Pond J (Fig. 1a) and the female of this pair (F Y) nested in a cavity within 50 m of Pond J. The other peripheral female (F B) was first individually recognized with her brood on a small pond adjacent to J, and then on Pond J.

In 1974 the three paired females resident on Pond J were all colour-marked. A peripheral female (F Or) nested nearby, and settled on Pond J with her brood. A second female may have been a peripheral breeder, because Pond C north of J was not occupied by any resident breeding pairs, but an unmarked female with a brood arrived there. Therefore on Pond J there were two and three resident breeding pairs in

Table 2. Numbers and densities of resident breeding pairs of buffleheads on the four study ponds from 1972 to 1974.

Pond Size (ha)	H 3.8		J 1.5		K 3.7		L 3.3	
	No. Pairs[a]	Pairs/ha	No. Pairs	Pairs/ha	No. Pairs	Pairs/ha	No. Pairs	Pairs/ha
1972	3[b]	0.8	2	1.3	3[c]	0.8	0[d]	0
1973	2	0.5	2	1.3	3	0.8	1[c]	0.3
1974	2[c]	0.5	3	2.0	3[c]	0.8	0[e]	0

[a]Based on at least eight censuses in May unless otherwise indicated.

[b]Based on maximum number of breeding pairs seen at any one time during six hours of observation on May 22 and May 23, and all day observations on June 5.

[c]Based on 3-5 censuses from May 10 to June 8.

[d]Based on one census on May 5.

[e]Based on one census on May 10.

1973 and 1974 respectively. In addition there was at least one and probably two peripheral breeding pairs in both years in the Pond J area.

The sample of breeding pairs in the Pond H area includes resident breeding pairs on Pond H, in addition to other females that settled on Pond H with their broods. With unmarked individuals it was not clear whether this latter group were resident pairs that settled on Pond H later than the known resident pairs, or were peripheral breeding pairs that occupied nearby lakes, rather than ponds (see Fig. 6). In 1972 there were an estimated three breeding pairs, and four broods on Pond H. However, it was not known whether these broods were with females of resident or peripheral breeding pairs.

In 1973 there were definitely two resident breeding pairs on Pond H, with one of the females colour-marked (F R-W). Female R-W arrived with her brood at Pond H, then another female with a brood arrived but left soon after. A third female with a brood arrived between July 19 and 21. This latter female had no pair-space on Pond H at the time she would have been laying, so she must have been a peripheral breeder that brought her brood to Pond H.

The sample of breeding pairs seen in the Pond K area included resident pairs that presumably nested, and late arriving pairs that settled on Pond K then dispersed. In 1973 three resident pairs settled, then two other pairs arrived later, but subsequently left. Without marked individuals it was not possible to know the exact status of breeding pairs. However, the number of resident pairs on Ponds K, L and I (Fig. 6) always exceeded the subsequent number of broods on these ponds, suggesting that few if any peripheral breeding pairs nested nearby.

SPACING BEHAVIOUR OF BREEDING PAIRS

Introduction

Spacing behaviour of breeding pairs is defined here as any behaviour that distributes pairs to different habitats and spaces out pairs within a given habitat. Spacing behaviour of breeding pairs of buffleheads on ponds involves two main elements: 1) the selection of a pond and nesting habitat, and 2) agonistic behaviour that may serve to disperse pairs to different ponds, or to space pairs on a single pond. Sexual behaviour on the breeding grounds, such as pair-maintenance display and copulatory behaviour, is included here as spacing behaviour because it is space-related. This section emphasizes agonistic and sexual behaviour of buffleheads on ponds in relation to space and time. For the present it seems preferable to use the term space (for example, pair-space or brood-space), rather than territory, to denote that part of a study pond held by a pair or individual. The territory concept has generated much controversy when applied to ducks, so use of this concept in relation to my findings will be evaluated later. The time referred to here is the nesting period from the arrival of pairs to the hatching of young.

Fighting between male buffleheads at more or less fixed positions in space, when their mates were both present and absent, was first recorded at one pond in 1972. At this pond (J) the two resident pairs were observed only during the incubation period. Most fights were recorded during the first two weeks of incubation, but fighting persisted into the third week, when the pair bond of one of the males apparently broke. These observations of use of the pair-space by paired females and fighting between their mates along a boundary zone

suggested that males maintain an exclusive pair-space for their mates for almost the entire nesting period.

Observations of bufflehead in 1973 at three ponds confirmed the above general nature of their agonistic behaviour patterns in relation to space, but showed that at different ponds the resident pairs maintained pair-spaces for varying periods relative to the breeding cycle.

In both years no individuals were marked during the nesting period while the pair-bond was intact and observations were incomplete at any one pond for all stages of the breeding cycle. Thus the exact nature of the spacing mechanism over time remained unclear.

In 1974, however, the spatial-temporal relationships between and within pairs were determined at one pond by daily recording the social interactions of marked individuals during all stages of the breeding cycle. The rest of this section consists of three parts. Part I describes the sexual and agonistic behaviour of breeding pairs, Part II describes and quantifies agonistic behaviour in space and time, and Part III deals with sexual behaviour in space and time.

Part I. Description of Sexual and Agonistic Behaviour

Sexual Behaviour

Sexual behaviour in buffleheads is space-related as it assists to maintain the pair-bond and the male's attachment to a space for the duration of that bond.

In describing sexual behaviour of buffleheads I have used the terminology of Myres (1959a; 1959b) and Johnsgard (1965), and have followed the ethological convention of capitalizing ritualized behaviour patterns which are considered to be displays.

Sexual behaviour of buffleheads has been described in detail (Myres, 1959a; 1959b) and summarized (Johnsgard, 1965; Erskine, 1972; Drury *et al.*, MS) so brief mention of their terms and display sequences supplemented by my own observations should suffice. Although pair-forming displays and sequences, such as Fly-over and Landing, Alternating and Cutting-out (Myres, 1959a), do occur on the breeding grounds they are not considered here as adult females were paired on arrival at the study ponds.

1. Pair-maintaining Displays

   a. Female

The two most common female displays are Head Display and Following (Myres, 1959a). Head Display is similar to Crest-erection of males. Following is the female's main response to male display. In response to Leading by a particular male the female rushes after, and follows him, gives a loud, gutteral call, and alternately extends and withdraws her neck (Myres, 1959a).

Drury *et al.*, (MS) describe two other female patterns of behaviour, the Side-to-Side and Sweep, both of which express

aggressive and sexual elements and occur when the pair are close together, either in the absence (Side-to-Side) or in the presence of another male (Sweep). In the Side-to-Side, Drury *et al.*, (MS) describe the female posture as intermediate between a crouch and Head-forward (Myres, 1959a) of the male, and that in the Sweep a female threatens a rival male. I observed an individual (F Y) with similar behaviour to the above patterns. This female adopted a crouched posture while fairly stationary and close to her mate engaged in a threat encounter with a neighbouring male. As her mate dove she called and stretched her neck in response to the approach of a rival male in the Head-forward posture. I did not distinguish between the Side-to-Side and Sweep.

b. Male

The most common male display is Head-bobbing (Myres, 1959a), perhaps more correctly termed Oblique-pumping (Johnsgard, 1965).

Three sequences of display, that apparently function to maintain the pair bond, occur on the breeding grounds. The first is an approach flight and/or approach swim - Head-bobbing - Leading (Myres, 1959a) with or without Lateral Head-turning and Bill-pointing (Johnsgard, 1965) by the male to the female, and Following by the female. Bill-pointing, the rapid bill movements by a Leading male back towards the female Following, has been termed Pecking (Myres, 1959a) or Ticking (Drury *et al.*, MS). I observed this sequence throughout the breeding cycle more often than those below.

The second sequence by a male is the Display Flight (Fly-over-Landing) - Headshake-forwards - Wing-lifting - Head-bobbing

(Myres, 1959a). Myres (1959a) states that Wing-lifting is sometimes not performed in the sequence but it always precedes high intensity Head-bobbing. Johnsgard (1965) reports that the Folded-wings-lifted posture (Wing-lifting) sometimes briefly interrupts Oblique-pumping, and then the latter display is usually resumed. He does not link Wing-lifting in the Display Flight sequence, instead he describes Short Flights ending in Wing-flaps (my sequence three). On a few occasions I saw Head-bobbing punctuated by Wing-lifting, but my observations agree more with those of Myres' since Wing-lifting was mostly seen in the Display Flight sequence preceding Head-bobbing, rather than following it. My 1974 observations of paired colour-marked females suggest that the Display Flight sequence with Wing-lifting mostly occurs during the prelaying and laying periods, and that the first sequence above is the more frequent one during the incubation period.

Johnsgard (1965) described a third sequence by a male as ritualized Short Flights followed by Wing-flaps as he lands near a female. I frequently observed this sequence especially after intra- and interspecific aggressive encounters. A male also performs this sequence of behaviour patterns in the absence of his mate, suggesting that the first two sequences have a more specific function in pair maintenance, whereas the third sequence has a more general function, perhaps in maintenance of space.

Other pair-maintaining displays are Crest-erection (Myres, 1959a) by males, and Diving-as-a-pair (Erskine, 1972). The latter display was seen more often during prelaying than during any other stage of the breeding cycle. Finally, evidence that copulatory

behaviour functions to maintain the pair bond is presented later.

Analysis of the frequency of these displays in various situations and in relation to the breeding cycle is needed to clarify their function in regards to maintenance of the pair bond.

2. Copulatory Behaviour

The female assumes a Prone posture while the male performs two precopulatory displays: the Water-twitch and Preen-dorsally. Then the male mounts the female, waggles the tail from side to side during copulation and may give a Wing-flick (Flick-of-the-wings) about the time of intromission. The sequence of post-copulatory behaviour is Rotations by the pair, then male Plunge and/or Splash-bathe, Upward-stretch, Wing-flap and Tail-wag, while the female bathes, and gives upward-stretch, wing-flap and tail-wag (Myres, 1959a; 1959b).

My observations agree with Myres (1959a; 1959b) and Johnsgard (1965) that Water-twitch is more frequent than Preen-dorsally. The sequence of copulatory behaviour I saw in June 1974 contradicts Erskine's (1972:33) statement that the two pre-copulatory displays "are each repeated several times, in no particular sequence". I observed that Water-twitch initiated the sequence and was followed either by Preen-dorsally, or mostly by one or more Water-twitches, then Preen-dorsally, and this sequence may be repeated one or more times. Water-twitch preceded and followed each Preen-dorsally. Mounting was preceded by the Water-twitch. Wing-flick was not seen. Post-copulatory behaviour varied among individuals. Pair Y performed faster Rotations than either pair W or pair B. The mate of F Y usually Splash-bathed with no Plunge, whereas M W and M B mostly Plunged.

Myres (1959a; 1959b) mentions that first attempts at mounting

on 2 of 12 occasions and apparently successive attempts were unsuccessful as Rotations and male Plunge were not seen. I observed many copulations in which the first attempt was unsuccessful, but most of these were followed by a successful copulation. When a male slipped off the back of a female with no Rotation or Plunge, he usually quickly gave either a Water-twitch, or Water-twitch - Preen-dorsally - Water-twitch followed by a successful mounting and post-copulatory behaviour. Copulatory behaviour in relation to space and time is dealt with later.

Intraspecific Agonistic Behaviour

In describing the agonistic behaviour of male buffleheads I have again capitalized ritualized behaviour patterns, such as the Head-forward posture, which are distinguished as displays by Myres (1959a) and Johnsgard (1965). I have not considered as displays any agonistic behaviour patterns that involved movement toward or away from an opponent (such as in an approach - withdrawal encounter) or behaviour patterns involving pure attack and escape elements (such as supplanting attacks, retreats, fighting, flap-paddle chasing on the water surface, and aerial pursuits). Therefore these behaviour patterns have not been capitalized.

With the exception of the Head-forward posture (Myres, 1959a), descriptions of agonistic behaviour have been brief, incomplete and mostly associated with pair-formation (Myres, 1959a; Erskine, 1972; Drury *et al.*, MS).

Agonistic behaviour patterns in relation to space will be described in terms of encounters between males. An encounter involving two paired males refers here to a continuous sequence of agonistic behaviour that ends when one male engages in other activity such as Wing-flap Display,

preening, swimming or flying away from his opponent. Encounters involving males were classified into five categories according to their intensity and sequence of behaviour patterns, and further subdivided according to the number and sex of other individuals involved. Agonistic behaviour is described below in order of increasing intensity.

1. Approach - Withdrawal

a. Male - male encounters

These encounters, either between paired males or a paired and an unpaired male, occur mostly within or near a boundary zone when the approach of one male results in prompt withdrawal or avoidance by another male. The most common form of approach - withdrawal is swimming and diving. Only the approaching male may assume a Head-forward posture unlike threat encounters where it is performed by both males.

Approach flights were distinguished when one bird flew toward and landed short of its opponent or its position, before the latter escaped, usually by a retreat flight or retreat swim underwater. When an unpaired male flew over the pair-space of a paired male the latter often made a short approach flight and landed as the intruder flew out of his pair-space.

b. Pair - male encounters

i. Paired male - pair boundary encounter

When a paired male swims and dives toward a neighbouring female or pair within or near a boundary zone, the male with the female withdraws by rapid Leading with his mate Following.

ii. Unpaired male - pair encounter inside the pair-space of the pair

This encounter occurs when an unpaired male performs the Display Flight sequence close to a paired female with her mate. The paired male responds by Leading his mate away and she responds by Following. The paired male may then attack the unpaired male.

2. Threat

Reciprocal threat encounters occur mostly between two paired neighbouring males along a boundary zone, but sometimes involve an unpaired male or three males. A male approaching a boundary zone by either swimming and diving and alternately surfacing in the Head-forward posture, or especially by an approach flight, provides a visual stimulus for a neighbouring male to respond with a similar approach and then a threat encounter ensues. Opponents then face each other in the Head-forward posture and maintain an individual distance of 20 to 30 m by diving attacks and escapes back and forth along a boundary zone. If the attacker C in the Head-forward posture turns and dives toward its opponent, the attacked D usually responds by an escape dive and retreat swim underwater either laterally or directly away from C. Both birds usually surface in the Head-forward posture. C usually responds in one of three ways: 1) C dives in escape in response to D's attack dive; 2) C turns and/or swims away from D and C responds by approach swimming and diving; or 3) when D escapes laterally C may dive in attack. In this way attack and escape movements may continue from 1 to 5 minutes, sometimes longer.

One bird usually ends an encounter by an avoidance flight or by swimming away and preening for a minute or more. Threat display along a boundary zone may be interrupted by momentary preening or wing-flick for

a few seconds and then be resumed.

During threat encounters I confirmed that interacting males capture invertebrates during diving because on many occasions they surfaced with green animals, presumably Chironomidae larvae, in their bills and mouthed them on turning away from their opponent. Feeding was especially noticeable when individual distance was maintained at 30 m or more. Presumably this feeding was displacement activity, but the possibility that it was functional cannot be excluded. Sometimes in encounters between paired males, one male remains close to his mate while she feeds and either performs quick shallow dives or remains in the Head-forward posture or crouched in response to his opponent's diving.

3. Attack - Retreat

This encounter is initiated when the attacker makes a supplanting attack directly at an intruder. The bird attacked retreats and the aggressor occupies its vacated or a nearby position a moment later. One attack is often sufficient to expel the intruder, but if it only retreats a short distance, the attacker makes repeated attacks until the trespasser flees from the pair-space. Retreat by the attacked ends the encounter. There is no aerial pursuit.

Three types of supplanting attacks can be distinguished, the attack underwater, attack rush and aerial attack, which increase in intensity from low to high, respectively. The bird attacked responds by escape dive and retreat swim underwater, retreat rush or retreat flight. All these responses were recorded for each intensity of attack. For example attack flight by the attacker usually elicited retreat flight by the attacked but sometimes the latter made an escape dive or retreat

rush to avoid an attack flight. Attack flights varied in length from 10 m to 100 m.

Most supplanting attacks were by paired males directed at unpaired males that intruded well within the pair-space of the former. Established paired males rarely intruded into their neighbour's pair-space much beyond the boundary zone. A supplanting attack by a male at a female is described later.

4. Fighting

Hinde (1952) and Marler (1956) used the term fighting to include both supplanting attacks (with no contact between individuals) and combats (with contact). Raveling (1970) and Ridpath (1972a) used fights to refer to situations where only contact occurs. An intermediate situation to the above is fighting in blue-winged ducks which McKinney (1970) describes as mainly posturing and attack lunges with little contact. Similarly in male buffleheads I use fighting to refer to reciprocal attacks at close quarters whether contact is seen or not. Contact is not conspicuous in underwater fighting, but is clearly seen during fights on the surface of the water when one bird sometimes seizes another.

Munro (1942) and Erskine (1972) each saw one fight, apparently associated with pair-formation. Myres (1959a) reports that threat may lead to fights but gives no description. Thus fighting has been rarely seen, and has not been described in any detail nor in relation to space.

Fighting between neighbouring males occurred in four situations according to their position in relation to boundary zones, and involvement of females.

a. Male - male encounters

i. Boundary fights

These fights, mainly between paired males, but also between a paired and an unpaired male, were seen often but much less frequently than threat. Most fights follow threat encounters and occur within a boundary zone when individual distance is reduced rapidly to 10 m or less. Opposing birds dive in attack and a fight erupts underwater accompanied by vigorous splashing and wing thrashing with the birds mostly submerged. Presumably contact often occurs underwater. When the combatants surface, one bird sometimes has hold of the tail, back or a wing of its opponent which vigorously flaps away to get free. When the attacked bird breaks free it may continue fighting or flap-paddle in retreat prompting its opponent to initiate a flap-paddle chase (described later). Males fighting on the surface of the water constantly change positions and repeatedly miss contact as they lunge at each other and jab down with open bills. During flap-paddle chases the pursuer sometimes grabs the pursued by the tail or back. Fights usually last less than a minute. Fighting encounters usually end with both males side by side giving an appeasement display then the Wing-flap Display (both described later).

ii. Fights inside a neighbour's space

A male, chasing an unpaired male out of his pair-space or attacking other species of ducks, may suddenly land within his neighbour's pair-space or within the boundary zone. In [redacted]e, the occupant promptly launches an aerial attack

directly at the intruder and fighting follows if the latter does not flee.

b. Pair - male encounters

i. Pair attacked inside their own space by male intruder

When a rival male directs an attack flight at a neighbouring female inside her pair-space, one response by her mate is to fly over in defence, intercept his opponent's attacks and fight with the intruding male.

ii. Intruding pair attacked inside their neighbour's space by resident male

A female intruder inside her neighbour's pair-space releases an attack flight by the resident male. The mate of the attacked female, if not by her side, flies over to defend her, and a fight between the males may break out.

c. Flap-paddle chasing

These chases between two males can be included as fighting because they often interrupt or terminate boundary fights and three-bird encounters within a pair-space. A flap-paddle chase refers to two males, one in pursuit of the other, rushing and flap-paddling with their wings over the water for a short distance. When the attacker makes a rush or lunges with open bill at an opponent, the attacked may flap-paddle in escape prompting the attacker to initiate a flap-paddle chase.

5. Aerial Pursuit Between Two Males

a. Paired male - unpaired male

In most aerial pursuits a paired male chases an unpaired male. When an unpaired male flies low with intent to land, or

lands within the pair-space of a paired male, the latter usually launches an immediate aerial attack and aerial pursuit of the intruder in retreat flight. The pursuing male breaks off the chase and lands near his boundary zone as the trespasser flees from his pair-space.

b. Paired males

Aerial pursuit is infrequent between established paired males. In contrast, aerial pursuits are frequent, energetic and long lasting when one male is re-establishing a pair-space after a temporary absence of several days because of disturbance or exclusion. In vigorous aerial pursuits the pursuer opens its bill and occasionally grabs the tail of the pursued in flight and they often plunge into the water.

6. Three-bird Attack and Pursuit Encounters

a. Pair - paired male neighbours

When an intruding paired male attacks a neighbouring female of a pair her mate flies over to defend her. Tactics preceding attack are as follows. During threat encounters between two paired neighbouring males C and D, male C swims and dives away from pair D and male D follows without his mate. Then male C dives toward female D, so that male C surfaces closer to female D than male D. When male D dives, male C (instead of diving in response) directs an aerial attack at female D while her mate is underwater. Counteracting tactics by the male of a pair are to stay close to his mate during threat encounters and to dive shallowly and surface quickly, so that he can fly to his mate and intercept any attacks by his opponent before the female takes flight. The attacked female dives

or lashes in escape, but also flies in retreat especially when her mate is slow to defend her. A three-bird pursuit-flight occurs when the female takes flight pursued by the attacking male with her mate following. During high intensity pursuit-flights the attacking male lunges at the female of a pair in the air, and when her mate catches up to them he buffers the attacks by constantly positioning himself between his mate and the attacker. Females appeared to be much more manoeuvrable in the air than males, so the attacking male rarely succeeded in grasping a female. The attacked pair may be temporarily forced off the pond but a tenacious female soon returns.

In high intensity three-bird encounters on the water, the attacker (male C), after making an aerial attack, repeatedly lunges at female D while her mate (male D) continually tries to intercept the attacks. Fighting often erupts between the two males. At the end of a fight the mate of the attacked female flies over to her, performs rapid Leading and she responds by Following. If the three birds land together after a pursuit-flight, the defender (male D) also performs rapid Leading with his mate Following. If the attacker still remains near the pair after Leading and Following, either at the end of a three-bird flight or a three-bird encounter on the water, the mate of the female usually dives in attack underwater. Male C usually responds with a retreat flight, but may flap-paddle in retreat prompting male D to initiate a short flap-paddle chase before male C flies in retreat to his pair-space.

Low intensity three-bird encounters occur on the water between established pairs. Male attacks at a paired female are not

persistent or vigorous and are inhibited when her mate flies over to defend her, and performs Leading with his mate Following. The sequences of behaviour patterns in high and low intensity three-bird attack and pursuit encounters are shown in Figure 7.

Three-bird pursuit-flights may also occur shortly before a resident pair flies toward the nest site. When the pair take flight and circle the pond, a neighbouring male flies up in attack and sometimes forces the pair to land again.

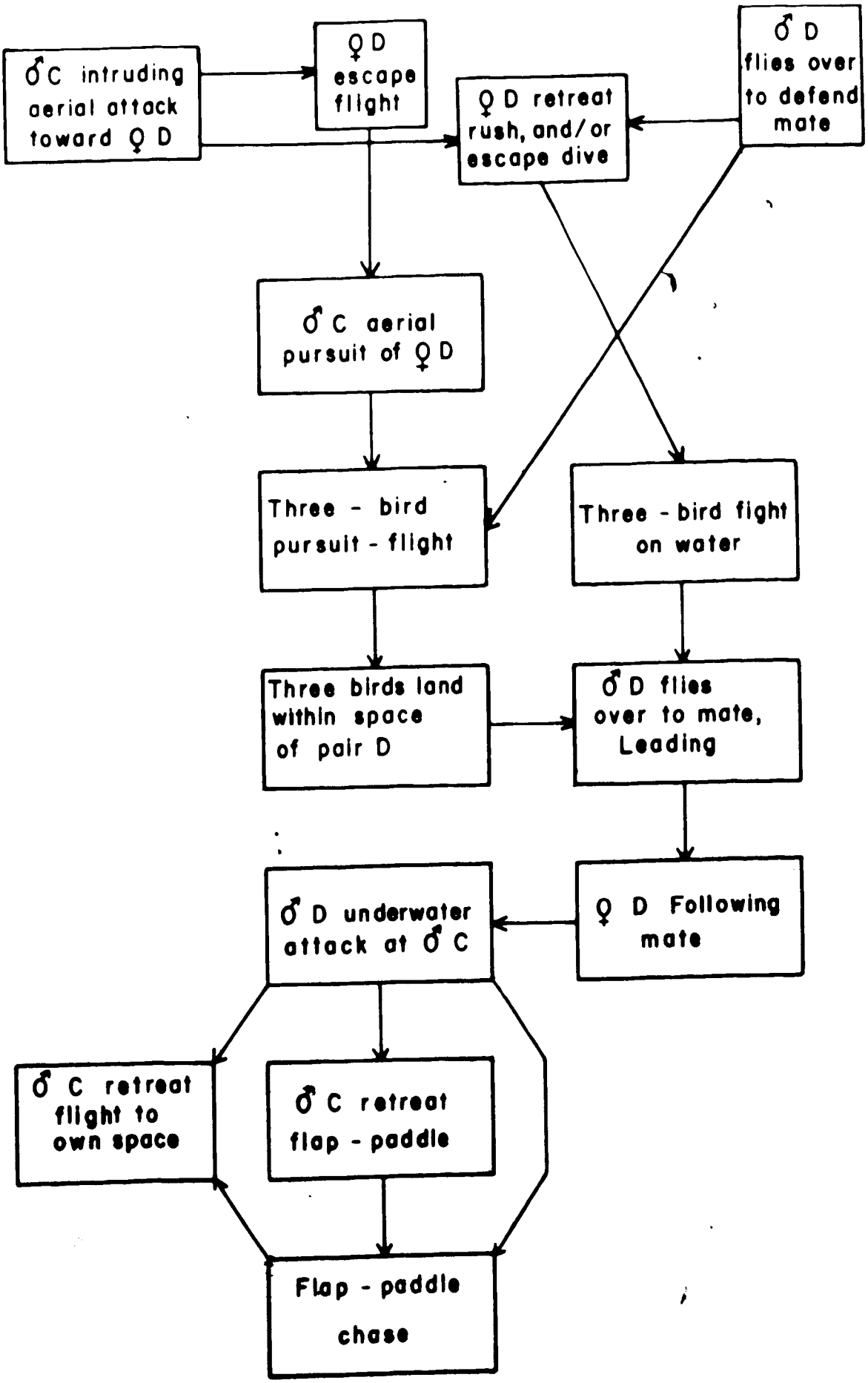
b. Strange pair - neighbouring male

A three-bird pursuit-flight occurs when a strange pair attempts to settle on a pond already occupied by resident conspecifics. As a strange pair flies over a pond and attempts to land in a pair-space, one resident male after another repeatedly chase the strange pair from their pair-spaces until eventually the strange pair leaves the pond.

7. Appeasement Display

Males give an appeasement display during fighting on the water. Two males cease attacking and orient themselves alongside each other in a parallel posture with the head forward, wings flicking and tail elevated. One bird, usually the loser of an encounter, turns his head away and they both swim apart. This appeasement display which I shall term Facing Away (after Tinbergen, 1959) serves to conceal the bill (fighting weapon) and inhibit attack (Cullen, 1957). The bird that initiated Facing Away swims away and may glance back at its opponent, who sometimes makes an attack rush. Another short fight or flap-paddle chase may occur, or the attacked male dives and retreat swims underwater before both birds swim apart and end the encounter. Similarly in the

Figure 7. Sequence of behaviour patterns in attack and pursuit encounters among a paired male and a neighbouring pair.


♂C intruding aerial attack toward ♀D
♀D escape flight
♀D retreat rush, and/or escape dive
♂D flies over to defend mate
♂C aerial pursuit of ♀D
Three - bird pursuit - flight
Three - bird fight on water
Three birds land within space of pair D
♂D flies over to mate, Leading
♂D underwater attack at ♂C
♀D Following mate
♂C retreat flight to own space
♂C retreat flap - paddle
Flap - paddle chase

kittiwake (*Rissa tridactyla*) Cullen (1957) observed that attack is not appeased completely and may continue on an opponent or be redirected at a mate.

The Facing Away appeasement posture is widespread among gulls (Moynihan, 1958; Tinbergen, 1959), but, except for Myres (1959a), appeasement display has not been described for ducks (Lorenz, 1951, 1952, 1953; McKinney, 1961, 1970; Johnsgard, 1965). In Canada geese (*Branta canadensis*) Raveling (1970) describes a Submissive posture which "serves the functions of identifying single geese, allowing approach, habituation, and ultimately pair formation" and "also serves to prevent violent attacks".

In bufflehead the Upward-stretch and Wing-flap following fighting and occurring during pair-formation were considered by Myres (1959a:186) to be an appeasement display. After fighting male bufflehead Face Away and do not perform the Wing-flap until they are well apart from each other. Thus it is unlikely that the Wing-flap Display would serve to inhibit attack at close quarters and therefore should not be considered an appeasement display.

8. Wing-flap Display

This display usually, but not always, terminates fighting, attack and pursuit encounters. The sequence of display components is Splash-bathing (Head-dipping - Wing-ruffling) - Upward-stretch - Wing-flap - Tail-wag. In male - male encounters Wing-flap seems to be usually initiated by the loser, then performed by the winner. In some situations, regardless of whether an apparent loser flies to his mate or stays near his opponent, the winner Wing-flaps first. Thus initiation of the Wing-flap is not a reliable indicator of the outcome of an

encounter. Further study of the context of the Wing-flap is needed before it can be used in predicting outcome.

Part II. Agonistic Behaviour in Space and Time

Introduction

These results deal firstly with selection of a particular part of a study pond by buffleheads and then emphasize the spatial-temporal relationships between and within pairs on these ponds.

The space occupied by four colour-marked adult females in successive years suggests that selection of a particular part of a pond may be initiated by the female of a pair. Three marked paired females returned to Pond J in 1974. Only one of these (F W) occupied the pond as a resident nesting female in 1973. The other two females (F B and F Y) were first resident on Pond J in 1973 as females with broods. In 1974 pair B arrived first and settled on the same space (east-end bay) selected by F B with a brood in 1973 (compare Fig. 10 - Map 1 and Fig. 20 - Maps 1 to 9). Pair W arrived next and settled nearest pair B's space, rather than in the north-west bay occupied apparently by two transient pairs (Fig. 10 - Map 1), perhaps because F W preferred to settle nearest the east-end bay which she occupied as a nesting female the previous year. On arrival F W repeatedly trespassed into the east-end bay strongly suggesting she preferred this space. Pair Y arrived last and settled in the north-west bay, the core area of the space occupied by F Y with a brood in 1973 (compare Fig. 10 - Map 2 and Fig. 20 - Maps 1 to 9). On Pond H in May 1974 a paired female (F R-W) settled on the same space she occupied while nesting and with a brood in the previous year. Thus the most important factor in selection of a particular pair-space appears to be the female's previous familiarity with it either while nesting or with a brood. Moreover, a female that successfully raises a brood on a particular pond or space may have a

stronger tendency, than a female that is unsuccessful, to return there as a nesting female the following year. Of the four marked females that returned to the study ponds in 1974, only F W failed to rear a brood in 1973. However, the nest cavity used by F W in 1973 was occupied the previous year by an unmarked female which arrived at Pond J with a brood of 12, nine of which apparently survived to fledging. Adult female buffleheads show a strong tendency to use the same nest cavity at least in two successive years (Erskine, 1961; 1972) and to return to the same ponds used previously (see above). Although F W deserted her clutch in 1973, it seems highly likely that this unmarked female that successfully reared a brood in 1972 and used the same nest cavity as F W did in 1973, was in fact F W. Therefore all marked females that apparently selected a pair-space on the study ponds in 1974 probably successfully reared broods there in previous years.

Selection of a particular pair-space appears to be modified by environmental stimuli at the time of settling. The most important of these stimuli probably is the density and location of other bufflehead pairs in relation to the suitable bays of the pond. Other pond characteristics such as the shoreline vegetation and availability of food and loafing sites are possible additional cues that birds use in selecting a space.

On the evidence presented, the female initiates selection of the pair-space. However, it is possible that at times paired male buffleheads select the space, for example, M B(K) occupied the same space in successive years but may have merely followed his mate to the space that she had selected.

For a detailed quantitative analysis of spatial-temporal

relationships between and within pairs at least one member of each pair should be colour-marked, the precise stage of the breeding cycle known for each pair and for statistical purposes there should be a large number of interactions recorded. Only the 1974 data for Pond J met these conditions. Analysis of these data first should provide a framework for comparing data for other years and habitat types. Unless otherwise mentioned all data refers to that for Pond J in 1974. The 1973 data revealed variations in the nature of spacing systems and differences in social behaviour in relation to the environment. These data are included where appropriate.

Establishment of Space - Pond J 1974

1. Introduction

Early arriving pairs that acquire a space on a pond by settling do not always remain to breed (Table 3). None of the early arriving unmarked pairs became residents, even though one unmarked pair occupied the pond on April 29 (ice-free date) and at least two unmarked pairs settled there before F W arrived about 4 days later. Also on May 4, the day before F Y settled on the pond, three unmarked pairs were present but none of these became residents. Thus arriving first does not ensure that a pair will establish a space on the pond.

Next, only previously marked paired females became residents (Table 3). In 1973 F B and F Y each reared a brood at Pond J, while F W was resident on Pond J during the nesting period. So only those males mated to females with breeding experience on Pond J the previous year succeeded in establishing a space there in 1974. The unmarked pairs that left the pond may have been transients or were evicted by the resident males. Thus these unmarked pairs may have dispersed to

Table 3. Numbers of pairs of buffleheads on Pond J during the period of establishment from April 28 to May 8, 1974.

Date	Number of pairs observed	Colour-marked paired females present
April 28[a]	0	-
29[b]	2	B
30	2	B
May 1	3	B
2	2	B
3	4	B, W
4[c]	5	B, W
5[d]	4	B, W, Y
6	4	B, W, Y
7	3	B, W, Y
8	3	B, W, Y

[a]Pond J partially ice-free. Female B and mate seen at 2000 at bog Pond M.

[b]Ice-free date for Pond J.

[c]Female Y and mate seen at peripheral pond near J at 1830.

[d]0800 1 red-necked grebe, 2 bufflehead pairs (B, Y) on pond
0930 1 unmarked bufflehead pair arrived
1015 Pair W arrived

other ponds or remained in the Pond J area as the peripheral pairs.

How then do pairs establish and maintain a space? The behavioural mechanisms involved appear to be complex so these should be most clearly identified by a detailed analysis of changes in agonistic behaviour between individuals in relation to space, time and the breeding cycle.

Agonistic encounters were classified into five categories described earlier: 1) approach - withdrawal, 2) threat, 3) attack - retreat, 4) fighting, and 5) aerial pursuit. These encounters were further subdivided mainly into male - male and male - pair encounters. The number and category of these agonistic encounters between individuals over time for different combinations of members of pairs are given in Figures 8 and 9.

The location of agonistic encounters between individuals changed over time, sometimes daily, resulting in changes in boundary zones and size of pair-spaces of the residents (Fig. 10 - Maps 1 to 11). In 1974 inaccuracies were greater in plotting the location of encounters between M W and M Y than those between M W and M B. To check the location of encounters involving M Y, on one afternoon I determined the positions of M Y from the west side of Pond J, and these were in general agreement to those I plotted from the blind on the south side. Thus despite the above inaccuracies in plotting positions of birds, I believe the maps accurately reflect changing spatial relationships between individuals.

To determine how space is established these daily changes, especially from May 4 to 7, are analyzed in more detail, with emphasis on the frequency, intensity and locations of agonistic encounters

Figure 8. Frequency and intensity of agonistic encounters among two males and their colour-marked mates on Pond J during May and early June, 1974.

The numbers 1 to 5 correspond to the following 5 categories of male - male and male - pair agonistic encounters described in the text.

1. Approach - withdrawal
2. Threat
3. Attack - retreat
4. Fight
5. Aerial pursuit

The relative stage in the breeding cycle of each of the two marked females is presented parallel to the abscissa and indicated by the following letters.

P - prelaying period

L - laying period

I - incubation period

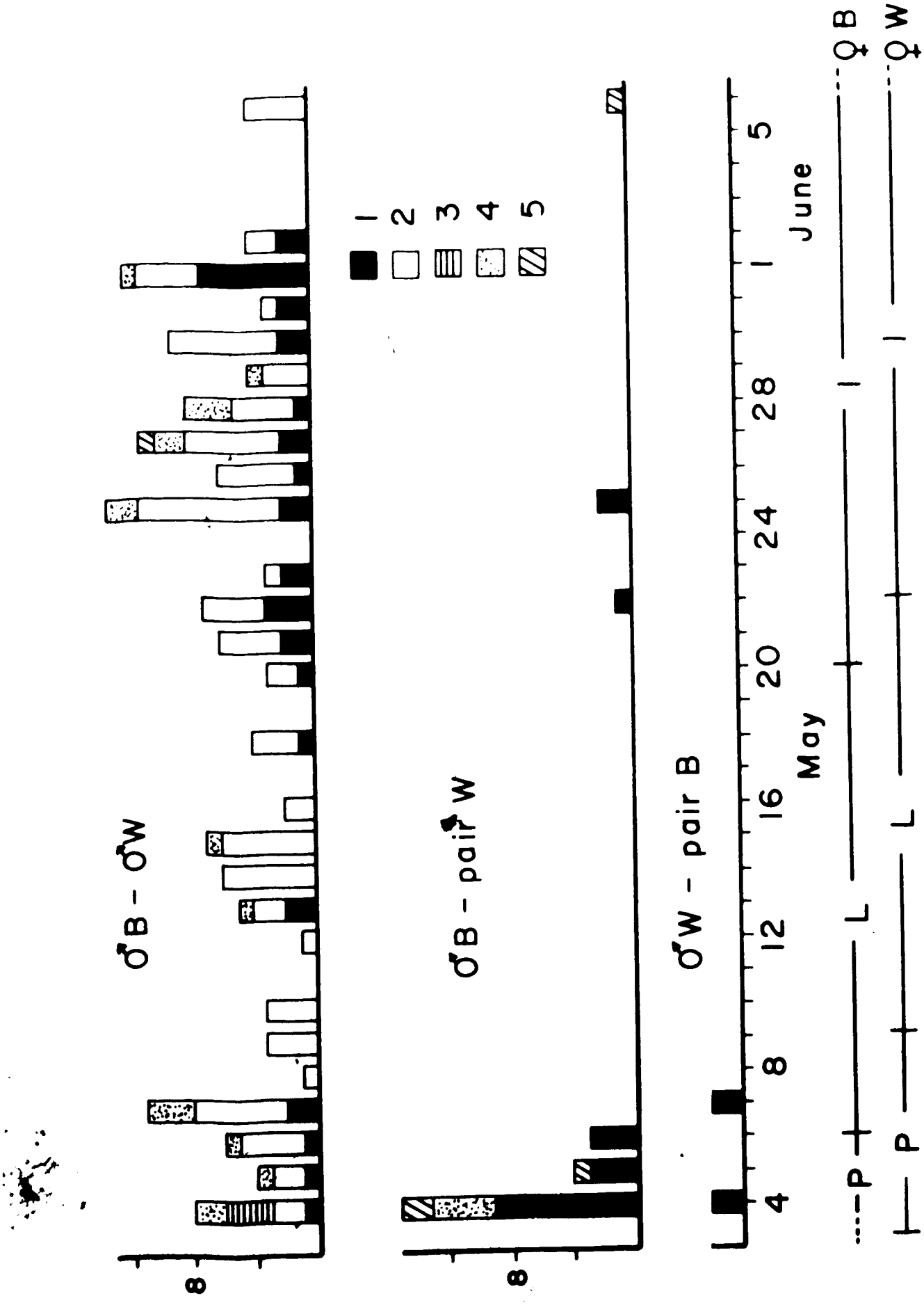

NUMBER OF ENCOUNTERS
♂B - ♂W
♂B - pair W
♂W - pair B
1
2
3
4
5
8
8
4
8
12
16
20
24
28
1
5
May
June
P
L
I
L
P
♀B
♀W

Figure 9. Frequency and intensity of agonistic encounters among two males and their colour-marked mates on Pond J during May and early June, 1974.

The numbers 1 to 5 correspond to the following 5 categories of male - male and male - pair agonistic encounters described in the text.

1. Approach - withdrawal
2. Threat
3. Attack - retreat
4. Fight
5. Aerial pursuit

The relative stage of the breeding cycle of each of the two marked females is presented parallel to the abscissa and indicated by the following letters.

P - prelaying period

L - laying period

I - incubation period

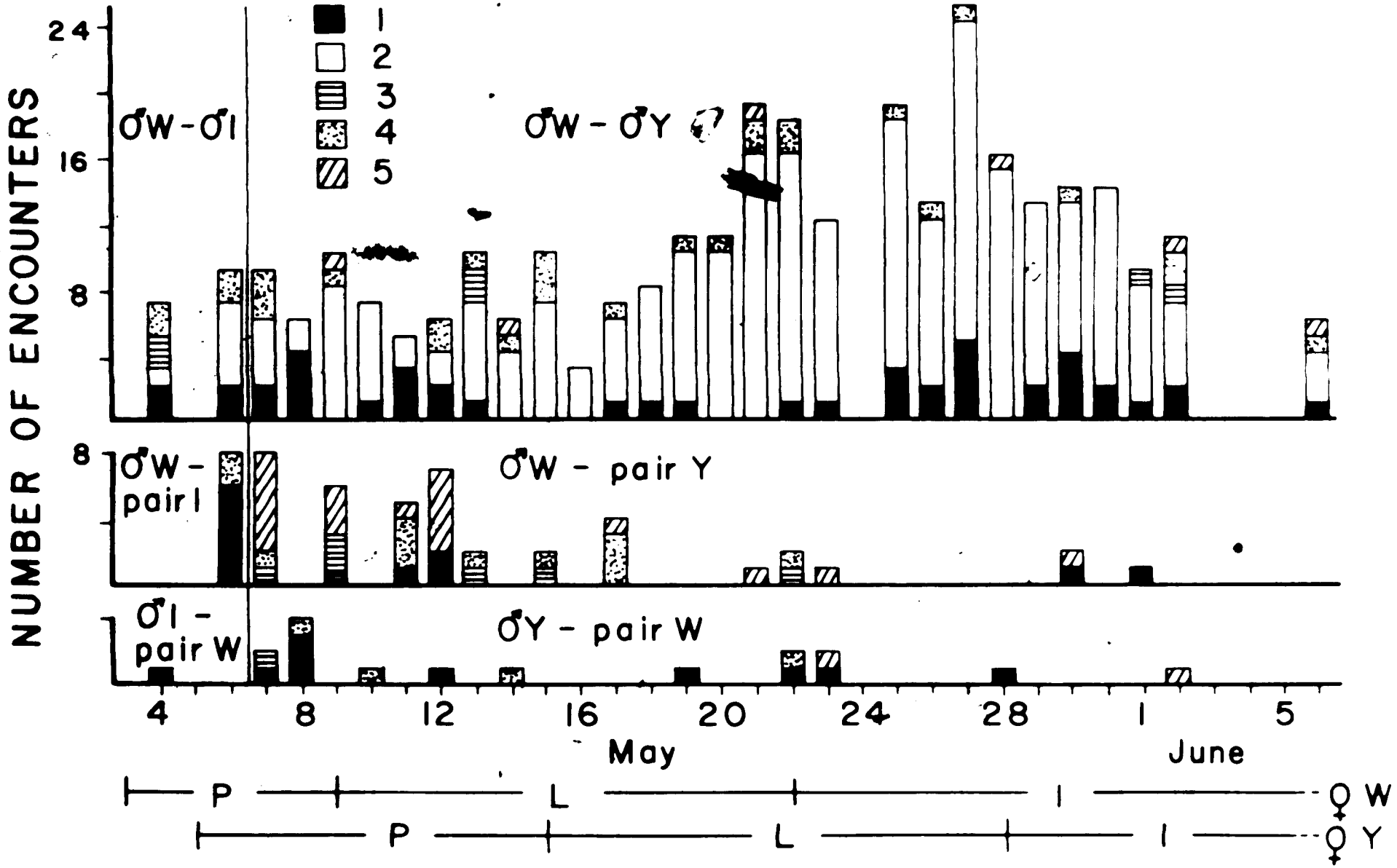

NUMBER OF ENCOUNTERS
24
16
8
1
2
3
4
5
♂W - ♂I
♂W - ♂Y
8
♂W - pair I
♂W - pair Y
♂I - pair W
♂Y - pair W
4
8
12
16
20
24
28
1
5
May
June
P
L
I
♀ W
P
L
I
♀ Y

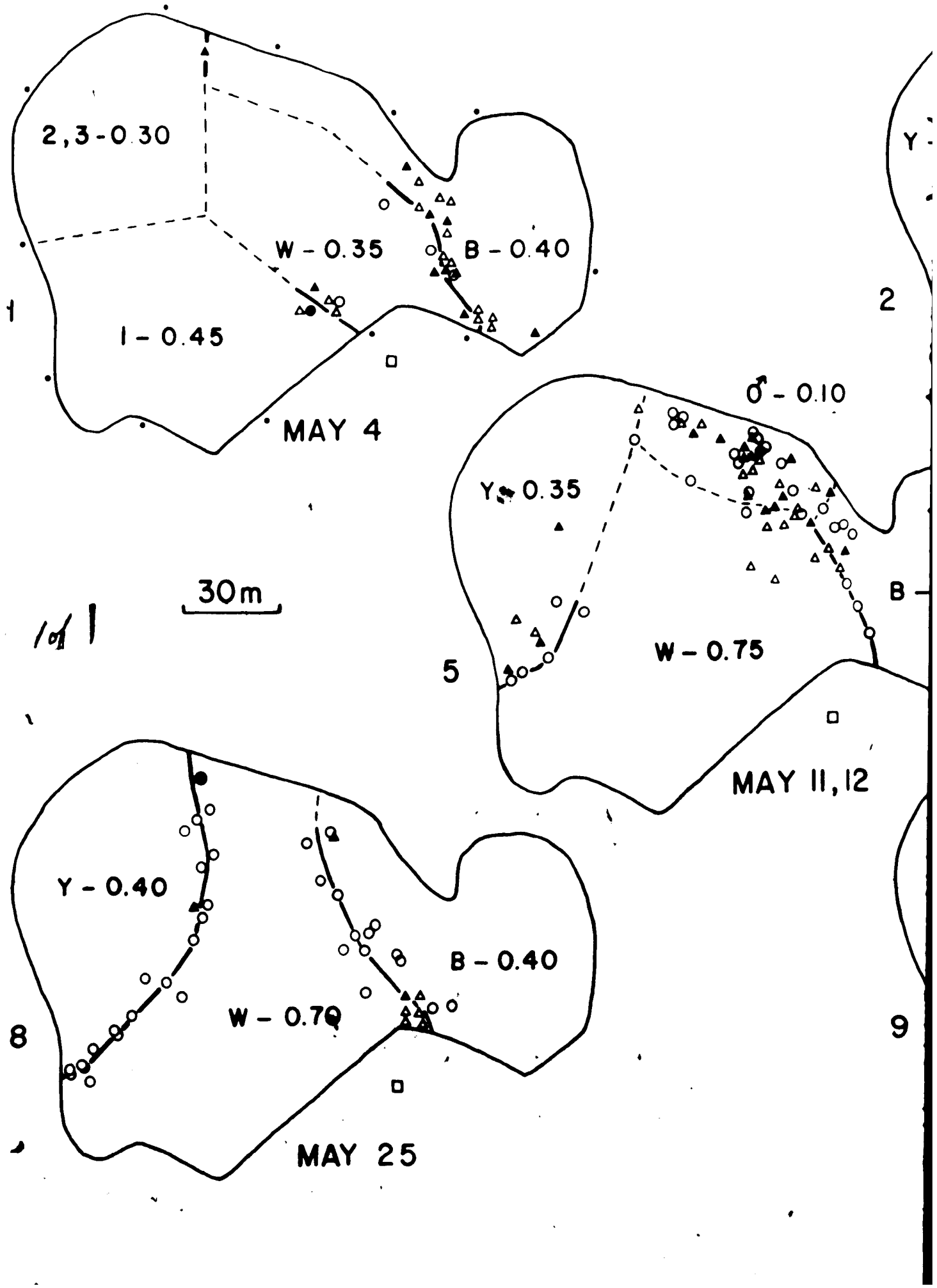
Figure 10. Spatial relationships among three resident males and their colour-marked mates on Pond J between May 4 and June 6, 1974.

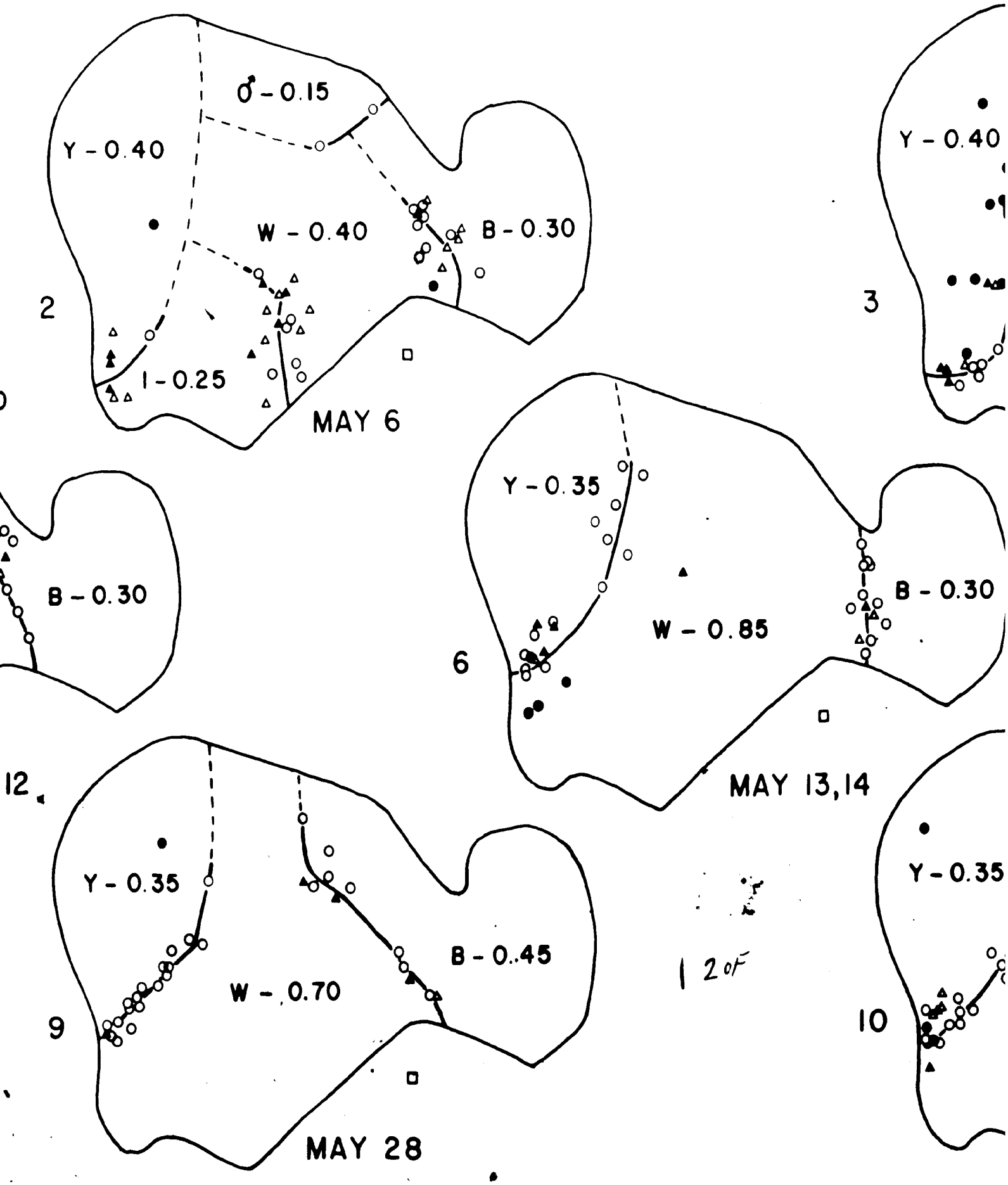
A male symbol, numbers or letters preceding decimal fractions and placed in each space on given days denotes the following individuals:

♂	unmarked unpaired male
1, 2 or 3	unmarked pairs
B, W or Y	females individually colour-marked with nasal saddles and their respective mates
B	female blue and her mate
W	female white and her mate
Y	female yellow and her mate

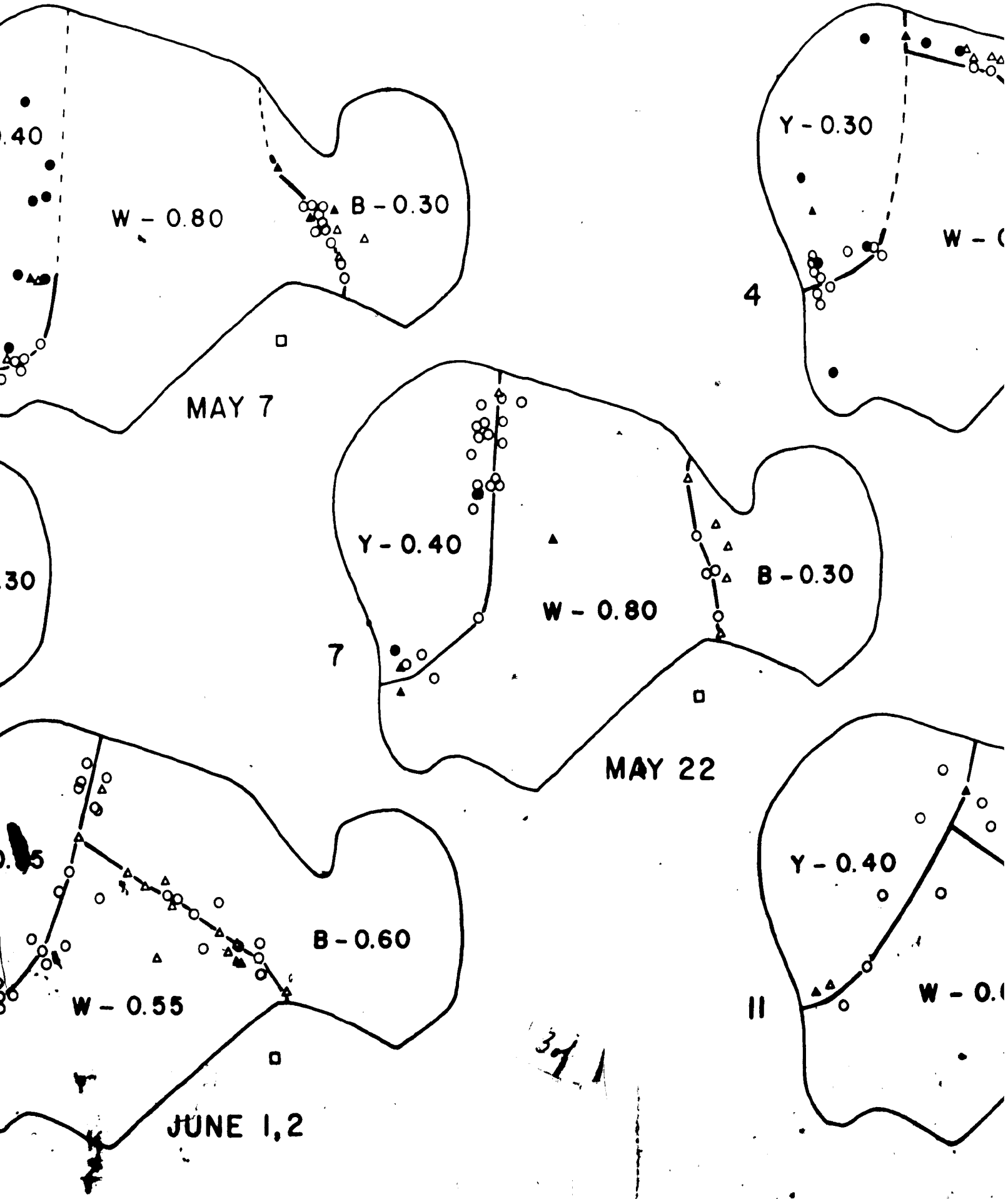
Decimal fractions following the above prefix represent the area of space expressed to the nearest 0.05 hectare (ha), held by each pair or individual on given days. For example, B-0.40, indicates a space of 0.40 ha held by pair B.

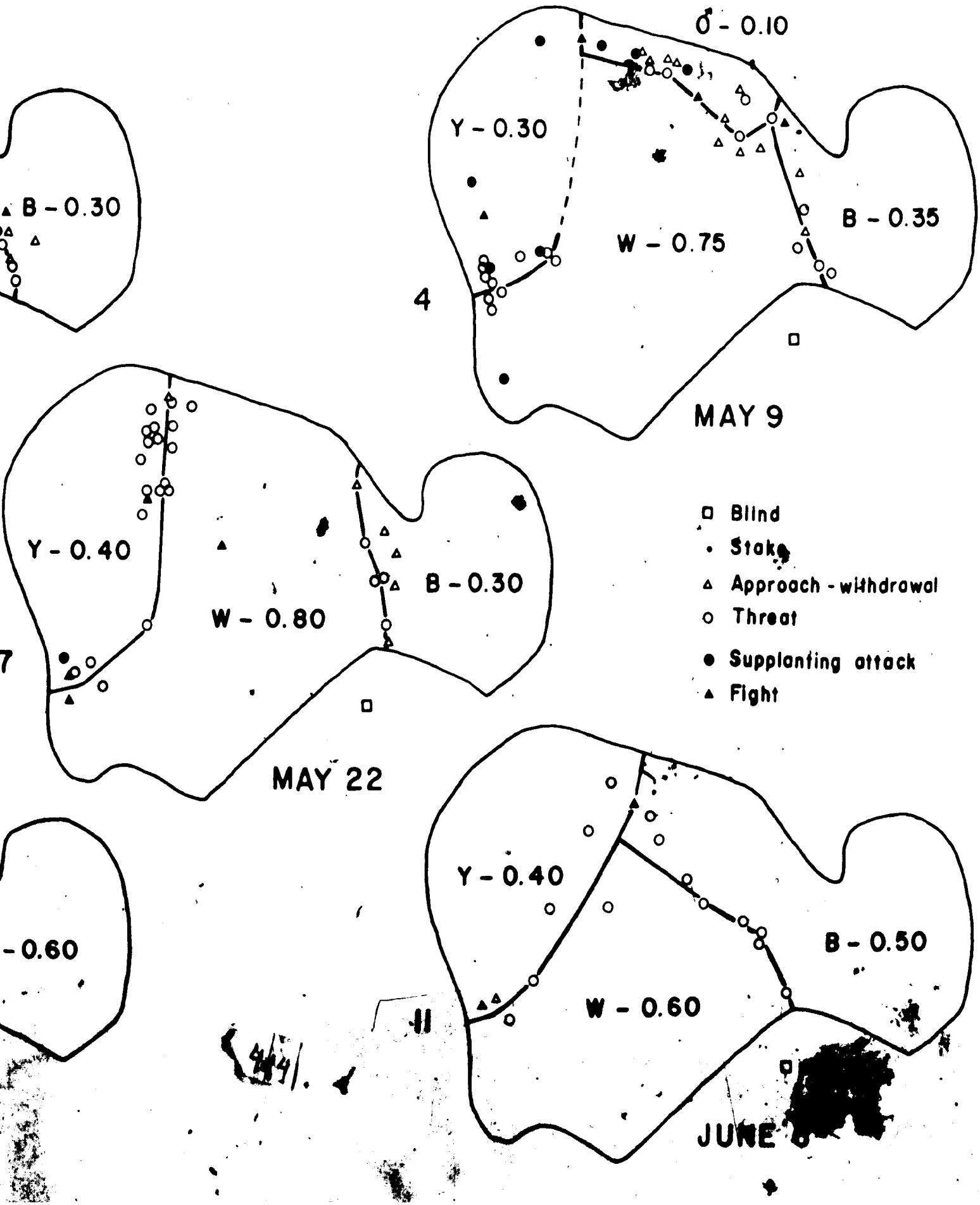
Solid lines are boundaries based on locations of interacting males engaged in threats and fights especially, and other agonistic encounters. Dashed lines are boundaries estimated from movements of individuals.


2,3-0.30
W - 0.35
B - 0.40
1
1 - 0.45
MAY 4
♂ - 0.10
Y - 0.35
30m
1 of 1
5
W - 0.75
MAY 11, 12
Y - 0.40
B - 0.40
W - 0.70
8
MAY 25
2
9


♂ - 0.15
Y - 0.40
W - 0.40
B - 0.30
2
I - 0.25
MAY 6
3
Y - 0.40
B - 0.30
Y - 0.35
W - 0.85
B - 0.30
6
MAY 13,14
12
Y - 0.35
B - 0.45
W - 0.70
9
MAY 28
Y - 0.35
10

1 2 of


.40
W - 0.80
B - 0.30
MAY 7
Y - 0.30
4
W - (
.30
Y - 0.40
B - 0.30
W - 0.80
7
MAY 22
Y - 0.40
B - 0.60
W - 0.55
JUNE 1, 2
11
W - 0.(


♂ - 0.10
Y - 0.30
B - 0.35
W - 0.75
4
MAY 9
B - 0.30
Y - 0.40
B - 0.30
W - 0.80
7
MAY 22
Blind
Stake
Approach - withdrawal
Threat
Supplanting attack
Fight
-0.60
Y - 0.40
B - 0.50
W - 0.60
11
JUNE

between individuals. Changes in size of space and agonistic behaviour in relation to the stages of the breeding cycle are emphasized later.

The establishment period was recognized as that interval from the arrival of breeding pairs to the establishment of stable boundary zones and the division of the open water area of the pond among the pairs. These conditions appear to be satisfied by May 7 (Fig. 10 - compare Maps 2 and 3), but from May 8 to 12 an unpaired male was again resident on the pond (Fig. 10 - Maps 4 and 5). Thus the pond was not totally divided up among the pairs until May 13 (Fig. 10 - Map 6) when the unpaired male was no longer resident. Therefore from April 29 to May 12 was chosen as the establishment period.

2. Interactions Among Paired Males

From pair B's arrival on April 29 to May 3, when pair W probably arrived, there was little aggression between the pairs. On May 4 hostility between pairs rose steeply as the newly arrived pair W challenged mostly pair B. There were ten fights involving M W, eight with M B and two with an unmarked paired male (M 1), more than any other day (Figs. 8 and 9). On May 4 F W repeatedly intruded into pair B's space resulting in more M B - pair W encounters than any other day (Fig. 8). Of eight M B - M W fights, six were caused by F W's position in space and two of these ended in a three-bird pursuit-flight. Even though pair W usurped some shoreline from pair B (Fig. 10 - Map 1), M B resisted the intrusion of pair W.

On May 5 the lull in interactions probably reflects the arrival of a red-necked grebe on the pond and the absence of pair W for nearly half the observation period. This grebe was gone from the pond by May 6.

On May 6 M W diverted aggression away from pair B to pair 1. Male W was involved in almost twice as many encounters with M 1 than with M B. There was only one fight between M W and M B, but four fights between M W and M 1. Male Y had three fights with M 1, so increased pressure from both neighbouring males was applied against M 1 (Fig. 10 - Map 2, Figs. 8 and 9). Pair 1 left the pond sometime between 1800 on May 6 and 0800 on May 7. Their departure probably resulted from increased encroachment and aggression toward them at both their boundary zones with neighbouring pairs, particularly the boundary zone with pair W, because pair 1's space and shoreline was about halved from May 4 to May 6. Thus pair W's strategy to expand their shoreline was first to encroach and exert pressure on pair B's boundary zone, and when this met with resistance, to apply pressure on their other neighbours.

On May 7, with the departure of pair 1, not only did M W interact more with M Y (19 encounters) than with M B (13 encounters), but the category of encounters differed markedly (Fig. 10 - Map 3, Figs. 8 and 9). Of the 13 encounters involving M B nearly all (11) were male - male, mostly threat. However, of 19 encounters involving M Y nearly half (9) were male - male. Only two of the 13 encounters involving M B were male - pair (M W - pair B), whereas more than half of the encounters involving M Y (10) were male - pair. Male W initiated all eight M W - pair Y encounters, by intruding aerial attacks at F Y. Six of these aerial attacks resulted in three-[illegible] pursuit-flights, because M Y was too slow to defend his mate nevertheless each time F Y returned to her space. Pair Y was forced off the pond once but soon returned. Female Y's strong tenacity to her pair-space probably

resulted largely from her previous experience with it. A female without previous breeding experience on the pond may have been less tenacious and more easily driven off the pond.

From May 8 to 12 (Fig. 10 - Maps 4 and 5) the increased hostility against the resident unpaired male by the paired males is described later. Among the paired males from May 8 to 12 (Figs. 8 and 9) there were few M B - M W encounters. Male W continued a high level of aggression toward F Y up to May 12, when I believe F Y entered a suitable nest cavity for the first time since her arrival. It is noteworthy that M W initiated attacks at F Y on May 9 and 11 when M W's mate was away from the pond, but not on May 8 and 10 when M W remained close to his mate on the days before she laid eggs. The fewer three-bird pursuit-flights reflects M Y's defence of his mate on the water. The high number of pursuit flights on May 12 are of a different nature. These were all initiated by M W while pair Y engaged in nest-searching flights and were not initiated by aerial attacks at F Y on the water. On May 10 M Y first made an intruding aerial attack at F W.

3. Locations of Paired Male Encounters

Paired males established wide boundary zones within which they interacted mostly by threat and fighting encounters. These zones were not fixed in space over time but sometimes changed from day to day. However, for any given day boundary zones were relatively stable because the locations of almost all male encounters were clustered along a definite boundary zone; most encounters occurred near the shoreline (Fig. 10 - Maps 1 to 6). The width of the zone was determined by the location of encounters which varied according to the position of the encroaching individual and the response of and distance to its opponent.

Paired males initiate aerial attacks at the female of a neighbouring pair, whereupon the mate of the attacked female flies over to defend her. The approach of a neighbouring paired female or pair may elicit attack by a neighbouring male. Thus even within boundary zones the position of agonistic encounters could result from defence of a mate or defence of a space. One way to distinguish between these two types of defence is to know the position in space of paired females in relation to their interacting mates, and to know the position in space of the birds that release aggression. Three examples were chosen to illustrate clearly the position of paired females in relation to their interacting mates and the boundary zones (Fig. 11). These examples occurred on May 4 when pair W actively challenged pair B both by deep intrusion and encroachment at the boundary zone. In all three cases it was the challenger's behaviour and position in space in relation to a boundary zone that released aggression by a paired male opponent. The approach flight of a challenging pair (pair W) to a boundary zone was a prime stimulus for the neighbouring male (M B) to respond with an approach flight (Fig. 11 - Map 1). Likewise the position of a neighbouring male (M W) at a boundary zone and his behaviour (swimming and diving in threat) elicited approach swimming and diving in threat by his opponent (Fig. 11 - Map 2). In the third case the position of the intruding pair W elicited a prompt direct aerial attack by the resident M B (Fig. 11 - Map 3). In all cases the male occupant initiating the encounters responded to the challenger's position in relation to a boundary zone and not to the latter's proximity to the former's mate. Thus M B excluded conspecifics from an area, and was not just defending the personal space around his mate from the approach and attacks of

Figure 11. Release of agonistic behaviour in response to positions in space and behaviour patterns of neighbouring males with respect to positions of their mates, boundary zones and area of space held by each pair.

Solid lines indicate the movements of male B. Dashed lines indicate the movements of pair W. Numbers inside each map of Pond J refer to the sequential positions, movements and behaviour patterns of opposing individuals during agonistic encounters on May 4, 1974 as follows:

Map 1.

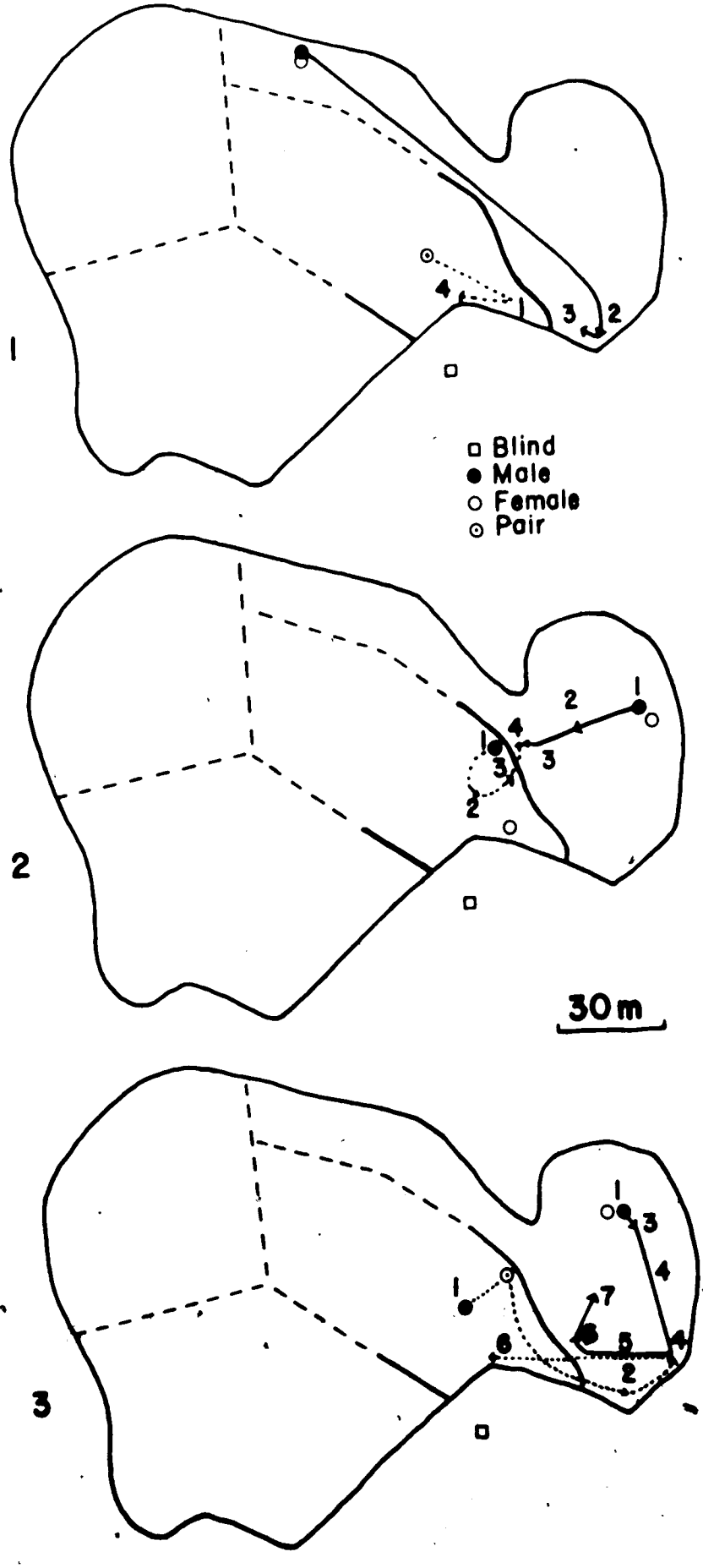
1 Pair W land at position 1 after being away from the pond.
2 Male B leaves mate and initiates an encounter by making an approach flight and landing at position 2.
3 Male B approach swims toward pair W.
4 Pair W withdraw with male W Leading and female W Following.

Map 2.

1 Male W at boundary away from his mate. Male B with his mate.
2 Male B initiates threat encounter by approach swimming and diving toward male W. Male W retreats, swimming and diving.
3 Male B continues approach swimming and diving. Male W approaches, swimming and diving.
4 Fight between male W and male B.

Map 3.

1 Pair B resting. Male W swims toward female W.
2 Pair W (female leading) swim toward and intrude along shoreline into pair B's space while pair B resting.
3 Male B alert, detects intruders. Male B swims a short distance towards trespassers.
4 Male B aerial attack at pair W. Brief fight between male W and male B, with male W intercepting male B's lunges at female W.
5 Three-bird pursuit-flight with male B the pursuer.
6 Male B breaks off pursuit and lands near the boundary zone as pair W flee into their own space.
7 Male B swims toward mate.


1
2
3
Blind
Male
Female
Pair
30m

neighbours. However, when a trespassing paired male attacks the female of a neighbouring pair, the mate of the attacked female defends her within their own space. Paired males even defend their mates within the space of a neighbouring pair. Thus defence of a mate occurs in certain contexts. Excluding conspecifics from an area and defence of a mate are not mutually exclusive; both occur.

4. Interactions Among Unpaired and Paired Males

Two unmated males were present on Pond J on April 30 and May 1, and one unpaired male from May 2 to 12, except for May 7. On May 4 and 5 a lone male was not attached to any particular area of the pond, rather it intruded within the pair-spaces and approached near the females of paired males, and was continuously attacked and chased by the latter (Fig. 10 - Map 1). By May 6 a lone male was localized on a space that presumably became vacant by the withdrawal of M B (Fig. 10 - Map 2). On May 7 there was no unpaired male on the pond. From May 8 to 12 an unmated male, presumably the same individual, occupied more or less the same space as that of a lone male on May 6 (Fig. 10 - Maps 4 and 5). This unpaired male engaged in threats and fights with paired males and initially excluded them from his space. This unmated male also continued to intrude into the space of paired males by approach and Display Flights to their mates. Once the unpaired male made an aerial attack and then pursued a strange pair attempting to settle within his space.

The hostility of all the paired males toward the unpaired male resident on his own space increased from May 8 to 12 (Fig. 10 - Maps 4 and 5). In the three days from May 8 to 10 there were a total of seven fights between the unpaired male and the paired males, whereas in the two days of May 11 and 12 there were 11 fights.

The unpaired male resisted eviction from the pond until May 12. Then there was a dramatic change in the intensity of hostility of the paired males and the response of the unpaired male. On May 13 at 0800 there was no unpaired male on the pond. On four occasions a lone male flew over the pond but quickly left after being attacked and pursued by the paired males. At 1000 an unpaired male flew over the pond and for the next 18 minutes before it left it continually retreated from the repeated aerial attacks and pursuit flights by one paired male after another, mostly M W and M B, whenever the unpaired male flew over or landed within their pair-space. From then on no unmated males established a space on the pond as they were always promptly attacked and pursued and forced off the pond by the paired males.

5. Locations of Paired Male - Unpaired Male Encounters

The boundary zone of the unpaired male's space was more distinct and the space more exclusive from May 8 to 10 than from May 11 to 12 (Fig. 10 - Maps 4 and 5). There was no distinct boundary zone on May 11 and 12 as most encounters were concentrated in a disputed area occupied by the unpaired male, and M W and M Y (Fig. 10 - Map 5).

Maintenance of Space - Pond J 1974

1. Interactions Among Paired Males

The period of maintenance of space refers here to that interval from May 13 to June 6. Two phases can be distinguished: phase I when boundary zones were fairly stable, and phase II when boundary zones were changing. Phase I corresponds to the eight days from May 13 to 20 from about mid-laying to about the start of incubation for two of the three paired females. Thus phase I could be called the late laying phase.

During phase I threat encounters comprised 70 percent of the 103 encounters involving paired males. Fighting accounted for 15 percent, approach - withdrawal 11 percent and attack - retreat and aerial pursuit each two percent of the total encounters. Thus space was maintained largely by threat, but also by fighting. At least one fight occurred on most days, and five fights occurred on two days (Figs. 8 and 9).

Male W maintained the central, larger space bordered on the east by pair B and on the west by pair Y (Fig. 10 - Map 6). Thus M W interacted with both M B and M Y. There were no M B - M Y interactions. In male - male interactions M W encountered M Y slightly more than twice as many times as M B. There were no male - pair encounters involving M B and M W, only those involving M W and M Y and their mates (Figs. 8 and 9). Male W interacted more with M Y for several possible reasons. The boundary zone of M W and M Y was about twice as long as that between M W and M B, perhaps requiring twice the maintenance. Pair B may have been a less visual stimulus than pair Y because, during this phase, all males stayed especially close to their mates as they foraged around the shoreline and over the open water. Possibly M W was more threatened by M Y and in order to defend the south-west bay adjoining pair Y's space, M W interacted more with M Y than M B.

Phase II involved maintenance of space even though boundary zones were changing because the paired males continued to maintain most or all of the original space they established and were resident continuously on the pond. Phase II extends from May 21 to June 6. On May 21 F B was incubating and F W was away from the pond for all the observation period, presumably laying her last egg. Thus two females

incubated clutches throughout phase II, and the other female for half of phase II. Hence this phase could be called the incubation phase.

During the incubation period females were at the nest site most of the time, while males were alone on the pond. As a result paired males, especially M W, spent more time patrolling their space and the number of interactions rose accordingly (Figs. 8 and 9).

During phase II (13 observation days) threat encounters comprised 69 percent of the 305 encounters involving paired males. Approach - withdrawal accounted for 19 percent, fighting 7 percent, aerial pursuits 4 percent and attack - retreat 1 percent of the total encounters. Thus, like phase I, space was maintained largely by threat. Fighting was proportionately less important, although fights occurred almost every observation day to June 6, except for May 23 and 31 (Figs. 8 and 9).

During the first 8 days of phase II there were about twice as many encounters (205) compared with phase I (103), a similar proportion of threat encounters (72 and 70 percent, respectively), proportionately more approach - withdrawal encounters (16 and 11 percent) and proportionately fewer fights (8 and 15 percent, respectively). However, the number of fights during the first 8 days of phase II (17) was more or less the same as during phase I (16), and fights continued almost daily at least until June 6, the third week of incubation for two females. Thus fighting was probably still necessary for maintaining space but also for expanding it because, during phase II, boundary zones changed and the size of pair-spaces expanded and contracted (details later) (Fig. 10 - Maps 7 to 11).

During phase II M W maintained the central space bordered by

M B and M Y, and until May 28 M B only interacted with M W, however from May 29 onwards M B and M Y interacted (Fig. 10 - Maps 10 and 11). Male W engaged in nearly three times as many threat encounters with M Y than with M B. Again, although reasons outlined earlier still apply, F W appeared to spend more time in the south-west bay and M W appeared to avoid M B. Thus it appeared to be more important for M W to defend and retain the south-west bay, rather than fight more with M B and try to retain the north shoreline.

2. Locations of Encounters Involving Paired Males

During phase I and II almost all encounters occurred within a boundary zone fixed in space for a given day (Fig. 10 - Maps 6 to 11). Locations of encounters, particularly those between M B and M W, were distributed along a boundary zone. However, for some days (Fig. 10 - Maps 7 and 9) most encounters between M W and M Y were clustered near the shoreline of the boundary zone.

To summarize, on Pond J in 1974 boundary zones and the pair-space were established during the prelaying period largely by fighting but also by threat encounters between paired males. Space was maintained during the laying and incubation periods largely by threat encounters but also by fighting between paired males within boundary zones. Paired males defended a space, but also defended their mates within this space and even within the space of neighbouring pairs.

Establishment and Maintenance of Space - Pond J - 1972, 1973; Ponds H and K - 1973.

To help determine how space is established and maintained on ponds in general it is necessary to compare the above findings at Pond J in 1974 with those obtained in other years and from other ponds. However,

the incomplete data obtained in 1972 and 1973 only permits a descriptive comparison.

1. Pond J - 1972 and 1973

On Pond J in 1973 the two pairs of buffleheads that had settled by May 2 were unmarked, thus it is not known if these were the same two pairs that became residents. Two pairs and a lone male occupied the pond when it was next visited from May 8 to 11. Pair 1 (F of the pair later marked as F R) occupied the east-end bay and pair 2 (F of the pair later marked as F W) and a lone male occupied the larger west-end bay. On May 8 and 9 M 2 repeatedly attacked and fought a resident lone male. On May 11 a lone male was not on the water, but one at the edge, apparently injured and unable to fly, retreated farther into the shoreline vegetation on being attacked by M 2. Presumably this lone male was injured by M 2, and not by a red-necked grebe which arrived on the pond on May 11. Injured buffleheads were not seen on any other occasions.

The estimated dates of clutch initiation were May 1 to 3 for F 1 and May 7 to 9 for F 2. The period of hostility by a paired male at an unpaired male corresponded with the early laying stage (eggs 1 to 3) of the female mated to the attacking male. Thus the timing of hostility was similar to that for the period of establishment on Pond J in 1974. Therefore the hostility against a resident unpaired male by a paired male appeared to be a response to the stage of the breeding cycle of his mate.

During the period of maintenance of space (late laying and incubation periods) there were few observations in 1973. Because of disruptions, first by grebes and then by trapping, the boundary zone between the paired males was not stable. However, on Pond J in 1972 a

boundary zone more or less fixed in space was maintained largely by threat, but also by fighting, by the two resident paired males throughout the incubation period of their mates when the pair bond remained intact. Thus the mechanism of establishment and maintenance of space was essentially similar for all three years on bog Pond J.

2. Pond H - 1973

On cattail Pond H in 1973 there were too few observations to identify any definite periods of establishment and maintenance of space. The two resident pairs seemed to acquire a space by settling; the males engaged in threat encounters within a wide boundary zone suggesting that this zone was established. Furthermore on May 7 when a third pair settled on the pond the nearest paired male promptly initiated an aerial attack at the female of the strange pair and a high intensity three-bird encounter on the water ensued, including male fighting and flap-paddle chasing, and the attacked pair were pursued from the pond. On two observation days (May 14 and 24) during the laying period, fighting between paired males was not seen. The exclusion of a third pair during the settlement period (prelaying) and the maintenance of space during the laying period, by threat encounters between the two resident paired males, suggests that the intensity of hostility may be higher during settlement.

On Pond H unpaired males, that were attacked and chased by the paired males, were not pursued off the pond but sought refuge in a central, apparently neutral, open water area. By comparison unpaired males were excluded from Pond J.

3. Pond K - 1973

On lily Pond K in 1973 the numbers of buffleheads rose from one male on May 3 to two pairs on May 4 and 7, three pairs on May 10 and 13, and five pairs on May 16. Two pairs subsequently left, thus there were an estimated three resident breeding pairs in 1973, and also in 1972 and 1974. It is not clear whether the apparent increase in pairs in 1973 resulted from more censusing, or was a response to the erection of nest boxes and artificial cavities, the social attraction of other buffleheads, or other stimuli at the pond.

Watches from the blind at Pond K began on May 16 when the five pairs maintained a stretch of shoreline or a bay by fighting and threat encounters mostly within established boundary zones. Trespassing paired females were attacked by the paired male occupant triggering a three-bird attack and pursuit encounter. The central, open water was occupied by an unpaired male, and some shoreline was not used much by the pairs. Any changes in length of shoreline per pair in response to the settling of late arrivals were not determined. Thus it is not known exactly whether the late arrivals established space with much aggression or settled with little hostility. However, at least four of the five paired males engaged in fighting so presumably fighting served to establish relatively stable boundary zones and pair-spaces. Space was maintained mainly by threat encounters. Unfortunately the stage of the breeding cycle of an individual unmarked female of a pair could not be estimated reliably. Four resident pairs on Ponds K and L were thought to have initiated clutches, yet only two unmarked females with broods arrived at Ponds K and L. Thus a specific female with a brood could not be recognized as an individual.

In summary, the basic behaviour patterns associated with the establishment and maintenance of space were similar for three different pond habitats with different densities of breeding pairs of buffleheads. At high densities (bog Pond J) agonistic behaviour, especially threat and fighting between paired males and paired male - pair attack and pursuit encounters, was much more frequent than at intermediate densities (lily Pond K) and apparently very infrequent at lower densities (cattail Pond H). The open water area of the smaller Pond J was totally divided among the resident breeding pairs and unpaired males were excluded from the pond. By comparison on the larger ponds (H and K) there was a central, neutral area sometimes occupied by unpaired males.

Agonistic Behaviour of Paired Males in Relation to the Reproductive State of Their Mates

The previous section emphasized how space was established and maintained at Pond J in particular, and at other ponds in general. In this section and the next I consider the effect of reproductive state of paired females on the behavioural responses among their mates as they in turn affect changes in size of pair-spaces on Pond J in 1974.

Frequency and intensity of agonistic behaviour of paired males varied according to the reproductive state of their mates. The total number of agonistic encounters involving paired males was generally high during prelaying; declined during laying, rose again during the first week of incubation, then tapered off until the end of intensive observations (June 6) while the pair bond remained intact (Fig. 12). A similar trend is evident between interacting individual males such as W and Y and W and B. Omitting the low number of encounters on May 5, when a

Figure 12. Frequency of agonistic encounters among three paired and one unpaired male resident on Pond J in 1974, in relation to the stage in the breeding cycle of their colour-marked mates.

The numbers 1 to 4 denote the nature of the encounters as follows:

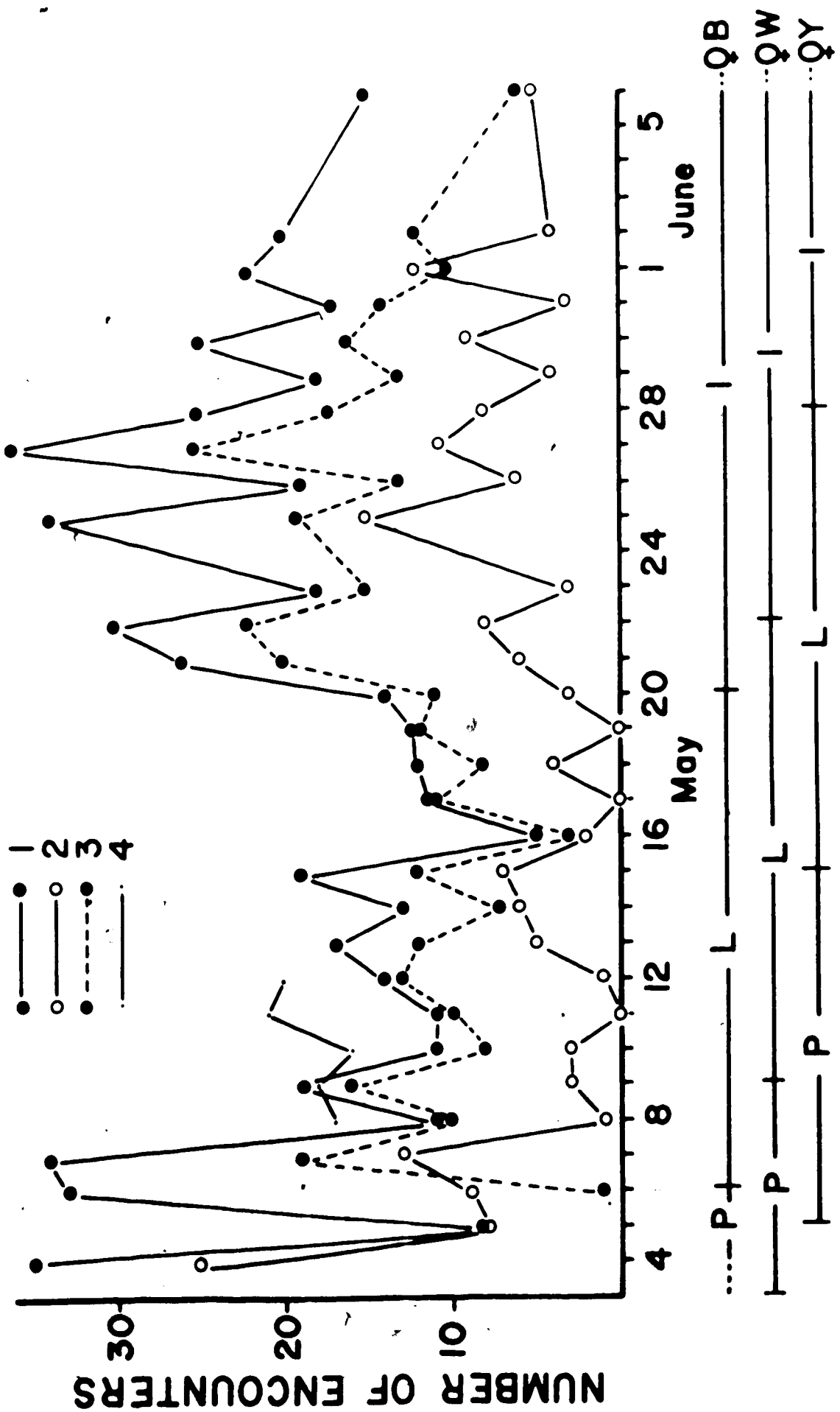
1. Total encounters involving at least two paired males.
2. Male - male and male - pair encounters among paired males W and B and their mates.
3. Male - male and male - pair encounters among paired males W and Y and their mates.
4. Encounters among paired males and an unpaired male.

The stage in the breeding cycle of each of the three colour-marked females is indicated by the following letters:

P - prelaying period

L - laying period

I - incubation period


NUMBER OF ENCOUNTERS
30
20
10
4
8
12
16
20
24
28
1
5
May
June
1 2 3 4
QB
QW
QY
P
L
I
P
L
I
P
L
I

red-necked grebe occupied the pond, but including encounters involving the resident lone male, it is evident that agonistic encounters were sustained at a high level until May 12 - the establishment period.

The agonistic responses of a paired male seemed to depend on the reproductive state of his mate, and the stimuli elicited from the responses of neighbouring males. These latter responses in turn seem related to the reproductive state of their respective mates. Because M W was involved in almost all agonistic encounters, changes in the intensity of these encounters relative to the breeding cycle, can be demonstrated by relating them to the reproductive state of F W.

Threat encounters among paired males rose from 23 percent of all encounters during prelaying to 64 percent and 68 percent during the laying and incubation periods, respectively. Fighting during male - male and male - pair encounters declined progressively from 20 percent during prelaying to 14 percent and 8 percent during laying and incubation, respectively. Approach - withdrawal encounters declined from 41 percent during prelaying to 11 percent during laying then rose to 20 percent during incubation. Changes in attack and pursuit encounters were insignificant.

Size of the Pair-Space

Size of the pair-space varied with pond size, pond topography, density of breeding pairs, reproductive state of paired females and male aggressiveness. Size of space can be measured in terms of area (ha) and length of shoreline (m), and expressed as a ratio of shoreline to area. For larger ponds with low densities of pairs, length of shoreline gives the best measure of occupied space. For smaller ponds with high densities of pairs, in which the pond area is totally divided up among

the pairs, size of space occupied can be measured in terms of area and shoreline.

Mean length of shoreline per breeding pair varied from 503 m on Pond H (3.8 ha) with low densities (0.5 pairs/ha) to 271 m (1.3 pairs/ha) and 181 m (2.0 pairs/ha) on Pond J (1.5 ha) with high densities. With two breeding pairs (1.3 pairs/ha) on Pond J the size of the pair-spaces seemed to be largely determined by topography of the pond. For instance, in 1972 the space of pair 1 occupying the smaller east-end bay was 0.3 ha, and that of pair 2 occupying the larger west-end bay was 1.2 ha. The ratio of shoreline to area was higher (5.3) for pair 1 with the smaller space, than for pair 2 (3.2). With two breeding pairs on Pond J the size of pair-spaces remained relatively constant throughout the breeding cycle while the pair bond was intact.

When the number of breeding pairs increased to three (2.0 pairs/ha) on Pond J in 1974 the size of pair-spaces changed throughout the breeding cycle. It is appropriate to describe these changes in relation to the reproductive state of the paired females. The size of pair Y's space was relatively constant at 0.30 to 0.40 ha, but the space occupied by pairs B and W changed concomitantly throughout the breeding cycle (Fig. 10 - Maps 1 to 11). Female B started laying 3 days before F W so their reproductive state was similar. During prelaying, and approximately the first half of their laying periods, pair W's space expanded from 0.35 ha to 0.85 ha, while pair B's space contracted slightly from 0.40 ha to 0.30 ha. Upon arrival at Pond J, pair W settled on a space with only a small amount of shoreline (Fig. 10 - Map 1). In order to establish a space on the pond the mate of F W responded aggressively and the expansion of shoreline and the pair-space

reflects that response (Fig. 10 - Maps 2 and 3). During the latter half of their laying periods the spaces of pairs W and B were relatively constant at 0.85 ha and 0.30 ha, respectively.

The expansion and compression of pair-spaces throughout incubation in relation to agonistic encounters suggest that size of space, reproductive state of paired females and male aggression are interrelated. Female B started incubation 2 days earlier than F W and 8 days before F Y. During the first 2 weeks of F B's incubation her mate appeared to win fights against M W and gradually encroached upon pair W's space. As a result, pair B's space gradually doubled from 0.30 ha May 20 to 0.60 ha on June 2 and their length of shoreline expanded considerably from 160 m to 245 m, while pair W's space gradually declined concomitantly by about a third from 0.85 ha to 0.55 ha and their length of shoreline contracted considerably from 260 m to 155 m. These changes in size of pair-spaces suggest that M B apparently became more aggressive and expanded his pair-space in response to his mate's onset of incubation. However, it is not clear whether M B's aggressiveness resulted primarily from the status of the gonads, or from external stimuli elicited by his mate, and/or the responses shown by M W.

From June 6 (day 18 of F B's incubation and day 10 of F Y's incubation) to June 10, pair Y continued to expand their shoreline by usurping the space of pair B and as a result pair B's space halved. By June 6 pair W had regained some open water space from pair B. Thereafter their space remained relatively constant.

The above concomitant changes in size of space of pairs B, W and Y in relation to reproductive state of the females, suggest that contraction and expansion of space, male aggressiveness and the female's stage

of incubation are interrelated. The aggressiveness of M B and M Y and the expansion of their spaces during the first 2 weeks of their respective mate's incubation suggests that the status of the gonads determined male aggression which in turn determined size of pair-space. However, the external stimuli of a female during her off-nest period at the pond and the agonistic responses of male opponents may be additional factors determining male aggression. For example, on one occasion while F B foraged along the shoreline attended by her mate, she intruded into pair W's space, followed by her mate. A fight, which then erupted between M W and M B, was won by M B. Possibly the outcome of the fight was affected by the presence of F B. If M W initially lost a boundary fight with M B in the presence of F B, then the outcome of the fight may have affected subsequent responses by M W.

Minimum size of pair-spaces on Pond J in 1972 and 1974 varied according to individual females and their reproductive state. The minimum space occupied by one female throughout the breeding cycle was 0.3 ha and 160 m shoreline. For two females size of pair-space was 0.3 and 0.4 ha during prelaying and laying, but expanded to 0.5 and 0.6 ha during the first 2 weeks of incubation.

Agonistic Responses Among Paired Residents

A total of 602 agonistic encounters involving paired residents at Pond J in 1974 were recorded throughout the breeding cycle and categorized according to components of agonistic behaviour and the number and sex of birds involved (Table 4). With the exception of one male - male and 15 male - female encounters between members of different pairs, all encounters involved at least two paired males in various combinations of two to four birds.

Table 4. Number of agonistic encounters among paired residents recorded during the breeding cycle at Pond J on 30 observation days between May 4 and June 6, 1974.

Encounter		Category of agonistic encounter					
		Approach - withdrawal[1]	Threat[2]	Attack - retreat[1]	Fight[2]	Aerial pursuit	Totals
Two-bird	Male - male	80	334	9	50	7	480
	Male - female	12				3	15
	Female - female	1					1
Three-bird	Male - pair	46		10	20	25	101
	Male - male - male	1	1				2
Four-bird	Pair - pair	3					3
Totals		143	335	19	70	35	602
		(24%)	(56%)	(3%)	(11%)	(6%)	(100%)

[1]These categories refer to non-reciprocal encounters in which one individual flees from the approach, attack or pursuit by its opponent.

[2]Threats and fights refer to reciprocal encounters in which interacting males both attack and escape from each other.

Male - male and male - pair encounters together comprised 96 percent of the total encounters. Reciprocal encounters accounted for 80 percent (threats 70 percent and fights 10 percent), and non-reciprocal encounters accounted for 20 percent of the 480 male - male encounters (Table 4). Reciprocal encounters refer to those encounters in which interacting males direct attacking movements at each other as in threat and fighting encounters. Non-reciprocal encounters refer to those encounters in which the approach, attack, or pursuit by a male elicits a fleeing response by an opponent male or pair. Thus resident paired males mainly respond to one another by threat.

By comparison, of 101 male - pair encounters, the main pair response (avoidance at the approach of a paired male) accounted for 45 percent, aerial pursuit of a pair by a paired male, 25 percent, and male - pair encounters ending in male - male fights, 20 percent of the encounters (Table 4). Thus 80 percent of male - pair encounters involved fleeing by the pairs and 20 percent, reciprocal attacks by males.

Combining all 602 encounters recorded, threat was the major agonistic response (56 percent), followed by avoidance (24 percent), then fights (11 percent).

Agonistic Responses Among Paired Residents and Unpaired Males

Throughout the breeding cycle of 1974 a total of 446 agonistic encounters involving paired residents and unpaired males were recorded at Pond J and categorized (Table 5). With the exception of four encounters between an unpaired male and a paired female, all encounters involved at least one unpaired and one paired male in various combinations of two to four birds.

Table 5. Number of agonistic encounters among paired residents and unpaired males recorded during the breeding cycle at Pond J on 30 observation days between May 4 and June 6, 1974.

Encounter		Category of agonistic encounter					
		Approach - withdrawal	Threat	Attack - retreat	Fight	Aerial pursuit	Totals
Two-bird	Paired male - unpaired male[1]	84	41	88	23	105	341
	Unpaired male - paired female			3		1	4
Three-bird	Unpaired male - pair	42		37		10	89
	Paired males - unpaired male	7	2	1		1	11
Four-bird	Paired male - unpaired male - pair	1					1
Totals		134 (30%)	43 (10%)	129 (29%)	23 (5%)	117 (26%)	446 (100%)

[1]The individual placed first generally refers to the one that approached or directed an attack at its opponent(s) first.

Encounters between an unpaired male and either a paired male or a pair comprised 96 percent of the total encounters. Reciprocal threat and fighting encounters accounted for 19 percent and non-reciprocal responses, 81 percent of all unpaired - paired male encounters. The latter were characterized by an unpaired male fleeing from the approach, attack or pursuit by a paired male. Aerial pursuit by a paired male was the most frequent of these non-reciprocal responses (31 percent).

By contrast in 89 unpaired male - pair encounters pair avoidance at the approach of an unpaired male accounted for 47 percent, and attack by a paired male against an unpaired male 42 percent of all encounters. A paired male leaving his mate to pursue an unpaired male was the least frequent response (11 percent), whereas in the absence of his mate, aerial pursuit was the most frequent response (Tables 4 and 5).

Combining all 446 encounters, fleeing responses comprised 85 percent and reciprocal threats and fights 15 percent of all encounters.

Comparison of Agonistic Responses by Paired Males and Unpaired Males

Differences in agonistic responses by paired and unpaired males were tested for significance using Chi-square (Table 6). In male - male encounters, threat encounters were significantly greater ($P<.001$) between two paired males than between a paired and an unpaired male. Fleeing by unpaired males from attack and aerial pursuit was significantly greater than that by paired males ($P<.001$).

In male - pair encounters supplanting attacks (category 3) by a paired male, with his mate, toward unpaired males were significantly greater than those toward paired males ($P<.001$). A paired male with his mate engaged in fights with a paired male but not with an unpaired

Table 6. Responses by a pair to a paired male compared with an unpaired male and responses by a paired male to another paired male compared with an unpaired male recorded during the breeding cycle of 1974 at Pond J.

Encounter	Category of agonistic encounter: Approach - withdrawal	Threat	Attack - retreat	Fight	Aerial pursuit	Totals
Male - male						
Paired male - paired male	80	334	9	50	7	480
Paired male - unpaired male	84	41	88	23	105	341
Level of significance[1]	P<.01	P<.001	P<.001	Not sig.	P<.001	
Male - pair						
Paired male - pair	46		10	20	25	101
Unpaired male - pair	42		37	0	10	89
Level of significance	Not sig.		P<.001	P<.001	P<.05	

[1] Differences between paired and unpaired males within each category of agonistic encounter in proportion to the totals were tested statistically with 2 x 2 Chi-square.

male ($P<.001$). There were significantly more aerial pursuits of a pair by a paired male, than those involving an unpaired male ($P<.05$).

Agonistic Responses by Resident Paired Males Toward Strange Pairs

Prompt aerial attack, aerial pursuit and expulsion by resident paired males prevented strange pairs from permanently settling on Pond J in 1974. If a resident male was temporarily absent from his space then a strange pair settling in the vacant space sometimes took much longer to be evicted on the return of the resident male. In these cases approach - withdrawal and attack - retreat encounters sometimes occurred before the strange pair was chased off the pond. On one occasion (described in detail later) a strange pair, that occupied a resident male's space during his absence, was not expelled from the pond until after the arrival of the mate of the resident male.

Excluding this one instance when a strange pair was not evicted during the morning observation period, then of 29 encounters involving resident males and strange pairs 21 (73 percent) were aerial pursuit of a strange pair, 4 (14 percent) were withdrawal of a strange pair by swimming away from a resident male, 3 (10 percent) were short distance retreat by a strange pair from attack by a resident male, and one encounter (3 percent) involved a fight between a resident male and a strange male with his mate.

On Pond H in 1973, hostility by the resident males during prelaying, and apparently during most of the laying periods of their mates, prevented strange pairs from permanently settling. Possibly during the late laying and early incubation periods hostility of the resident males declined so that late arriving pairs were able to settle but there was no conclusive evidence that these pairs initiated clutches.

On Pond K in 1973, again except for two late arriving pairs that settled but departed several days later, strange pairs were chased off the pond by the resident males.

Male Aggression in the Presence and Absence of Mate

Male aggression in the presence and absence of a mate was recorded at Pond J in 1974, with marked individuals. On entering the blind shortly before 0800 on May 18, I noted an unmarked female bufflehead in the trap in the south-east corner (see Fig. 10) of the east-end bay and, in addition to M W and M Y in the west end, there were three males in the east end, with one of them presumably the mate of the caught female waiting alongside the trap. Evidently this strange pair and the two lone males occupied the east end during pair B's absence, because while the female was being removed from the trap a male bufflehead, later confirmed as M B, expelled the three males from the east end. After marking the trapped bird (F Or-Bk), she was chased by the resident males. I re-entered the blind shortly before 0900. Female Or-Bk, now accompanied by a male, occupied the south-east corner of the east-end bay (hereafter referred to as the south-east corner) after being repeatedly attacked and pursued by M B. From 0900 to 1800 all agonistic encounters involving M B and F Or-Bk and/or her mate were recorded and categorized (Fig. 13).

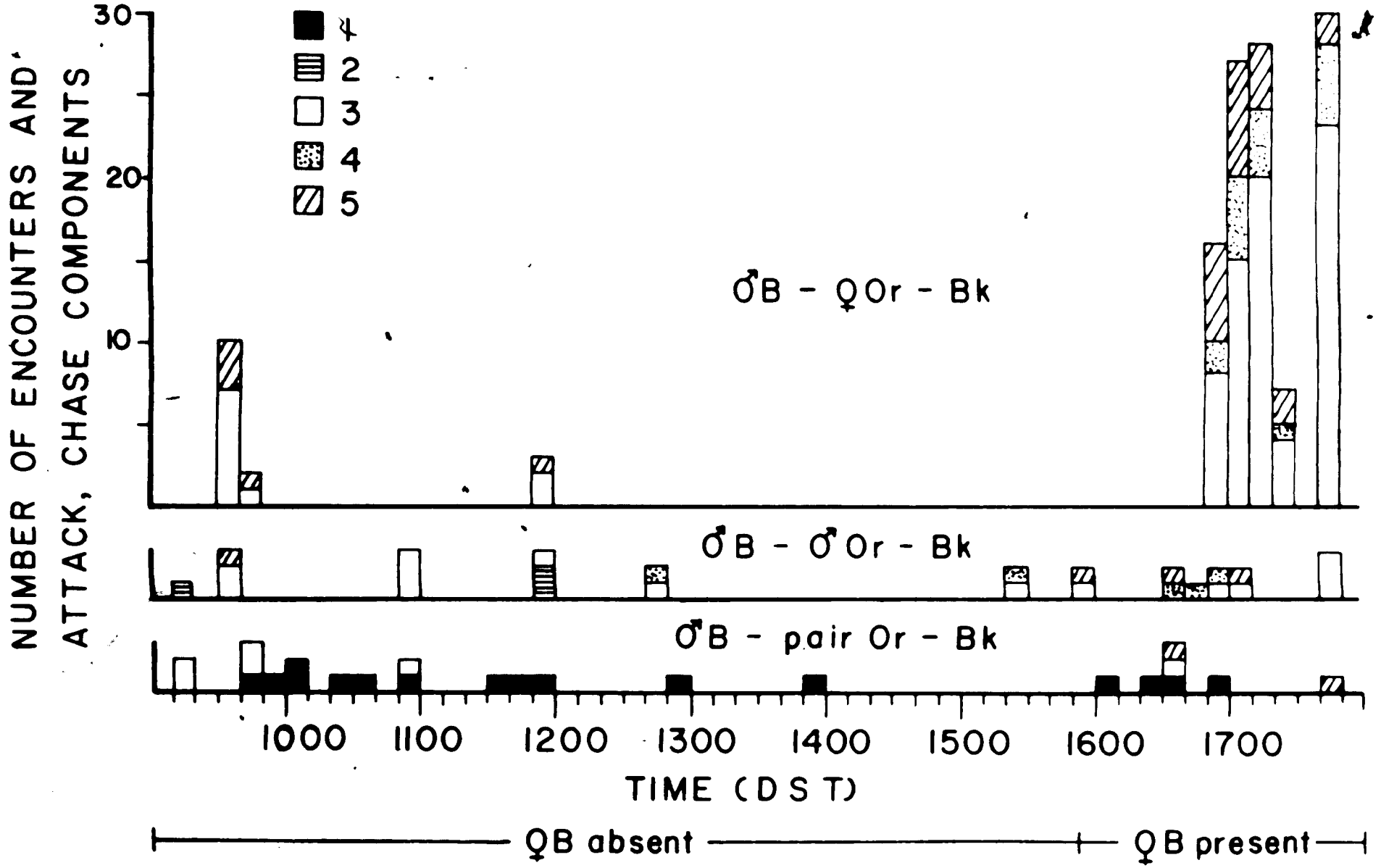
During F B's absence her mate was unable to expel F Or-Bk and her mate from the south-east corner, despite an initial burst of aerial attacks (Fig. 13). During the first recorded encounter two aerial attacks by M B at F Or-Bk were intercepted by the female's mate. In the second encounter the first two aerial attacks at F Or-Bk and one at her mate by M B were promptly followed by aerial pursuit with M B the

Figure 13. Aggression by a resident male (B) toward a strange pair (Or-Bk) in the absence and presence of his mate (F B) on Pond J for nine observation hours on May 18, 1974.

The numbers 1, 2 and 4 correspond to three categories of entire agonistic encounters, and 3 to 5 to separate components of attack and pursuit in high intensity encounters as described in the text and as follows:

1. Approach - withdrawal
2. Threat
3. Aerial attack, attack rush
4. Fight
5. Aerial pursuit

The above encounters and attack and chase components are almost mutually exclusive. For instance, an aerial pursuit initiated by an aerial attack was tallied as one aerial pursuit and one aerial attack. Fights between males included attack rushes but these latter components were not recorded.


NUMBER OF ENCOUNTERS AND ATTACK, CHASE COMPONENTS
30
20
10
4
2
3
4
5
♂B - ♀Or - Bk
♂B - ♂Or - Bk
♂B - pair Or - Bk
1000
1100
1200
1300
1400
1500
1600
1700
TIME (D S T)
QB absent
QB present

pursuer. Following the last aerial attack by M B, F Or-Bk made short retreat flights from four attack rushes by M B before there was an aerial pursuit. Each time M B pursued F Or-Bk around the east end her mate stayed on the water. This suggests that the pair bond of F Or-Bk and her mate was weak, because F Or-Bk's mate did not follow her and try to protect her from M B's attacks. After each pursuit F Or-Bk tenaciously returned to the south-east corner prompting her pursuer to initiate repeated attacks at her. For the rest of the period from 0938 to 1552 while F B was away from the pond there were few attacks and pursuits, mostly withdrawal of pair Or-Bk in response to M B's approach (Fig. 13).

On the return of F B to her pair-space at 1552 two males (her mate and the mate of F Or-Bk) approached her Head-bobbing followed by M B Leading, F B Following and a pair B copulation at 1553. Female B spent the next hour mainly feeding, closely attended by her mate, though this activity was interrupted several times by the approach of F Or-Bk's mate followed by M B Head-bobbing, Leading and F B Following, male - male fights and aerial pursuit, and male - pair attack and pursuit encounters with M B the attacker (Fig. 13).

A marked rise in the frequency of attacks by M B, directed almost solely at the intruding F Or-Bk, occurred about one hour after M B was reunited with his mate (Fig. 13). There were two intensified bursts of aggression, one relatively long and one short, before F Or-Bk and her mate were finally expelled from the pond. The first burst began at 1655, lasted for nearly half an hour, and ended with an aerial pursuit at 1723 in which F Or-Bk left the pond with her mate following. The return of F Or-Bk and her mate 18 minutes later at 1742 triggered off

the second burst of aggression. Prompt, persistent attacks by M B for the next eight minutes culminated in pair Or-Bk being forced off the pond at 1749. Female Or-Bk was not seen again at Pond J, or anywhere else.

Further analysis of the components of these bursts of aggressive behaviour by the resident male reveal its special nature, intensity and directionality. During the first burst of aggression by M B there were nine encounters all initiated by aerial attacks by M B and all terminated when M B flew back to his mate and performed Head-bobbing or swam toward her. Of 82 attack and pursuit components, 78 (95 percent) were directed solely at F Or-Bk and four (five percent) at her mate. Aerial attacks comprised 46 percent, all attacks (60 percent), and all pursuits (40 percent) of the 78 attack and pursuit components directed at F Or-Bk by the resident M B. The intensity of male attack and the female flight response resulting in aerial pursuit declined with time. For example, in the first one third of the encounters lasting one third of the time there were nearly one half of the total attack and pursuit components and proportionately more aerial attacks (73 percent) ending in aerial pursuit than those in the last six encounters (38 percent).

Of the 34 attack and pursuit components of the two encounters during the second burst of aggression, 30 (88 percent) were directed solely at the female, 3 (nine percent) at the male and one (three percent) was a three-bird pursuit-flight. The first encounter consisted of an aerial attack followed by an aerial pursuit. The second more vigorous encounter consisted of 22 attack and six pursuit components. Combining these two encounters, aerial attacks comprised about 53 percent, all attacks (77 percent) and all pursuits (23 percent) of the 30

aggressive components directed at F Or-Bk by M B. The greater proportion of attacks during the second burst of aggression, especially the second and last encounter before F Or-Bk finally left the pond, can be attributed to two interrelated factors. The first of these was the tendency of F Or-Bk to respond to the attacking male's aerial attacks by short retreat rushes and flap-paddles, and short retreat flights and landing within the south-east corner instead of a retreat flight that prompted the attacking male to initiate an aerial pursuit. The second factor was F Or-Bk's great tenacity for the south-east corner despite her mate's lack of protection from the attacks of M B.

In summary, the release of aggression by a resident male in the absence of his mate in response to the external stimuli of an intruding strange pair within his space was not sufficient to expel the strange pair. The tenacity of the intruding female to a space on Pond J must have been reinforced by only a short period of familiarity with it. The presence of the mate of the resident male combined with the external stimuli of the position in space of the intruding pair elicited persistent, continued attacks by the resident male at the strange pair until they were expelled from the pond. The marked increase in the rate of attacks by the resident male directed almost solely at the intruding female, the fleeing response by the attacked female and her mate's almost complete lack of protection of her, suggest that these attacks by the resident male can be interpreted as increased aggression in response to the external stimuli of his mate.

Exclusiveness of the Pair-Space

Each pair-space at Pond J in 1974 was an exclusive area in the sense that a particular paired male spent virtually all his time within

it throughout each day of the breeding cycle while the pair bond remained strong. The female of the pair used only the pair-space of her mate during her off-nest periods at the pond. A pair sometimes vacated their space briefly, especially during the prelaying period, but established neighbouring resident pairs rarely intruded into it in their absence. Strange pairs did settle in a vacant pair-space, but were expelled on the return of the resident male.

Resident pairs exclusively occupied their space, with the exception of strange, lone females which were probably incubating. Males excluded all other conspecifics from their pair-space, whether they were neighbouring or strange pairs, unpaired males or lone sub-adults. On Pond J with a high density of pairs in 1974, paired males established and maintained an exclusive space by expelling conspecifics from within their boundaries on any given day, despite the fact that boundary zones shifted over time with the compression and expansion of pair-spaces. Again in 1972 and 1973 on Pond J paired males maintained an exclusive pair-space with respect to conspecifics.

On Ponds H and K with lower densities of pairs, resident paired males appeared to maintain an exclusive shoreline by expelling all conspecifics. Boundary zones became less distinct with increasing distances from the shoreline toward the centre of the pond, where unpaired males were tolerated and not excluded from the pond. Thus the centre of the pond was probably a neutral area.

Interspecific Agonistic Behaviour

1. Buffleheads and Other Ducks

I frequently saw paired male buffleheads attacking other species of diving ducks, such as common goldeneye, lesser scaup and

ring-necked ducks, and occasionally dabbling ducks such as mallard, American wigeon, blue-winged teal and green-winged teal. Three types of attack were distinguished; underwater attack (low intensity), attack rush (intermediate intensity), and aerial attack (high intensity). Any one encounter with other ducks may involve all three types of attack.

Low intensity attacks were recognized when male buffleheads swam toward other species of ducks which responded by swimming away in retreat. A male bufflehead usually continues swimming until his target is about five m away, then alternately dives and surfaces in the Head-forward posture until it is close enough for an underwater attack. The attacked duck usually responds by a short or long retreat flight. If the retreat is short, usually the male bufflehead continues the attack, mostly approach swimming and diving and attack underwater, but may also rush or fly in attack until the intruder flees from his space.

When a pair of lesser scaups retreat to the shoreline of a pond on the approach swim of a male bufflehead, the female scaup usually retreats out of sight well into the shoreline vegetation, while her mate stays on guard facing the adversary. The male bufflehead approaches in the Head-forward posture to within a metre of the male scaup, dives, surfaces quickly and either repeats the process or dives in attack underwater, until either the male scaup takes flight or the bufflehead turns away. A male scaup that flies away from his mate usually swims back along the shoreline to his mate. The male scaup may again be chased off without his mate or eventually the pair is chased off by the male bufflehead.

In high intensity attacks at other pairs of ducks an aerial attack by a male bufflehead is often followed by aerial pursuit. The

pursuing bufflehead usually lands near his boundary zone or at the edge of the pond as the intruders flee from his space or into the shoreline vegetation.

Accounts of hostility by a male bufflehead toward other species of ducks are meagre. Erskine (1972:27) reported that a male bufflehead drove off a pair of goldeneye by directing an underwater attack at the female, but he did not specify the type of attack he saw by a male bufflehead against redhead (*Aythya americana*), lesser scaup and common eider (*Somateria mollissima*). Myres (1959a:185) saw a male bufflehead "fly at and drive off a pair of lesser scaup" and mentions that goldeneyes are attacked. Dice (1920) saw a male bufflehead attack a male pintail (*Anas acuta*).

Data on interactions between buffleheads and other ducks were incomplete, because I concentrated on intraspecific interactions, and are not suitable for detailed quantitative analysis. Interspecific interactions, especially those involving lesser scaups, appeared to be complex in terms of motivation of attack. Breeding pairs of common goldeneyes were transients at all study ponds, and were usually promptly chased off by male buffleheads, especially from Pond J. Breeding pairs of lesser scaups were resident at all study ponds and were not excluded from the ponds by male buffleheads. Nevertheless, lesser scaups were harrassed by male buffleheads particularly at Pond J, but also at Pond K.

At Pond J in 1974, for example, my impression was that two male buffleheads, W and B, eventually chased off all scaups from their pair-spaces, and those scaups sought refuge amongst the shoreline vegetation in pair Y's space and near the boundary zones. Motivation of attacks by

buffleheads upon scaups was not clear. Buffleheads attacked conspecific intruders promptly, whereas scaup intruders were often ignored initially then eventually attacked. Presumably these differences in motivation depends on a complex combination of factors such as internal state (activity of buffleheads), external stimuli (position of scaups in space and their activity), and also the reproductive state of the buffleheads and the phenomenon of redirected aggression.

2. Buffleheads and Grebes

Three species of breeding grebes occurred on the study ponds, the large, common red-necked grebe, and two small, less common ones similar in size to buffleheads, the horned grebe (*Podiceps auritus*) and the pied-billed grebe (*Podilymbus podiceps*). I saw all three species of grebes attack pairs of buffleheads. Both sexes of horned and pied-billed grebes attack buffleheads from below the surface by diving under them (attack underwater), or by rushing at them over the water in a hunched posture (attack rush). The attacked buffleheads usually fled by short retreat flights or rushes. Myres' (1959a:85) report of a horned grebe diving and rushing at two males and a female bufflehead seems to be the only account of bufflehead - grebe interactions.

The larger red-necked grebe is a greater threat to buffleheads because of its larger bill. Both sexes of red-necked grebes attack buffleheads, but it is probably the male grebe that forages farther away from the nest and usually attacks buffleheads whenever they are encountered. A patrolling red-necked grebe in Low Threat (Kevan, 1970) approaches and dives toward a pair of buffleheads which stay alert in an upright posture. Long underwater attacks by a red-necked grebe are initiated 20 to 30 m away from buffleheads but sometimes a grebe

surfaces short of its target and dives again. In response a bufflehead pair usually fly in retreat, land in an upright posture and resume other activity when the grebe swims away. The close approach toward a pair of buffleheads by a threatening grebe, with its bill pointing toward them ready to make an underwater attack, elicits the following response from buffleheads. The male flies toward the grebe, the latter submerges and the bufflehead patters over the water surface in figure-of-eight, semi-circular or circular motions with the grebe submersed beneath it, then flies to its mate, lands and the pair remain motionless in upright posture. When the grebe surfaces it usually withdraws.

A breeding pair of red-necked grebes and breeding pairs of buffleheads coexisted on some ponds. The following evidence suggests that at least on one occasion a pair of red-necked grebes excluded two pairs of buffleheads from Pond J in 1973. Two resident pairs of buffleheads and a pair of grebes occupied Pond J on May 16, but on May 19 the two pairs of buffleheads were absent, being present on two peripheral ponds near J. By May 20 one male bufflehead had reoccupied Pond J. despite the presence of the pair of grebes. On May 22 I saw a red-necked grebe, presumably the male, direct an underwater attack at a paired male bufflehead attending two females. The grebe grabbed hold of the male bufflehead underwater, but the bufflehead escaped. The three buffleheads took flight and retreated from the pond. This was the only occasion I saw any grebe make contact with a bufflehead. This pair of grebes on Pond J were then shot and one male bufflehead, presumably M 2, reoccupied Pond J the same day (May 22). On May 27 a second male bufflehead, presumably M 1, re-established a pair-space on Pond J. Thus two paired male buffleheads reoccupied the pond only in the absence of

the grebes. A pair of grebes were also shot at Pond J in 1974 so that they would not interfere with the spacing behaviour of buffleheads.

3. Other Ducks and Grebes

Kilham (1954) observed a territorial pied-billed grebe repeatedly direct underwater attacks at a female ring-necked duck and less persistent attacks at a female hooded merganser (*Lophodytes cucullatus*).

In Norway and Iceland, Fjeldsa (1973) observed horned grebes dive in attack and drive away from their nest area 13 species of ducks, including Barrow's goldeneye (*Bucephala islandica*). Fjeldsa mentions that similar behaviour also occurs in red-necked grebes.

In Finland, Raitasuo (1964) observed that great crested grebes (*Podiceps cristatus*) defended a nest area by diving attacks at mallards and all other intruding ducks. Interspecific aggression by the grebes began during nest building and was greatest during late incubation and hatching. Raitasuo (1964) reported similar hostility by horned grebes toward mallards, and other species of ducks of the genus *Anas*, and the genus *Aythya*. All the above accounts show that attacks by grebes elicit fleeing by ducks. Only the bufflehead is known to respond to a grebe's intention to attack by initially flying toward the grebe rather than fleeing. Goldeneyes may also react in a similar way so grebe - goldeneye interactions deserve closer study.

Part III. Sexual Behaviour in Space and Time

Duration of Pair Bond

Pair bond tenure varied markedly between at least two different study ponds, but not between years for the same pond, suggesting that it is a response to different pond environments and not just to changing chronology between years. Duration of the pair bond was relatively short on cattail Pond H, short to intermediate on lily Pond K and longest on bog Pond J.

Pair bond was considered to be strong if a resident male occupied a particular pair-space for all or almost all of an observation day and attended an individual female using the same space throughout all stages of the breeding cycle. Pair bond was considered to be weak if a resident male was absent from his pair-space for more than half an observation day, even though he attended an individual female in that space for part of the day.

On cattail Pond H, in both 1973 and 1974, there were two breeding pairs, one of the paired females being F R-W in both years. In 1973 the pair bond of F R-W and her mate was definitely strong on May 24 (late laying) and May 28 to 29 (early during week 1 of incubation). On June 1 (end of week 1 of incubation) pair bond was still intact but weak as the male seen with F R-W was usually absent from the pond. On June 5 and 7 (end of week 2 of incubation) there were no resident males on Pond H and F R-W was unattached. These data show that the pair bond and male attachment to the pair-space declined during week 1 of incubation and probably broke completely by early in week 2 of incubation.

The duration of the pair bond of F R-W and her mate was similar in 1974. On June 3 an incubating F R-W flushed from her nest site to join

a male waiting on her pair-space. On June 4 when F R-W was flushed from her nest site there was no male waiting for her. The pair bond was still intact at least during week 1 of incubation. Assuming that the nesting chronology of F R-W was similar to that in 1973, then the weak pair bond by June 4 suggests that pair bond tenure was similar to that in 1973. A similar trend was evident for the other pair on Pond H in both years.

On bog Pond J from 1972 to 1974 inclusive the pair bond of all residents usually lasted throughout week 3 of incubation and at times into week 4. In 1972 the pair bond of the east-end occupants was strong during the first 2 weeks of incubation, then weakened and broke completely during week 3. The bond of the west-end pair was strong during week 3 of incubation but probably persisted into week 4 because, on June 10 (about day 24 of incubation), a male was absent in the morning but accompanied F 2 in the afternoon.

In 1973 the pair bond of the two resident females (later F R and F W) was strong during week 3 of incubation, but then an influx of pairs made it difficult to determine exactly when the pair bond broke.

In 1974 daily observations of the spatial relationships of males mated to colour-marked females showed that pair bond remained strong until early in week 4 of incubation. Male B was with F B on June 11 (day 23 of incubation) but absent from his pair-space on the morning of June 12 suggesting a weakening or a break in the pair bond about this time. The pair bond of pair W was definitely strong on the morning of June 12 (day 22 of incubation). When Pond J was next visited on June 19 F B had a brood, F W was present without her mate, but F Y was accompanied by her mate (day 23 of incubation). No males were seen

with F Y thereafter so the pair bond must have been weak by June 19 or then broke abruptly. Interestingly, the pair bond of F Y persisted until June 19. Thus, the pair bond tenure at Pond J was related to the reproductive state of the female, and not determined by chronology of nesting. However, at Pond K the pair bond of females that nested later lasted until about the same time (no later than June 13) as early-nesting females. Dzubin (in McKinney, 1965) found that in mallards apparently duration of the pair bond was influenced by chronology of nesting, for many males accompanied broods in a year with an early spring but not in most other years. McKinney (1965) reports that in pairs of ducks nesting later, the male leaves earlier during the breeding cycle than early nesting ones.

On Pond K in 1973 the pair bond was crudely estimated to have lasted to week 2 of incubation for one pair and week 1 for the other two pairs. These data partly support previous findings on pair bond tenure that "breeding drakes abandon their mates at onset or very early during incubation" (Drury *et al.*, MS), but show that the pair bond lasts considerably longer at certain ponds.

To summarize, on a cattail pond the pair bond of at least one pair, possibly the other, remained strong during week 1 of incubation, probably no later, for 2 years. On a bog pond during all 3 years the pair bond of all resident pairs (except for one pair in 1 year) remained strong for the first 3 weeks of incubation. The pair bond lasted 2 weeks longer on Pond J than H with those on Pond K apparently intermediate. On Pond J the pair bond of all resident pairs apparently lasted 2 to 3 days longer (day 23 of incubation) in 1974, when density of pairs was highest, than in other years.

Copulatory Behaviour Between Members of a Pair

Successful copulations, in which the complete sequence of post-copulatory behaviour was performed, were seen in 1973 at Pond H on 1 day during the laying period and at Pond J on 4 days during the incubation period. This suggested that copulations might be performed daily and function to maintain the pair bond during laying and part of incubation. For example at Pond H on May 24 from 0800 to 2100 the two resident pairs each copulated twice. At Pond J the two resident pairs each copulated one to three times on each of the 4 observation days during the first 3 weeks of incubation.

In 1974 the three marked females on Pond J were watched daily to determine their rates of copulation in relation to the stage of the breeding cycle. On 18 days between May 4 and June 6 I recorded the number of copulations observed during a minimum period of 10 hours for one to three pairs, mostly two. The data are more accurate for pairs W and Y, but frequency of copulations is probably underestimated for pair B.

Breeding pairs of buffleheads copulated more during prelaying, but in the period from prelaying to week 2 of incubation each pair on average copulated at least twice per day (Table 7). Each pair observed copulated at least once per day. One day during prelaying (May 6) pair W copulated five times.

The daily occurrence of copulations during incubation is of considerable interest. Incubating females returned to the pond two to four times per day. Females B and W copulated with their mates at least once, sometimes twice, during each visit to the pond for feeding, whereas, F Y copulated an average of only once per day, although she

Table 7. Frequency of successful copulations by three resident pairs in relation to stage of breeding cycle.

Stage in Reproductive Cycle	Colour-marked females			Mean no. copulations/ pair/10-hr. observation period
	B	W	Y	
Prelaying Period (Days 1-7)				
No. 10-hr. observation periods	1	3	3	
Total no. copulations observed	2	12	7	3.0
Laying Period (Days 1-6)				
No. 10-hr. observation periods	1	2	3	
Total no. copulations observed	1	6	5	2.0
(Days 7-13)				
No. 10-hr. observation periods	3	4	2	
Total no. copulations observed	3	8	3	1.6
Incubation Period (Week 1)				
No. 10-hr. observation periods	3	3	4	
Total no. copulations observed	5	7	5	1.7
Mean no. copulations observed/visit/day	1.0	1.2	0.5	
(Week 2)				
No. 10-hr. observation periods	5	3	1	
Total no. copulations observed	8	8	1	1.9
Mean no. copulations observed/visit/day	1.1	1.0	0.3	
(Week 3)				
No. 10-hr. observation periods	1	1		
Total no. copulations observed	1	1		1.0
Mean no. copulations observed/visit/day	0.5	0.5		

sometimes visited the pond at least three times in a day. During visits to the pond by F Y in which no copulations were recorded, the mate of F Y continued to perform pre-copulatory displays but F Y did not respond with a Prone posture. On the other hand, each time F B and F W visited the pond they adopted the Prone posture, while their respective mates performed pre-copulatory displays, followed by mounting and successful copulation. Females W and B were probably more sexually responsive to their mates than F Y. Pair B's rate of copulations was probably underestimated for all stages of the breeding cycle. Underestimates during incubation arose through two circumstances. Female B often visited the pond only once during the observation period, and there tended to be more copulations per visit during week 1 of incubation, yet careful watches of pair B copulations only began on May 29 (day 10 of F B's incubation) with the onset of F Y's incubation. Female W copulated twice on her first visit to the pond on day 1, 2, 4, and 9 of incubation suggesting that two copulations per visit were more likely during week 1 of incubation. So probably F B copulated at least 2 to 3 times per day during the incubation period.

All observed copulations between a pair of buffleheads occurred within their pair-space, sometimes near the boundary zone. As mentioned earlier although first attempts at copulation were often unsuccessful these were nearly always quickly followed by a successful one. I never saw any copulations interrupted by an intruding male.

There are probably few accounts of the frequency of copulations in wild ducks in relation to the breeding cycle. McKinney (1967) reports the frequency of copulations in captive shovelers. To compare my data with McKinney's I too calculated the rate of copulations on the basis

of 24 observation hours that females were available for copulation (Table 8). Shovelers usually copulated twice per day during prelaying, much less often during laying and rarely during the incubation period, when females were less available. Based on the time female buffleheads were available the rate of copulation was relatively constant during the prelaying and laying periods, then more than doubled during the first 2 weeks of incubation (Table 8). This rise reflects the fact that although females spent less time on the pond the average number of copulations per pair during this period was similar to that during other stages of the breeding cycle. Clearly, by this analysis, buffleheads copulate much more frequently than shovelers.

Bigamy With Neighbours

Monogamy is the only documented mating system of buffleheads. Bigamy with neighbours, a resident male simultaneously mated to his own mate and a neighbouring female, occurred on Pond J in 1973. No other cases of bigamy with neighbours were recorded at other ponds. However, bigamy with strange females was confirmed at Pond J in 1974.

In 1973 a breeding pair of red-necked grebes on Pond J apparently excluded both resident pairs of buffleheads between May 17 and 19 (see Page 106). By May 20 only one male bufflehead, presumably M 2, reoccupied the pond in the presence of the grebes. Exclusion by the grebes of two male buffleheads and reoccupation by one of them provided a situation for bigamy to occur. On May 22 M 2 accompanied two incubating females, F 1 and F 2, at the same time during their off-nest periods. Bigamy again prevailed on May 23 but not on May 27 when another male, presumably F 1's mate, reoccupied the pond and the mating system reverted to monogamy. A bigamous situation lasted at least 2

Table 8. Frequency [redacted]leheads and captive northern shovelers in relation to stage of the breeding cycle

Buffleheads	Prelaying Period (Days before laying) 5-8	Prelaying Period (Days before laying) 1-4	Laying Period (Days) 1-6	Laying Period (Days) 7-13	Incubation Period (Week) 1	Incubation Period (Week) 2	Incubation Period (Week) 3
No. of pairs observed	2	3	2	2	3	3	2
Successful copulations observed	8	23	18	17	25	22	2
Hours:minutes of observation that females were on Pond J	33:52	77:50	74:44	68:33	29:22	25:49	05:36
Rate of copulations per female available per 24 hrs. of observation	2.82	2.85	2.90	2.98	6.82	6.77	4.36
Rate of copulations per female shoveler available per 24 hrs. of observation (after McKinney, 1967)	0.29	0.23	0.08	0.19	-	-	-

days, probably 5.

On May 23 from 0800 to 1800, F 2 visited the pond thrice and F 1, twice. Male 2 copulated once with his own mate (F 2) and once with his neighbour's mate (F 1) when the respective females were alone with him. No copulations were seen when the trio was on the pond together on parts of two visits. Thus a paired male attended two incubating females, his own mate and his neighbour's mate, while the neighbouring male was absent, but only copulated when one female was with him.

Bigamy With Strangers

Copulation with strange females was suspected in 1973 at Pond J on June 5. Male 2 copulated with his own mate (F 2) at 1618, accompanied her as she fed until 1632, then flew over to a different nearby female and copulated with her twice in rapid succession. Male 2 flew back to his own mate then launched an aerial attack at the female that he had previously twice copulated with and pursued her from his pair-space. Possibly the pursued female would have been tolerated if the male's mate was not on the pond at the same time. No individuals were marked thus it was not known if the female with which he twice copulated was the other resident female (F 1), or a different female.

Conclusive evidence that resident paired males form a temporary pair bond and copulate with strange females as well as their own mate on the same day was obtained at Pond J on 3 days in 1974. The females mated to the resident males were all colour marked, thus any lone unmarked females were readily recognized. Throughout May paired males chased off all lone females from their space. On June 1 at 1244, while F B was on the pond and F W away from the pond, M W and M B in turn attacked and pursued a lone female. At 1248 M W flew over to a

lone unmarked female in his space, possibly the same one. [illegible] performed Head-bobbing, Leading, successfully copulated with her twice, attended her to 1320 while she fed then copulated with her a third time. At 1325, he mounted her again but the copulation was unsuccessful as there was no Rotation. This lone female resumed feeding, then after a short preening and loafing bout, left the pond at 1407.

On June 2 at 1003, while F B was away from the pond, a lone unmarked female landed in the east-end bay; M B performed Head-bobbing, Leading, copulated with her twice then accompanied her while she fed. After preening and loafing the lone female left the pond at 1054.

On June 6 M B copulated with a lone unmarked female at 1352, and attended her while she fed. During the female's preening and loafing bout, until she left the pond at 1518, M W made two separate approach flights toward her, but M B promptly attacked and pursued the intruder from his space. The Prone posture adopted by a lone intruding female and subsequent copulation with the resident male presumably serves to appease his aggression.

Thus on June 1, 2 and 6 a lone unmarked female spent periods at the pond of 80, 50 and 87 minutes respectively, exclusively within the pair-space of M W (June 1) and M B (June 2 and 6) while their respective mates were away from the pond. The lone female intruder initially copulated twice with the male occupant (M W on June 1 and M B on June 2), once with M B on June 6 before engaging in a long bout of feeding accompanied by a resident male. This activity rhythm of the lone female and the duration of her periods at the pond was similar to that of the marked incubating females. This suggests that the lone unmarked female probably was also incubating.

NEST SITE CHARACTERISTICS AND BEHAVIOUR AT NEST SITE

Characteristics of Nest Sites

Some characteristics of nest cavities used by female buffleheads occupying the study ponds are presented in Table 9. All cavities were in stubs (usually dead), five in aspen stubs near Pond J, and one in a balsam stub near Pond H. The dimensions of the nest-hole entrance of cavities 1 to 5 indicated they were excavated by common flickers. The larger nest-hole entrance (10 x 10 cm) of cavity 6 suggests that it was a flicker hole enlarged by rot or a hole of a pileated woodpecker (*Dryocopus pileatus*).

Height above ground of entrance holes ranged from 6.9 m to 14.3 m, an average height of 9.6 m. Including the heights (range 2.7 m to 7.0 m) of four holes in stubs used by buffleheads in 1964, also in the Atikameg area (A.J. Erskine, pers. comm.), the average height above ground of entrance holes was 7.9 m (26 ft). Thus in the Atikameg area, Alberta nearly all nest sites were in aspen stubs, more than 6 m (about 20 ft) above ground. By contrast in Interior British Columbia nest sites of buffleheads were found mostly in aspen trees at relatively low heights, 54 percent of them being two to ten ft (0.6 to 3.2 m) above ground (Erskine, 1972:65).

Only two nest sites near the study ponds were less than 75 m from the nearest pond or lakeshore, while the other four were 200 to 300 m or more distant (Table 9). Based on the distance that individual females flew from the pond, the nest site of F B, though not found, was at least 600 m from Pond J. The nest site of four other females at Ponds K and H, again not located, were mostly more than 300 m distant. These data support Erskine's (1972:63) findings that nest sites are

Table 9. Characteristics and use of nest cavities and nest-site tenacity of individual female bufflehead

Cavity No.	Height of nest-hole entrance above ground in metres (feet)	Distance in metres (feet) from nearest study pond	Type of poplar stub	Occupants 1972	1973	1974
1	14.3 (47.0)	69 (225)	aspen	F 1	F W	Flickers
2	6.9 (22.5)	46 (150)	aspen	-	F Y	F Y
3	9.5 (31.0)	380 (1250)	aspen	-	F R	?
4	11.6 (38.0)	375 (1230)	aspen	-	Flickers	F W
5	8.4 (27.7)	425 (1400)	aspen	-	-	F Or
6	6.9 (22.5)	213 (700)	balsam	-	F R-W	F R-W

farther away from water in Alberta, particularly in forested areas, than in parkland habitat in British Columbia. Erskine (1972:63) found that nearly half of 23 nest sites examined were between 25 and 75 ft (7.6 and 22.8 m) from water and most of the rest were up to 350 m distant, whereas in British Columbia about three quarters of 150 nest sites were within 25 m of water.

Availability and Use of Suitable Nest Sites

In this study no special effort was made to determine the availability and use of all suitable nest sites within an area or to assess factors affecting them. We searched for the nest cavities of particular females at all ponds, but mostly J. In this way a crude estimate was obtained of flicker cavities in patches of forest where buffleheads nested.

To estimate whether sufficient nest sites were available for buffleheads in the vicinity of the study ponds, I determined the number and proportion of available sites used by them and compared these data with Erskine's findings. In the Pond J area, from 1972 to 1974 inclusive, of 12 apparently suitable sites buffleheads used at least six (two of which were also used by flickers), flickers used two additional sites and four were apparently unoccupied. I believe most nest sites of buffleheads were found with the possible exception of one to two sites of peripheral females but the number of apparently unoccupied cavities and those used by flickers were probably underestimated. Assuming a maximum of four breeding pairs of buffleheads in the Pond J area (two to three resident pairs and one to two peripheral pairs) the number of nest sites (six) used by females over a period of 3 years represents 1.5 times the maximum breeding pairs in any one year.

Similarly, Erskine (1972:69) found that in aspen groves at Watson Lake, British Columbia, of 79 potential nest sites 28 (or 1.5 times the maximum breeding pairs of 18) were used by buffleheads over a period of 6 years. Furthermore, Erskine (1972:73) found that of the sites used by buffleheads in 1 year nearly half of those still available the next year were not used. Changes in use of nest sites resulted from deaths of females and new recruits into the population, desertion the previous year and competition from flickers, and other birds and mammals (Erskine, 1972). A minimum of two sites were used by buffleheads and two others were apparently unoccupied in the Pond H area during 1973. There were four and three broods on Pond H in 1972 and 1973, respectively, thus the number of sites used by buffleheads and those unoccupied is obviously underestimated. In the vicinity of Ponds J and H half the nest sites known to be available were used by buffleheads, but the number of sites available was probably underestimated at Pond H. By comparison in British Columbia, buffleheads used 35 percent of 79 available sites in aspen parkland at Watson Lake and 50 percent of about 40 available sites in Douglas fir forest at Philillo Lake (Erskine, 1972:69).

Erskine (1972:186) considered that sufficient flicker cavities were available for buffleheads and their competitors in parkland habitat in British Columbia, but that in forested areas in British Columbia and Alberta, because fewer sites were available and proportionately more used by buffleheads, the availability of nest sites may limit the number of breeding buffleheads.

Evidence in this study, such as the number of nest sites available, the proportion used by buffleheads and flickers and the availability of

aspen forest, suggest that nest holes *per se* were not limiting the number of breeding buffleheads in the Pond J area, and possibly the Pond H area. In the Pond K area no nest sites were found. The fewer flickers seen, the smaller areas of aspen forest suitable for excavation of cavities by flickers, the long distances that female buffleheads flew to the nest site suggest that fewer cavities were available in the immediate vicinity of Pond K than Ponds J and H. Tree swallows (*Iridoprocne bicolor*) used all three nest boxes, and flickers and starlings (*Sturnus vulgaris*) used two of three artificial cavities put up at Pond K to increase the number of sites available for buffleheads. One artificial cavity was apparently not used, perhaps because it was not as conspicuous as the other sites. The failure by buffleheads to use these sites does not necessarily indicate that sufficient natural cavities were available for them. Three pairs of buffleheads were resident on Pond K, then two more pairs settled but subsequently left possibly because they were unable to find a suitable nest cavity. They may have been deterred from using the artificial sites because most of these sites already were occupied by other species of hole-nesting birds and also resident male buffleheads attacked female conspecifics attempting to inspect nest sites (described below). These factors, then, could have prevented buffleheads using these nest sites and thus the presence of artificial nest sites at the edge of the pond may not, in fact, have increased their availability to the ducks.

Nest-site Tenacity

Individual female buffleheads have a strong tendency to use the same nest cavity at least in two successive years. In this study, of three females caught and marked at the nest site in 1973, two used the

same nest site the following year and one changed nest sites following desertion (Table 9). These findings agree with those of Erskine (1972). Erskine (1972:214) compiled nest-site histories for 45 female bufflehead. Of these, 38 females (84 percent) used the same nest site at least two years in succession irrespective of earlier or later changes in nest site. Erskine (1972:74) reported that females handled more than twice changed nest sites more often. Only 12 of 45 females (27 percent) used the same nest site in three successive years, however this represents 57 percent of all females with a history of three years or more (Erskine, 1972:214). Therefore to evaluate natural nest-site tenacity over time many factors such as competition for nest sites, suitability of sites, disturbance, desertion and female survival have to be considered.

Male Aggression at Nest Sites

Aerial attacks by a resident paired male bufflehead directed at a female conspecific trying to inspect a nest site were seen in 1973 and 1974 at Pond J. On May 11, 1973 an unmarked lone female flew toward cavity number 2 about 50 m from Pond J, paused at the entrance hole but an aerial attack by M 2 caused her to flutter toward the ground. I estimated that F Y laid egg 1 in that cavity on May 18, so the attacked female was most likely F Y (at that time unmarked).

Nest-searching flights by a female bufflehead, mostly accompanied by her mate, may elicit aerial attacks and pursuit by a neighbouring paired male. In early May 1974 F Y at first avoided inspecting nest site number 2 she used the previous year and searched elsewhere, perhaps because this site was nearest pair W's space and a flight to it may have released aggression from M W.

On May 12, presumably because F Y failed to find a suitable alternative site, pair Y made search flights over Pond J and in patches of forest near cavity number 2, and then approach flights directly toward this cavity. These flights, particularly the approach ones, sometimes released aerial attacks by M W and ended in a three-bird flight (TBF). The sequence of these flights by pair Y and the response of M W during 1 hour was 5 search (1 - TBF), 2 approach (2 - TBF), 2 search (1 - TBF) and 2 approach (1 - TBF). During the last approach flight by pair Y, M Y intercepted M W's aerial attack and engaged in a two male aerial pursuit, then F Y flew alone toward the entrance hole. However, she failed to alight at the hole and descended to a nearby peripheral pond. Then F Y made an approach flight from the peripheral pond alone and successfully entered the cavity. Thereafter no more search flights were seen.

Behaviour of Females During the Laying Period

The short interval between arrival of pairs and start of laying was 7, 6 and 10 days, respectively for females B, W and Y at Pond J in 1974.

Dates of laying were much less accurately determined in 1973 than in 1974. In 1973 at Pond H the estimated date of clutch initiation for F R-W was between May 12 and 14. I estimated that at Pond J, F R and F W initiated clutches in 1973 between May 1 and 3, and May 7 and 9, respectively, a mean date of May 4 to 6, 8 to 10 days earlier than F R-W. By contrast at Pond J in 1974 the three females, B, W and Y, started laying on May 6, 9 and 15, respectively, a mean date of clutch initiation of May 10 for three females and May 7 to 8 for the two earliest laying females, 3 to 4 days later than in 1973.

The intervals between laying varied with individual females (Figs. 14 and 15). For F B, clutch size was unknown, hence the rate of laying could not be estimated accurately. Female Y laid on alternate days at intervals of about 48 hours, whereas F W appeared to lay eggs at varying intervals. For example, for F W the interval between laying egg 1 and 2 was apparently about 40 to 45 hours, eggs 3 and 4 were laid at about 48 hour intervals, and eggs 5 to 8 were laid at about 35 hour intervals. Female W's increased rate of laying for eggs 5 to 8 of the clutch supports Erskine's (1972:80) finding, suggesting "a shift from laying on alternate days early in the clutch to laying on successive days towards the end of the clutch".

Most eggs appear to be laid in the morning (Figs. 14 and 15), agreeing with Erskine's (1972:80) findings. Time spent in the nest cavity during the laying period varies with individual females (Figs. 14

Figure 14. Presence of female Y on Pond J between May 13 and 28, 1974.

Start and end of observation periods are indicated by vertical bars, and the time between them is the observation period.

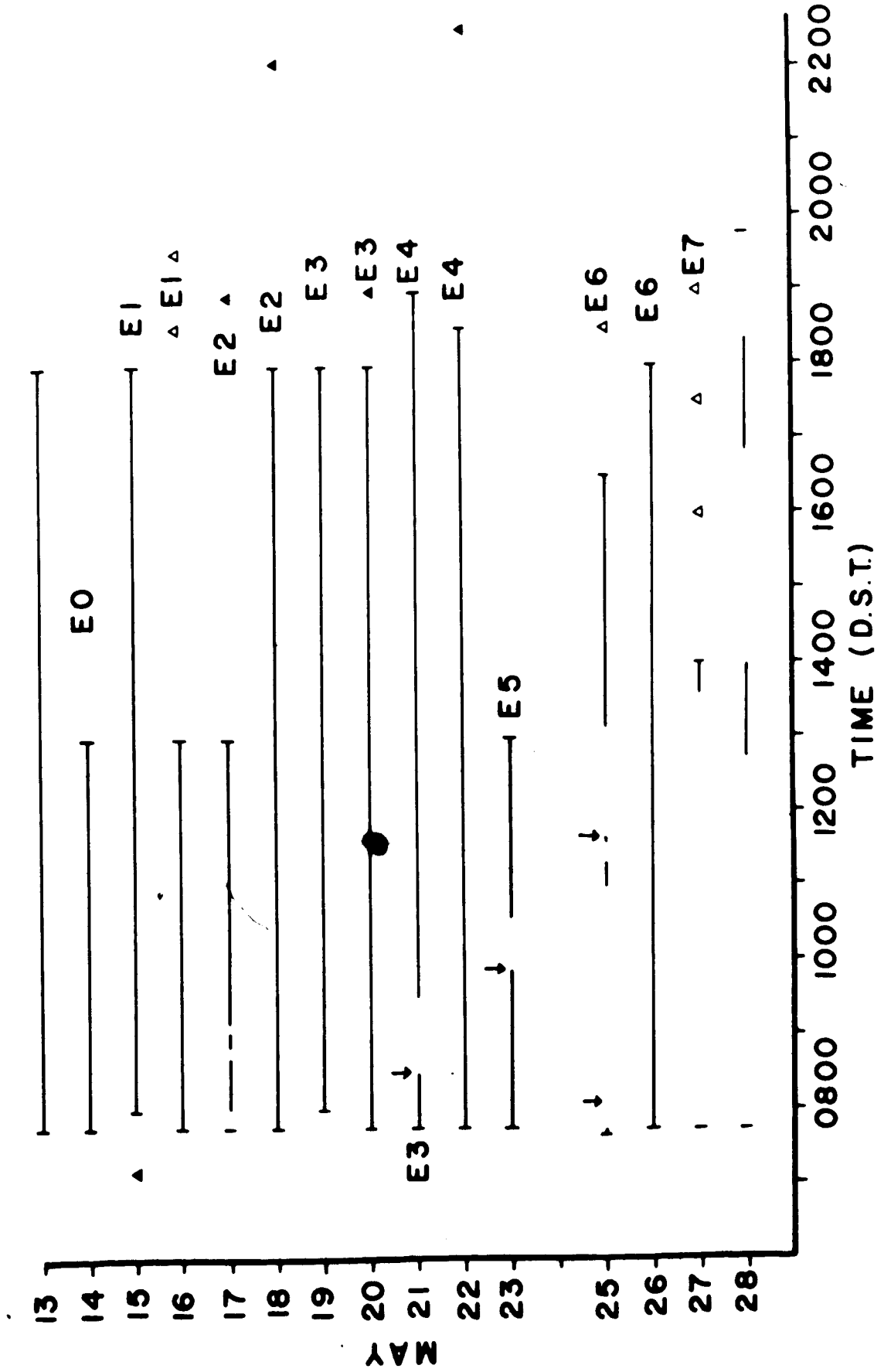
Solid horizontal lines represent presence of female on pond, and break in line, absence from pond.

Numbers after E refer to number of eggs in cavity at time of inspection.

▲ female present when pond checked briefly

△ female absent when pond checked briefly

↓ female seen to enter nest cavity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TIME (D.S.T.)
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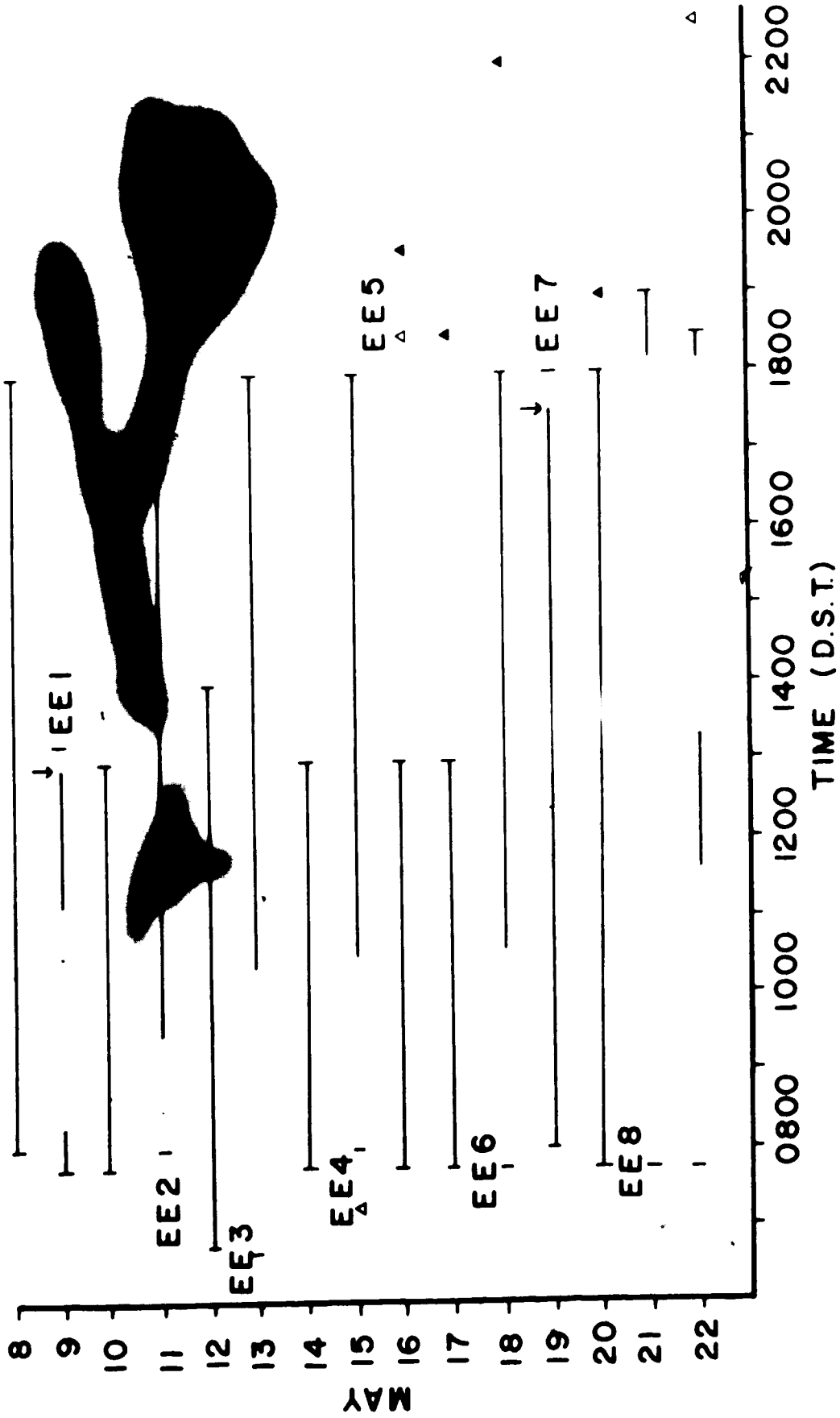
E3
E4
E4
E5
E6
E6
E7

Figure 15. Presence of female W on Pond J between May 8 and 22, 1974.

See Figure 14 for explanation of vertical bars, solid horizontal lines and breaks in lines.

Numbers after EE refer to the estimated number of eggs in the nest cavity on given days.

↓ female flew toward nest cavity.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EE2
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EE5
EE6
EE7
EE8

and 15). During the laying period females apparently occupy the cavity only on those days eggs are laid (Figs. 14 and 15). Apparently F Y spent very little time in the cavity laying eggs 1 to 5, but then spent increasing time in the cavity on the days eggs 6 and 7 were laid (Fig. 14). Incubation apparently started the same day as F Y laid the last egg. Female W probably spent 4 to 5 daylight hours in the nest cavity on mornings when eggs were laid, but probably less time when eggs were laid in late afternoon (Fig. 15). However, on May 21 when F W presumably laid her last egg she was away from the pond all day until 1800 (Fig. 15). Similarly F B spent a morning and part of an afternoon (May 18) away from the pond when the last or second last egg was laid (Fig. 13)

Female buffleheads spent the entire 5 and 10-hour observation periods on the pond (Figs. 14 and 15) within their own space on the days they apparently did not lay eggs. On days when eggs were laid females spent from 40 minutes to nearly 3 hours away from the pond (Figs. 14 and 15), and the rest of the 5 and 10-hour observation periods were spent within their own space. During the laying period, especially the latter half, each paired male attended his mate closely while she fed.

Clutch Size

Clutch size of three individuals in each of 2 years is presented in Table 10. Mean clutch size was constant at 7.7 for each year, but less than that of 8.75 for Alberta (Erskine, 1972:83).

Maximum size of the four largest class Ia broods in 1972 at three study ponds was 12 (J), 11 and 9 (H) and 10 (K). By contrast, in 1973 maximum brood size was 8 (L), 7 (J), and 7 and 7 (H). These few data suggest that clutch size may vary between years for the same habitats.

Erskine (1972:86) reported that mean clutch size of buffleheads showed relatively little change between years. However, annual variations in clutch size have been demonstrated in other diving ducks, for example, the ring-necked duck (Mendall, 1958), and the tufted duck (*Aythya fuligula*) and scaup (*A. marila*) (Hildén, 1964).

Clutch size of individual buffleheads was relatively constant between years (Table 10), however this may reflect the similarity in mean clutch size for these 2 years. Erskine (1972:87) found that clutch size of individual buffleheads varied markedly between years.

The laying of smaller clutches as the season progresses, an initial rise then a decline, has been shown in buffleheads (Erskine, 1972:86). This trend is similar to that in passerines (Klomp, 1970), however, clutch size declined from the start of the breeding season in other diving ducks, for example, the tufted duck and the pochard (*Aythya ferina*) (Havlin, 1966), and in species of dabbling ducks of the genus *Anas* (Sowls, 1955).

Behaviour of Females During the Incubation Period

During the incubation period three colour-marked females spent from two to at least four off-nest periods per day at Pond J in 1974. When a female alighted in her pair-space her mate swam or flew over to her and she either started feeding straight away or the pair copulated. The two most sexually responsive females, W and B, copulated with their respective mates, usually within a few minutes of their arrival on the pond. During each visit to the pond a female engaged in a long bout of feeding, usually foraging along the shoreline, closely attended by her mate. She then spent a short period of preening and loafing before returning to her nest site.

Table 10. Clutch size of three individual bufflehead in 1973 and 1974

Colour-marked female	1973	1974	Mean
R-W	8[1]	8[1]	8
W	7[2]	8[1]	7.5
Y	8[3]	7[1]	7.5
Mean	7.7	7.7	7.7

[1] Actual clutch size determined from inspecting the nest cavity during the incubation period.

[2] Clutch size determined from inspecting the cavity after the female deserted the eggs.

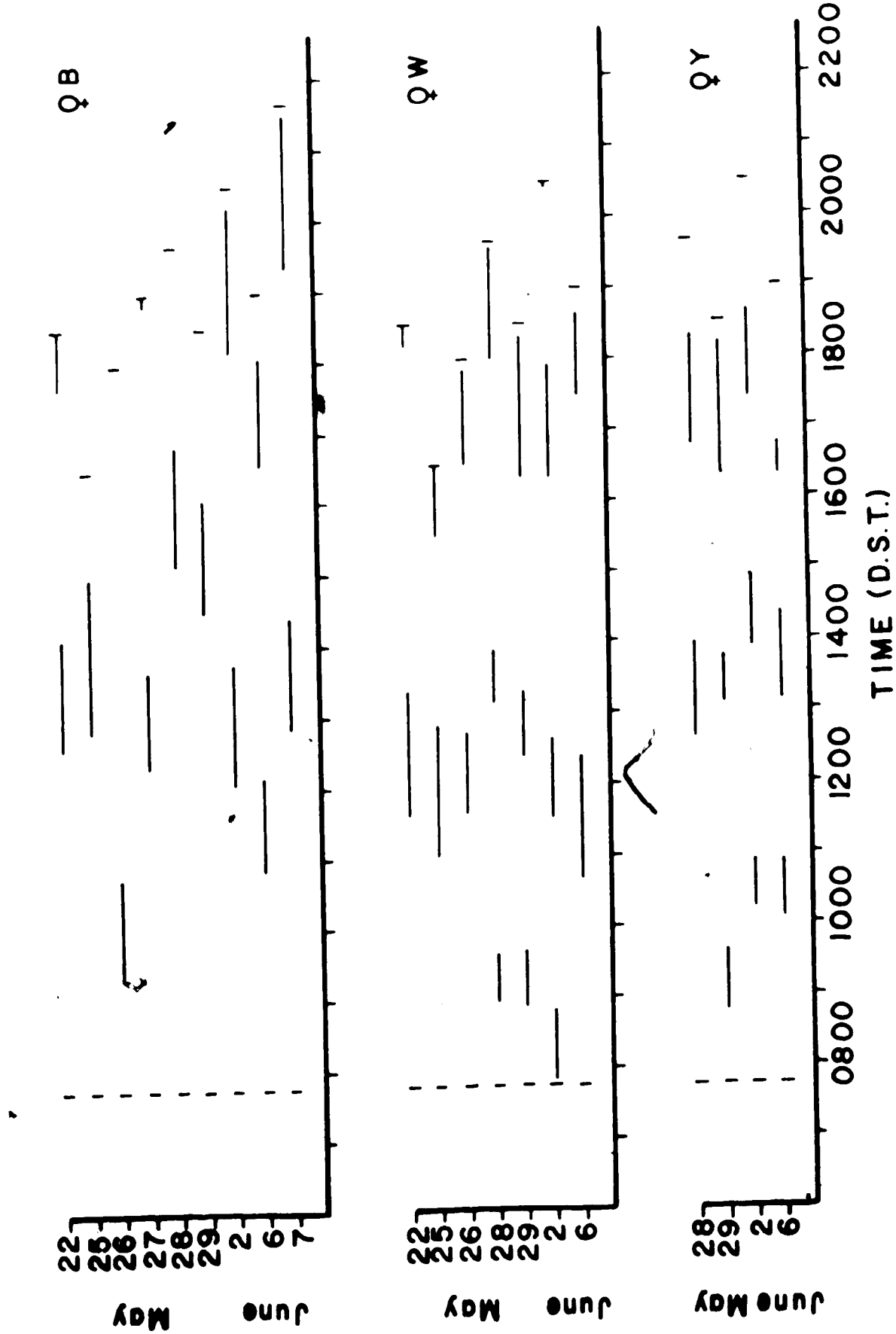
[3] Clutch size estimated from a class Ia brood of seven plus one egg remaining in the cavity. The ducklings were counted on the day they arrived at the pond within 50 m of their cavity, so I assumed no ducklings were lost travelling on land.

Incubation rhythm, the pattern of off-nest periods at the pond, was determined for three marked females for most hours of the day (Fig. 16). These data were gathered during mornings, incidental to recording interactions among males, and continued on throughout the afternoon until sometime after 1800 when there were no further females on the pond. No observations were made during the first 2 hours after sunrise. Thus it was not known for certain if females visited the pond during the early morning hours. Other evidence suggests that incubating females stay in the nest cavity at this time. For example, at Pond J in 1972 there were five morning watches, four began 1 hour and one, half an hour after sunrise, during the incubation period of two females, and at no time did females arrive at the pond within the period 4 hours after sunrise. Furthermore Erskine (1972:91) found females in the nest cavity on all of five visits within about 2 hours after sunrise. Incubation rhythm of the bufflehead, based on automatic recording, has not been documented. However, in Finland, Sirén (1952) used automatic apparatus to continually record the incubation rhythm of a congeneric female common goldeneye throughout her entire incubation period. In the period 2 hours after sunrise this goldeneye was never off the nest, and in the period 4 hours after sunrise she was off the nest only once in 30 mornings. I suspect that female buffleheads and goldeneyes only rarely leave the nest in the early morning. However, it is possible that individual females deviate from this pattern.

From Figure 16 it can be seen that the off-nest periods varied somewhat among individuals. If we assume that there were no off-nest periods in the early morning, then it appears that F B spent two periods at the pond per day, whereas the other two females, F W and F Y,

Figure 16. Presence of three colour-marked females on Pond J during part of their respective incubation periods in 1974.

See Figure 14 for explanation of vertical bars, solid horizontal lines, and breaks in lines.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22 25 26 28 29 2 6
28 29 2 6

spent three to four periods (Fig. 16). The data for June 2 and 7 indicate that F B most likely spent only two off-nest periods at the pond on each of those days.

The percentage and total time that F B spent on the pond per day during her off-nest periods closely coincides with those of F W on each day that these data were recorded for F B for either two periods or part of the second period (Table 11, Fig. 16). Female Y spent a similar proportion of time on the pond each day (Table 11). The relatively constant and high mean time per off-nest period for F B reflects her incubation rhythm of two visits per day to the pond (Table 11). By contrast the mean time per off-nest period for F W was shorter on those days she visited the pond three times (Table 11).

It is not clear whether these differences in incubation rhythm resulted from individual variation among females, their reproductive state and/or changes in the environment. However, during the first 2 weeks of their respective incubation periods, F B's space and shoreline expanded as those of F W contracted concomitantly. Thus the fewer off-nest periods of F B in association with a high mean time per off-nest period could be related to her greater foraging space and shoreline. Female W's mean time per off-nest period was low when foraging space declined, then rose as her space increased slightly. It is tempting to suggest that F W visited the pond more often for shorter periods in response to her contracting space. However, there was no evidence to support or refute this idea, and a similar rhythm may have occurred even without a change in space.

Table 11. Time spent by three marked females on Pond J during their incubation periods in 1974.

Date	Observation time (mins)	FEMALES B: Day of Incubation	B: Total time at pond (mins)	B: % time at pond	B: No. complete off-nest periods	B: Mean time per off-nest period (mins)	W: Day of Incubation	W: Total time at pond (mins)	W: % time at pond	W: No. complete off-nest periods	W: Mean time per off-nest period	Y: Day of Incubation	Y: Total time at pond (mins)	Y: % time at pond	Y: No. complete off-nest periods	Y: Mean time per off-nest period
May 22	640	3	135	21.1	1	92	1	120	18.8	1	103					
25	525	6	131	25.0	1	131	4	171	32.6	1	111					
26	615	7	84	13.7	1	84	5	149	24.2	2	74					
28	715	9	100	14.0	1	100	7	177	24.8	3	59	1	167	23.4	2	83
29	645	10	99	15.3	1	99	8	164	25.4	3	55	2	153	23.7	3	51
June 2	765	14	225	29.4	2	113	12	225	25.4	3	63	6	183	23.9	3	61
6	675	18	173	25.6	2	87	16	167	24.7	2	84	10	142	21.0	3	47
7	840	19	216	25.7	2	109	-	-	-	-	-	-	-	-	-	-

SPACING BEHAVIOUR OF FEMALES WITH BROODS

Arrival of Broods

Date of arrival of all class Ia (2 to 6 days old) bufflehead broods seen on 6 ponds in 1972 and 4 ponds in 1973 is shown in Figure 17. The actual day of arrival was known for one third of newly hatched broods, presumably 2 days old, and was estimated to ±1 day or less for most other broods.

The arrival of broods was staggered over 5.5 weeks, with the earliest brood arriving on June 13 and the latest between July 19 and 21. Staggering of arrival of broods is clearly seen on ponds with more than two broods. For example, arrival dates of broods with number of broods in parentheses for Pond H were in 1972: June 22 to 26 (2), July 5 to 9 (2); in 1973, June 27 to July 2 (2), July 19 to 21 (1); at Pond J in 1973, June 13 to 22 (2), and July 3 (1).

Homing

In 1972 the number of resident pairs on a pond mostly coincided with the subsequent number of broods suggesting that an individual female returned to the same pond with her brood that she had occupied a few weeks earlier with her mate.

The homing tendency was confirmed the following year with colour-marked females. Of two resident pairs on Pond H, F R-W returned there with her brood, and an unmarked female with a brood, possibly the other resident female (F 2), was seen on Pond H on July 2 but subsequently moved, possibly to a nearby lake, in response to the presence of a pair of red-necked grebes resident on Pond H (discussed later). At Pond J one of two resident females (F R) homed a distance of about 300 m with her brood, while the other female (F W) deserted her eggs. Two

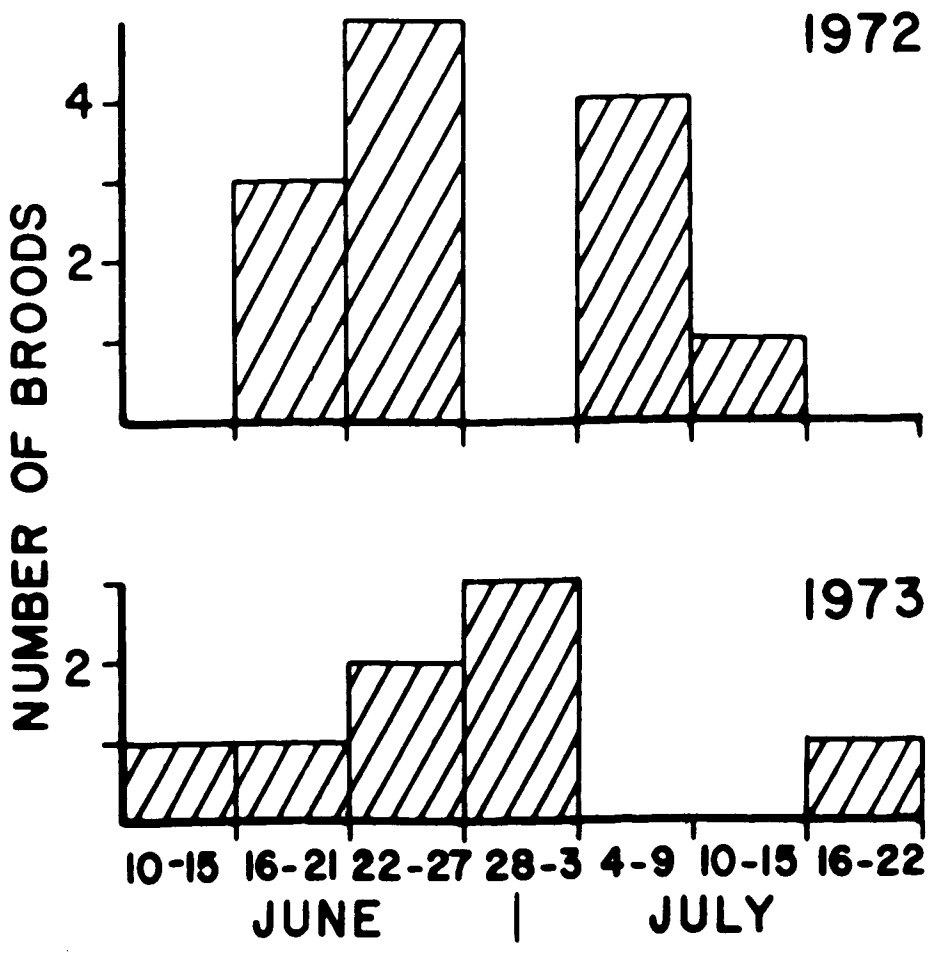


Figure 17. Number of class Ia bufflehead broods on ponds in relation to date of arrival.

peripheral females (F Y and F B) arrived at Pond J with their broods. There were four unmarked resident pairs on Ponds K and L combined, yet only two unmarked females arrived with broods. These observations confirm a homing tendency in females with broods to Ponds J and H, and possibly K.

In 1974, however, of three colour-marked females resident on Pond J, and one on Pond H (F R-W), only one (F B) returned with her brood, a distance of at least 600 m. Evidence presented later suggests that the homing response is modified by environmental stimuli at the pond near the time of settlement.

Introduction to Spacing Behaviour

Hostility between female buffleheads with broods, and the resulting spacing of them, has not been documented. Erskine (1972:101) suggests females with broods only establish home ranges. I first saw hostility between females with broods at Pond H in 1972. At that time (July 10) I saw a fight between two of the four females with broods, and two more fights on July 14 involving three different females. All day observations (0630 to 2200) on July 16 of four unmarked females with broods (two with class Ib broods and two with IIa broods) confirmed that fights occurred at fixed positions in space near the shoreline and that each female with a brood restricted its activities to a particular space (Fig. 18). This behaviour suggested that these females maintained a stable, exclusive area by fighting and threat. However, on July 20 one female with a brood, probably F 3, was not on the pond. Her abandoned brood joined F 1's brood of similar age (IIb); other broods appeared to mix but no further fights were seen. Unmarked individuals, broods of similar age and number, and mixing of broods all made it difficult

Figure 18. Spatial relationships among four unmarked females with broods on Pond H on July 16, 1972.

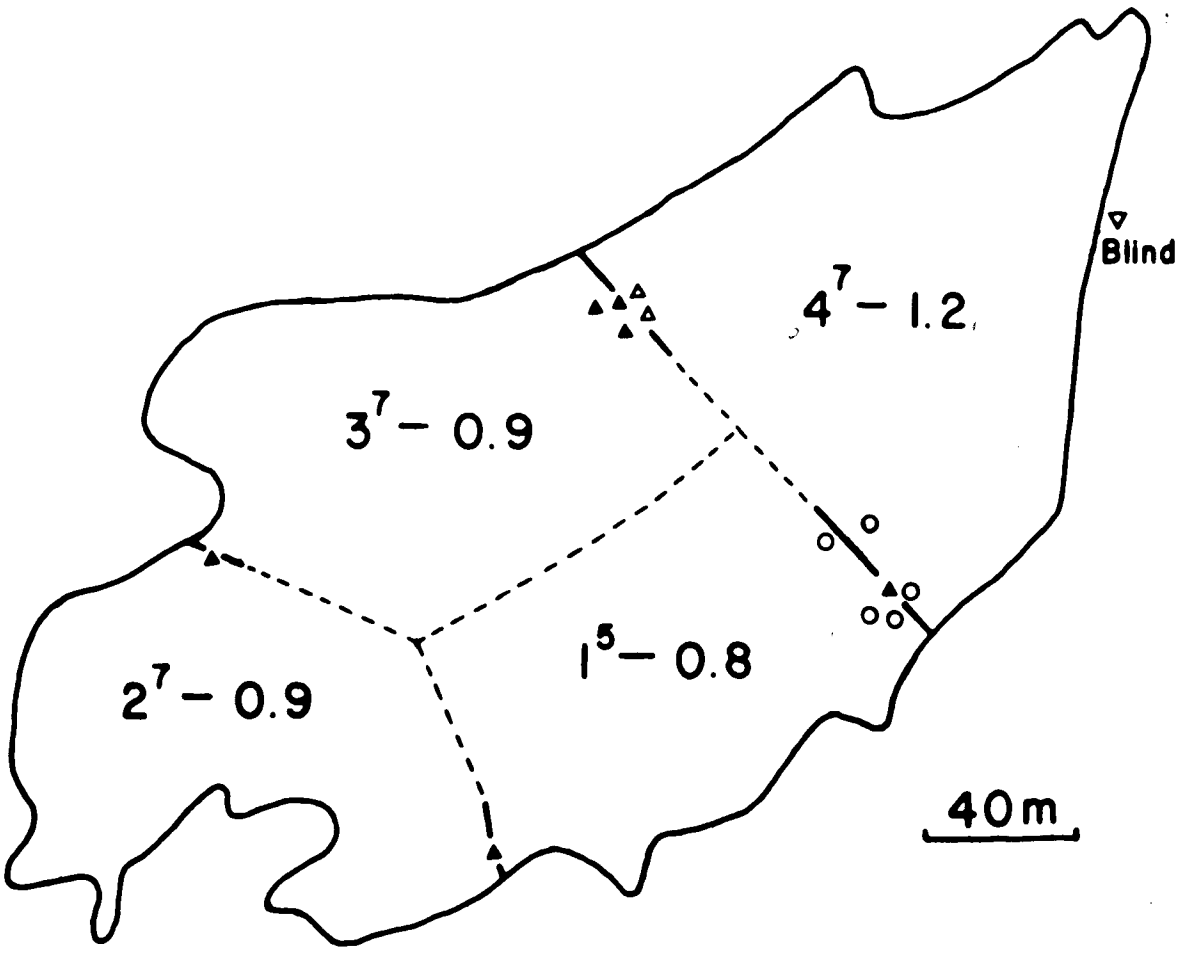
A number, followed by a superscript number then a decimal fraction, located within the centre of each brood-space denotes an unmarked individual female with a brood. The superscript indicates the number of ducklings in each female's brood. Decimal fractions represent the area of space, expressed to the nearest 0.1 hectare (ha), held by each female with a brood.

For example, 4^{7}-1.2 indicates a brood-space of 1.2 ha held by female 4 with 7 ducklings.

The age classes of the respective broods on July 16, 1972 were as follows:

Female	Age class
1	IIa
2	Ib
3	IIa
4	Ib

Solid lines are boundaries based on locations of threats and fights between females with broods. Dashed lines are boundaries estimated from movements of females and their broods.



△ Approach — withdrawal

○ Threat

▲ Fight

to determine conclusively a degree of attachment to a specific space by a female with a brood.

Fortunately, in 1973 at Pond J all three females, with broods of different size and age, were colour-marked and their social interactions recorded over a 20-day period in which the brood-space of one female expanded as another contracted, while that of the third was relatively stable. Interactions between females with broods were recorded for shorter periods at Ponds H and L in 1973, and at Pond J in 1974.

Description of Intraspecific Agonistic Behaviour

Brief descriptions will suffice as the agonistic behaviour of females with broods is essentially similar to that of males described in detail earlier.

1. Approach - Withdrawal

In these encounters the approach of a female with a brood usually by swimming and alternately diving and surfacing in the Head-forward posture or by an approach flight, prompts its opponent to withdraw by an avoidance flight or by swimming away.

2. Threat

Neighbouring females with broods engage in reciprocal threat encounters, within and along a boundary zone by alternately diving and surfacing in the Head-forward posture in essentially the same manner as males.

3. Attack - Retreat

Supplanting attacks, as described for males, may be directed by females with broods at each other or by a female with a brood at a lone [redacted], presumably a yearling. A female expanding her

brood-space directs aerial attacks at her opponent in two situations, when the attacker intrudes into the space of its opponent and when the latter trespasses into the newly acquired space.

4. Fighting

Fighting between neighbouring females with broods is usually preceded by threat encounters and occurs within a boundary zone. Fights are often initiated by aerial attacks and mostly erupt on the water surface, unlike those of males which erupt underwater. Fighting on the water surface mostly consists of attack lunges with little contact very similar to that described for males. Fights may also be interrupted or terminated by flap-paddle chases. Fights usually last about half a minute, but one was recorded lasting nearly 2 minutes. Fighting encounters usually end with an appeasement display then the Wing-flap Display. The side by side appeasement posture of males is not performed by females. Females with broods usually end fighting with Facing Away then move apart to give the Wing-flap Display (see males) or fly to their broods.

5. Aerial Pursuit

An intruding lone female may be attacked then pursued by a female with a brood until the trespasser flees from her space. Vigorous aerial pursuits occur between females with broods when one female attempts to establish a brood-space on a pond, or expand its existing space and its opponent tries to resist the intrusion. As in aerial pursuits between males, the pursuer occasionally grabs the pursued in flight. In situations with relatively stable boundary zones aerial pursuit was not seen.

Agonistic Behaviour in Space and Time

1. Introduction

Only the 1973 data for Pond J were suitable for a detailed quantitative analysis of spatial-temporal relationships between females with broods. To determine the nature of the spacing mechanism and the relationships between individuals in time and space, the frequency, intensity, location and outcome of agonistic encounters in relation to changes in size of brood-space are analyzed first for Pond J in 1973. Then the interrelationships between aggression, size of brood-space, size of brood and age of brood are examined.

An encounter between two females with broods refers here to a continuous sequence of agonistic behaviour that ended when one female engaged in other activity such as Wing-flap Display, preening or swimming away from her opponent. Encounters between these females were classified into six categories according to their intensity and sequence of behaviour patterns.

Approach by one individual and withdrawal or avoidance by the other was recognized as category 1.

Reciprocal threat encounters were assigned to category 2, supplanting attacks with no aerial pursuit to category 3, and fighting with or without flap-paddle chases but no aerial pursuit, to category 4.

Encounters with only one aerial pursuit that may be preceded by supplanting attacks, fighting and/or flap-paddle chases with one individual dominant were recognized as category 5.

Category 6, the most intense encounters with one individual dominant, consisted of a mixture of supplanting attacks, chases and fighting on the water surface together with either a) more than one

ter of pursuit, or [illegible] further attacks after an aerial pursuit.

2. Spacing Behaviour of Three Colour-marked Females on Pond J in 1973

Three females with their broods arrived at Pond J over a period of 21 days. Female R and her brood arrived first on June 13. An unmarked female (marked F B on July 3) and her brood arrived next and occupied a peripheral pond adjacent to J between June 21 and 22, and then Pond J by June 25. Female Y and her brood arrived last on July 3. The ages of the broods differed considerably. Female R's brood was 8 days older than that of F B, and 20 days older than that of F Y. Hereafter, R or red refers to F R, B or blue to F B and Y or yellow to F Y.

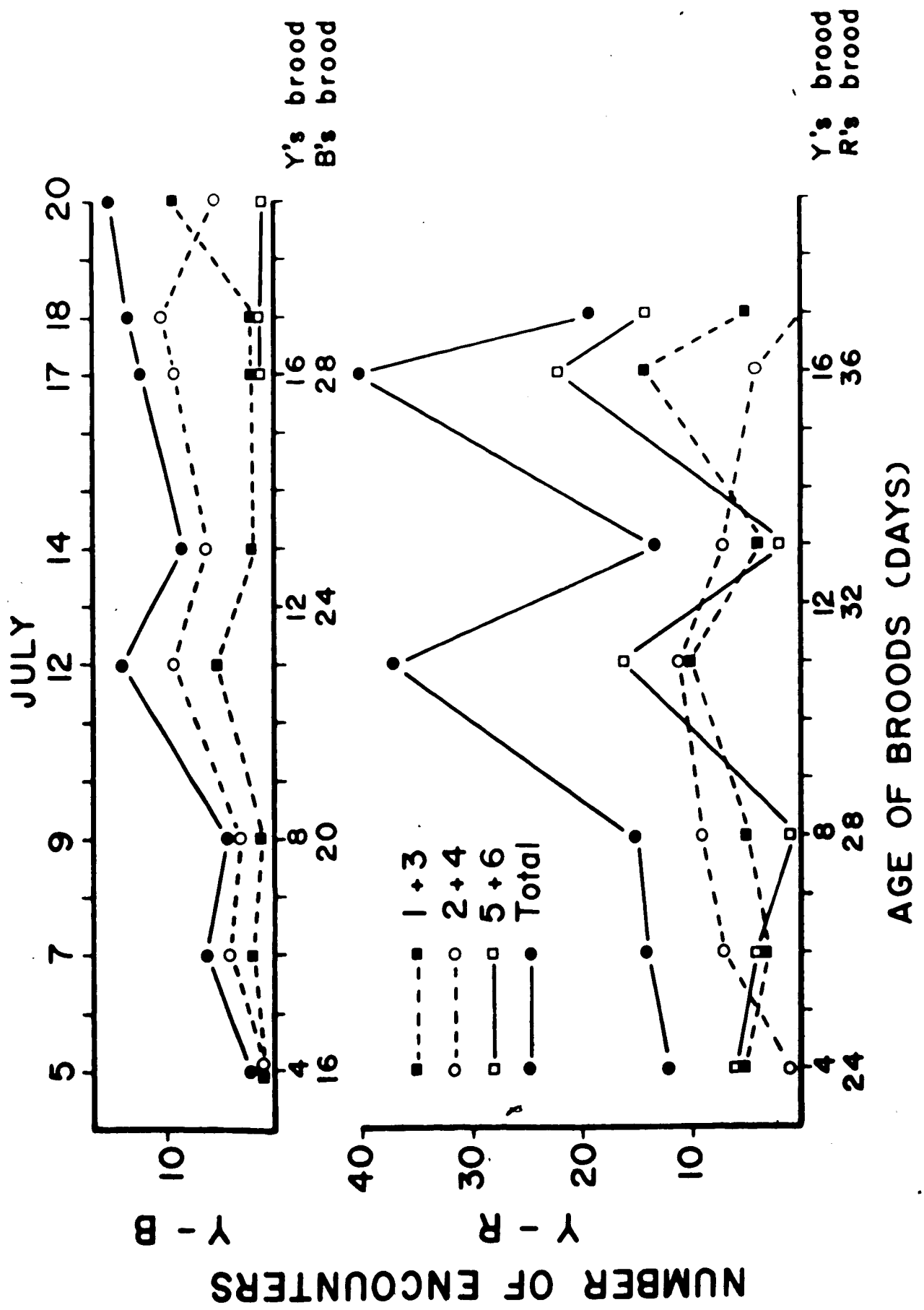
Figure 19 depicts the frequency and intensity of agonistic encounters between three marked females during a period in which Y gradually expanded her brood-space, first forcing R off the pond, then occupying the whole pond when B no longer maintained her brood-space. In general the total number of encounters increased with time. Yellow occupied a central space and interacted about twice as much with R as with B. There were virtually no interactions between B and R. To quantify more simply the changes in agonistic behaviour in terms of maintenance of space I combined a) reciprocal encounters characteristic of maintaining space, categories 2 and 4; b) milder non-reciprocal encounters, categories 1 and 3; and c) more intense non-reciprocal encounters, categories 5 and 6 (Fig. 19). The agonistic responses of Y differed markedly between encounters with R and those with B.

Encounters between Y and B characterize agonistic behaviour associated with maintenance of a relatively stable brood-space. Even though B's space contracted considerably at first, it then expanded and

Figure 19. Frequency and intensity of agonistic encounters between three colour-marked females with broods on Pond J between July 5 and 20, 1973.

The numbers 1 to 6 represent six categories of agonistic encounters described in the text.

1. Approach - withdrawal
2. Threat
3. Attack - retreat
4. Fight
5. Aerial pursuit - low intensity
6. Aerial pursuit - high intensity


NUMBER OF ENCOUNTERS
Y - B
Y - R
JULY
5
7
9
12
14
17
18
20
4
16
8
20
12
24
16
28
Y's brood
B's brood
Y's brood
R's brood
4
24
8
28
12
32
16
36
AGE OF BROODS (DAYS)
1+3
2+4
5+6
Total
10
20
30
40

remained relatively constant. The greater proportion of threat and fighting encounters (categories 2 and 4) up to July 18 were associated with B's maintenance of her brood-space. Aerial pursuits were infrequent and not recorded until July 17. On July 20 a decline in the proportion of reciprocal encounters was accompanied by a rise in supplanting attacks by Y and retreats by B until B no longer excluded conspecifics from space.

Agonistic responses in encounters between Y and R illustrate an expansion-contraction-eviction situation in which Y's space continually expanded as that of R's contracted, then R was evicted from the pond by Y. Fleeing by R in response to Y's attacks and pursuits increased with time, while threat and fighting encounters, associated with defence of space, declined (Fig. 19). Aerial pursuits occurred each observation day, but were most frequent on those days with a high number of encounters associated with major gains in space.

Changes in sizes of brood-space and the location of agonistic encounters are shown in Figure 20 - Maps 1 to 9. Three phases can be distinguished during the period that sizes of brood-spaces changed: Phase I refers to the period before the arrival of Y; Phase II to the period from July 5 to 9 when B's space contracted considerably and that of R was relatively stable; and Phase III refers to the period from July 12 to 20 when R was evicted and B's space was relatively stable.

During phase I, before Y arrived, the open water area of the pond was totally divided between R and B, with B occupying the larger brood-space (Fig. 20 - Map 1). Phase II, the observation period from July 5 to July 9, began when Y and her brood arrived at Pond J on July 3. Yellow settled in the north-west bay where a boundary zone had

Figure 20. Spatial relationships among three colour-marked females with broods on Pond J between June 28 and July 20, 1973.

A letter followed by a superscript number then a decimal fraction represents females individually colour-marked with nasal saddles as follows:

R red

B blue

Y yellow

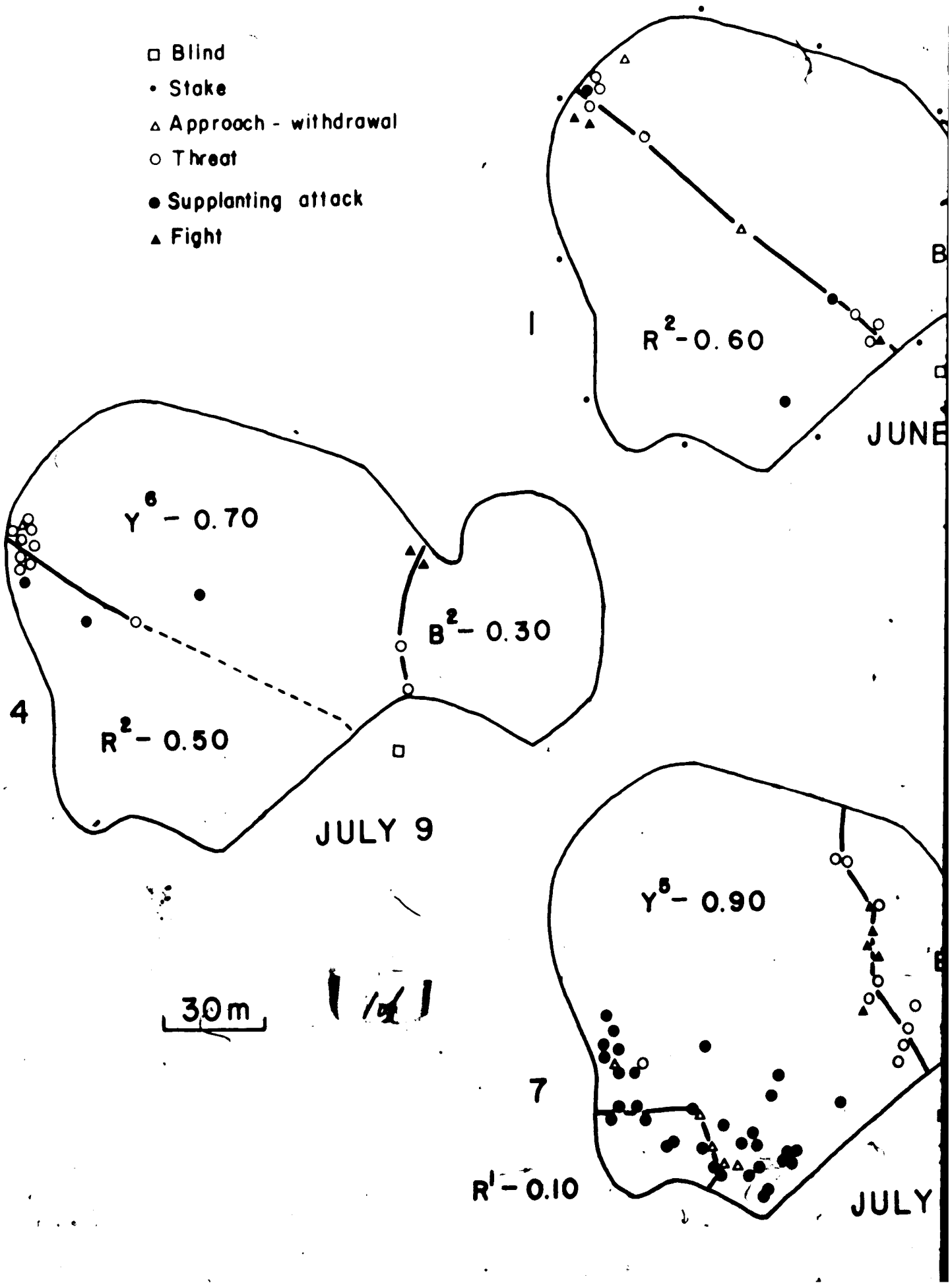
The superscript indicates the number of ducklings in each female's brood on given days.

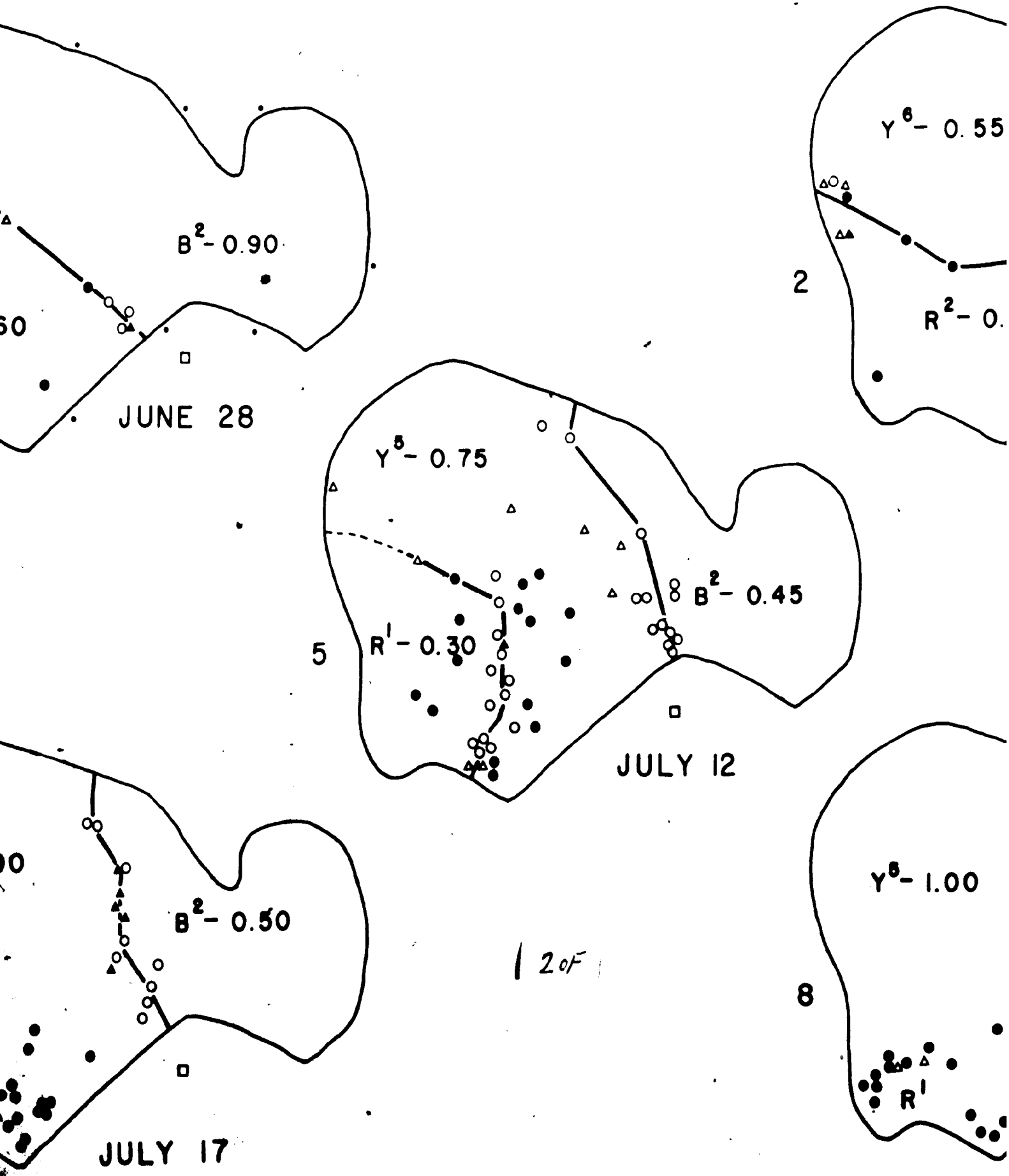
Decimal fractions denote the area of space, expressed to the nearest 0.05 hectare (ha), held by each female with a brood on given days.

For example, Y^{6}-0.55, indicates a brood-space of 0.55 ha held by female Y with 6 ducklings.

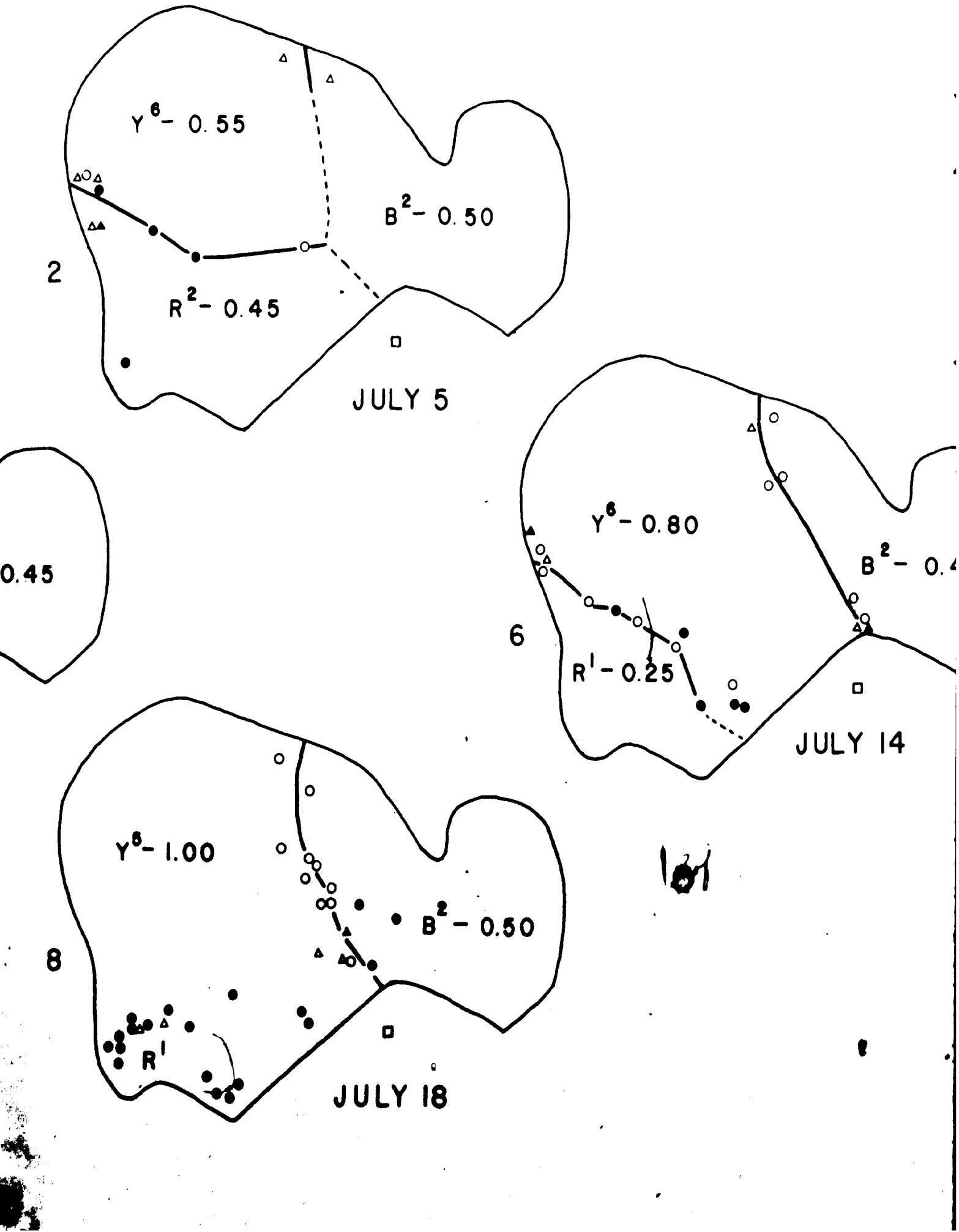
Solid lines are boundaries based on the locations of agonistic encounters between females with broods.

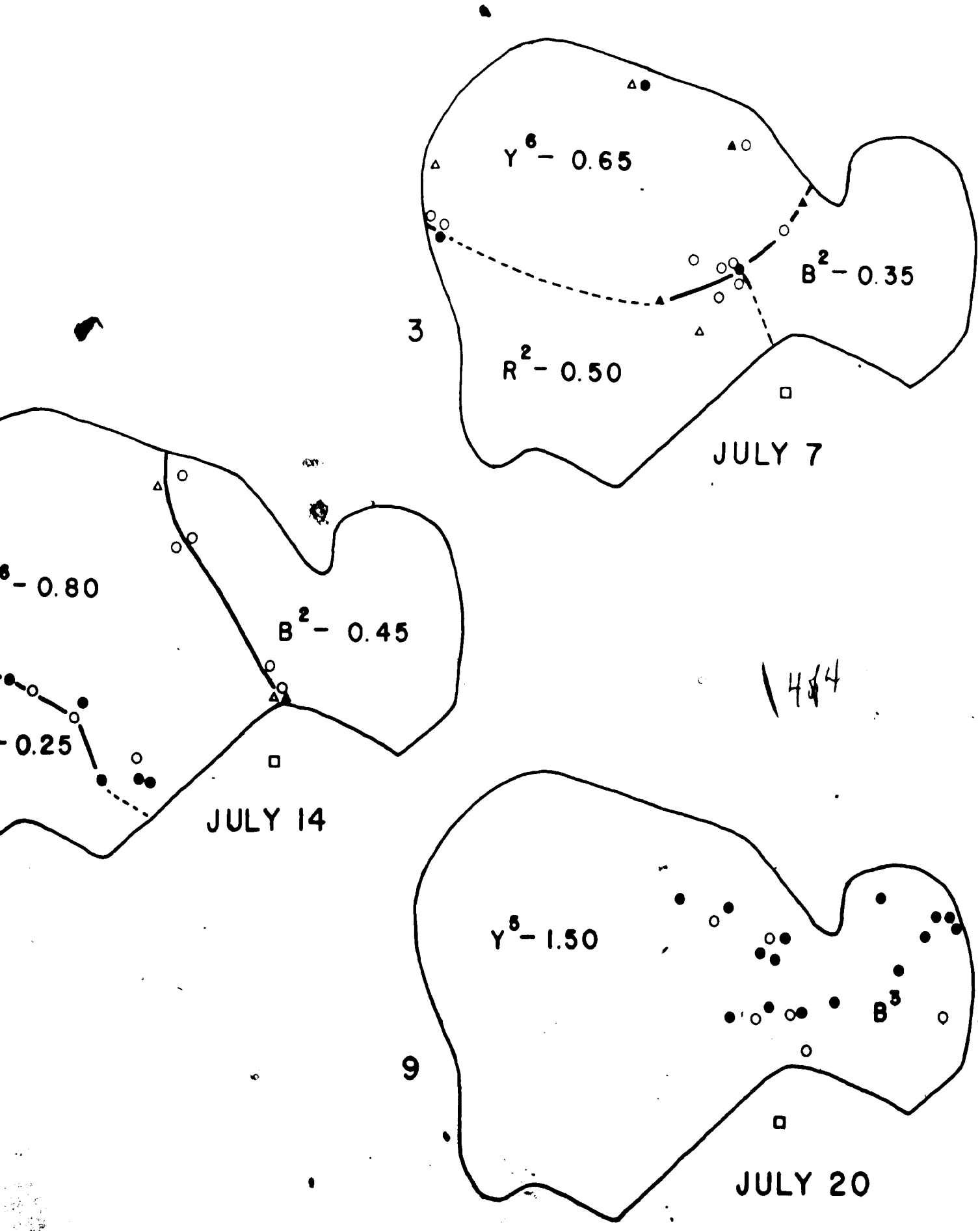
Dashed lines are boundaries estimated from movements of females and their broods.


□ Blind
• Stake
△ Approoch - withdrawal
○ Threat
● Supplanting attack
▲ Fight
1
R² - 0.60
JUNE
4
Y⁶ - 0.70
B² - 0.30
R² - 0.50
JULY 9
30m
7
Y⁵ - 0.90
R¹ - 0.10
JULY


B2- 0.90
JUNE 28
Y6- 0.55
2
R2- 0.
Y5- 0.75
B2- 0.45
5
R1- 0.30
JULY 12
B2- 0.50
JULY 17
Y6- 1.00
8
R1

1 2 of


Y⁶- 0.55
B²- 0.50
2
R²- 0.45
JULY 5
0.45
Y⁶- 0.80
B²- 0.4
6
R¹- 0.25
JULY 14
Y⁶- 1.00
B²- 0.50
8
R¹
JULY 18


Y 6 - 0.65
B 2 - 0.35
R 2 - 0.50
3
JULY 7
- 0.80
B 2 - 0.45
- 0.25
JULY 14
Y 6 - 1.50
B 3
9
JULY 20

existed between B and R. Thus Y established a brood-space both where resistance to her establishment was weakest and the pond topography most suitable (Fig. 20 - Maps 1 and 2). From the arrival of Y until July 9, B's brood-space contracted by two thirds, whereas that of R remained relatively stable, declining by only one sixth (Fig. 20 - Maps 2 to 4). This suggests that Y's encroachment was resisted more by R than B, even though there were proportionately fewer threats and fights and more fleeing from attack and pursuit in encounters between Y and R, than those between Y and B. By July 9, Y had encroached upon the boundary between R and B and penetrated to the shoreline, thus partitioning B's space from that of R (Fig. 20 - Maps 2 to 4). Thus Y occupied a central space and interacted along one boundary with B and along the other with R.

Most encounters occurred within a boundary zone and intrusions within brood-spaces were infrequent. Clustering of encounters near the shoreline of the north-west boundary zone suggests this site was a focal point of R's defence, or Y's attacks (Fig. 20 - Maps 2 to 4).

During phase III, the observation period from July 12 to 20, there was a marked rise in the frequency and intensity of attacks by Y against R. On both July 12 and 17 Y's aggression towards R intensified (Fig. 19). Continual fleeing by R in response to Y's increased aerial attacks and pursuits resulted in considerable compression of R's brood-space on both these days (Fig. 20 - Maps 5 to 7). Finally on July 18 repeated aerial attacks and pursuits by Y forced R off the pond (Fig. 20 - Map 8).

The concentrated aerial attacks by Y upon R along part of a boundary zone (Fig. 20 - Map 5), then along the entire boundary zone

(Fig. 20 - Map 7), first led to R's expulsion from a bay, then forced R to retreat farther into the south-west bay, her core area.

Meanwhile as Y intensified her attacks toward R, B expanded her brood-space and maintained a relatively stable boundary zone by threat and fighting encounters until the morning of July 20 (Fig. 20 - Maps 5 to 9). Then, for the first time recorded, an aerial attack by Y upon B within the boundary zone, released a long retreat swim underwater then a retreat flight by B. Thereafter Y intruded into the east end attacking and pursuing B, and for the first time, B failed to expel Y from the east end. Yellow's attacks upon the ducklings of B elicited no defence response from B. By mid-day Y and her brood occupied the east end; B avoided Y and no longer accompanied her brood. This rapid breakdown in the maintenance of B's brood-space was accompanied by a complete breakdown in her attendance and defence of her brood. By July 22 B had abandoned the pond and her brood.

Differences in behaviour patterns involving Y in two different situations: 1) maintenance of space, and 2) expansion of space and eviction of an opponent were tested for significance using Chi-square (Table 12). There were significant differences in four agonistic behaviour patterns (categories 2, 4, 5 and 6) exhibited by two different females in response to Y's aggression. Red responded to Y's aggression significantly more by fleeing ($P<.001$ and $P<.005$) for two categories of aerial pursuit, 5 and 6 respectively. Blue responded to Y's aggression significantly more by threat and fighting ($P<.005$ and $P<.001$, respectively). The above analysis emphasizes how space is established and maintained. However, to evaluate determinants of size of space and aggression and their interrelationships it is first necessary to

Table 12. Comparison of agonistic encounters recorded among female bufflehead with broods at Pond J during eight observation days from July 5 to 20, 1973.

Interacting colour-marked females	Category of agonistic encounter[1] 1 Approach - withdrawal	2 Threat	3 Attack - retreat	4 Fight	5 Aerial pursuit Low Intensity	6 Aerial pursuit High Intensity	Totals
Y-R	22	28	24	1	38	27	150
	15%	25%	16%	1%	25%	18%	100%
Y-B	15	35	9	12	1	2	74
	20%	48%	12%	16%	1%	3%	100%
Level of significance[2]	Not sig.	P<.005	Not sig.	P<.001	P<.001	P<.005	

[1] Numbers correspond to the six categories described in the text.

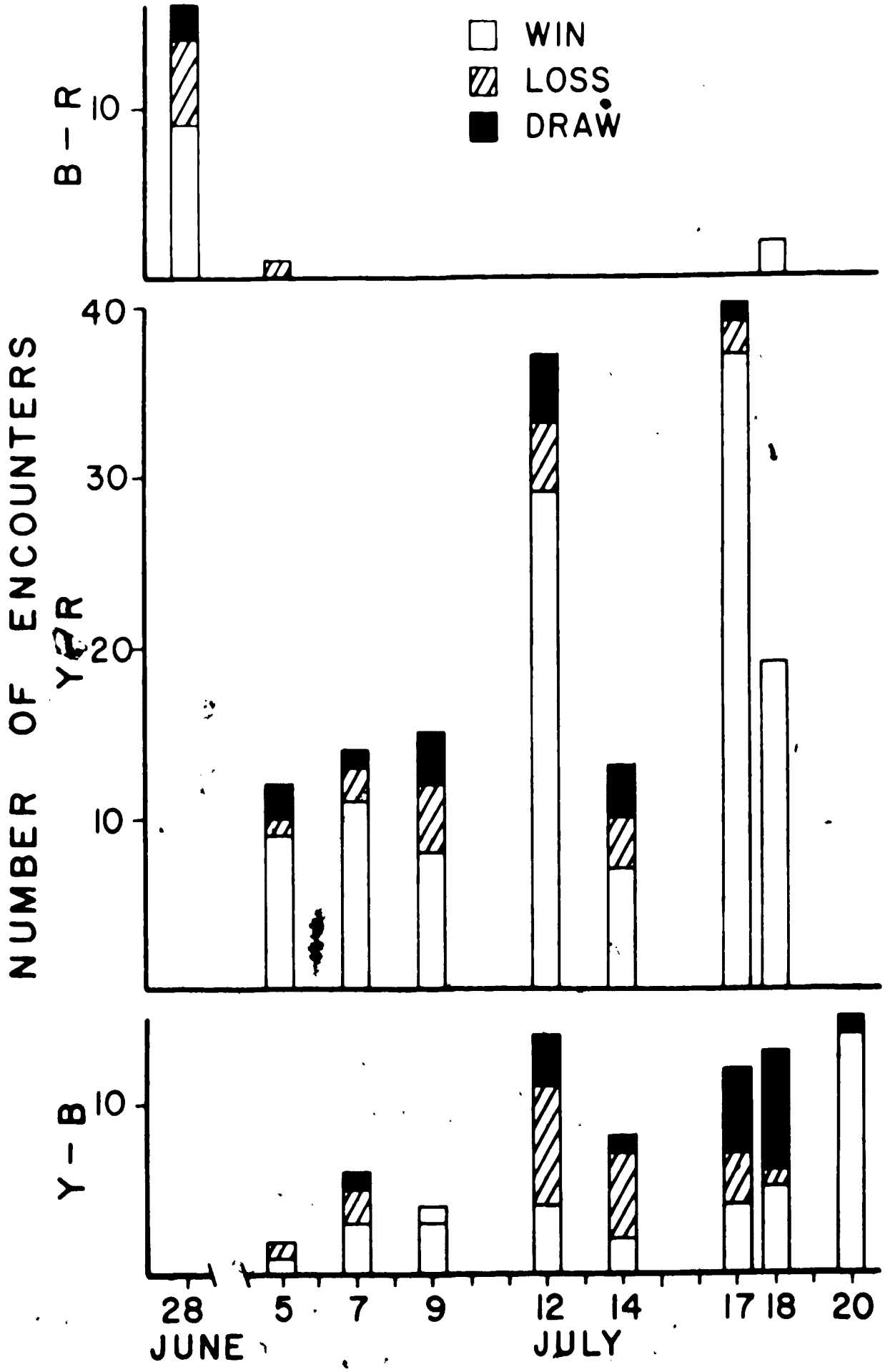
[2] Differences between females within each category of agonistic encounter in proportion to the totals were tested statistically with a 2 x 2 Chi-square.

quantify aggression. One component of aggression is the outcome of an encounter, which was classified as a win, loss or draw for each interacting individual. With three colour-marked females the attacker and attacked were clearly recognized. In non-reciprocal encounters (categories 1, 3, 5 and 6), for example those between Y and R where Y was clearly dominant, the attacker and/or pursuer was termed the winner, and the individual fleeing from its attacker and/or pursuer, the loser. In threat encounters a loss was recorded for that individual ending the encounter first by withdrawal, redirected aggression or other activity away from its opponent. In fighting a win was determined by a number of criteria such as an individual's frequency of attacks, grabbing, flap-paddle pursuits, and the vigour and sequence of the Wing-flap Display relative to its opponent. A draw was recognized for inconclusive encounters such as threats, when both opponents showed mutual withdrawal, and some fights.

Figure 21 shows the success of Y in encounters with her neighbours and success of B in encounters with R. Yellow and B were dominant over R. Overall Y was dominant over B. Yellow won 80 percent of 150 encounters with R. Of the total encounters with R, Y initiated 70 percent and of these, won 94 percent.

In encounters with B, including July 20 when the spacing mechanism broke down, Y won nearly half and about a quarter each were a loss and a draw. However, in encounters between Y and B up to July 18 when B maintained her brood-space, Y won 37 percent, lost 34 percent and 29 percent of encounters were a draw. Thus up to July 18 B and Y appeared to be equally dominant in terms of outcome of encounters, but not in initiating them. Yellow initiated about twice as many encounters

Figure 21. Success of blue in B-R agonistic encounters and success of yellow in Y-R and Y-B agonistic encounters.


WIN
LOSS
DRAW
B-R
10
NUMBER OF ENCOUNTERS
40
30
20
10
Y-R
Y-B
10
28
JUNE
5
7
9
12
14
17
18
20
JULY

as B suggesting Y was more aggressive. The individual initiating an encounter usually won it. In encounters between Y and B, Y won 71 percent of 24 encounters she initiated, and B won 69 percent of 13 encounters she initiated.

Outcome of encounters determines dominance relationships between individuals but not necessarily their aggressiveness. To measure aggression in red grouse (*Lagopus l. scoticus*) Watson (1964) scored the number and outcome of encounters over time and expressed the score as an index of aggression. Similarly for female buffleheads with broods I calculated an index of aggression (total points scored per bird per average observation hour) for each female per observation day by assigning a bird three points for a win, two points for a draw and one point for a loss as did Watson (1964).

Figure 22 depicts the relationship between aggression and size of brood-space over time for three colour-marked females. Clearly Y was much more aggressive than either R or B. Yellow held a central space and interacted with both her neighbours whereas they rarely interacted with each other. Yellow's total index of aggression was nearly four times that of either of her opponents. In 16 days, from July 5 to 20, Y expanded her brood-space by nearly three times through eviction of R from the pond and overlapping B's brood-space shortly before B abandoned her brood. Thus Y's expanding larger brood-space was clearly related to her relatively greater aggression over time. Red's higher index of aggression than B results from her greater number of encounters with Y and was no indication that R was more aggressive than B.

The younger, larger brood of Y and her greater aggression and

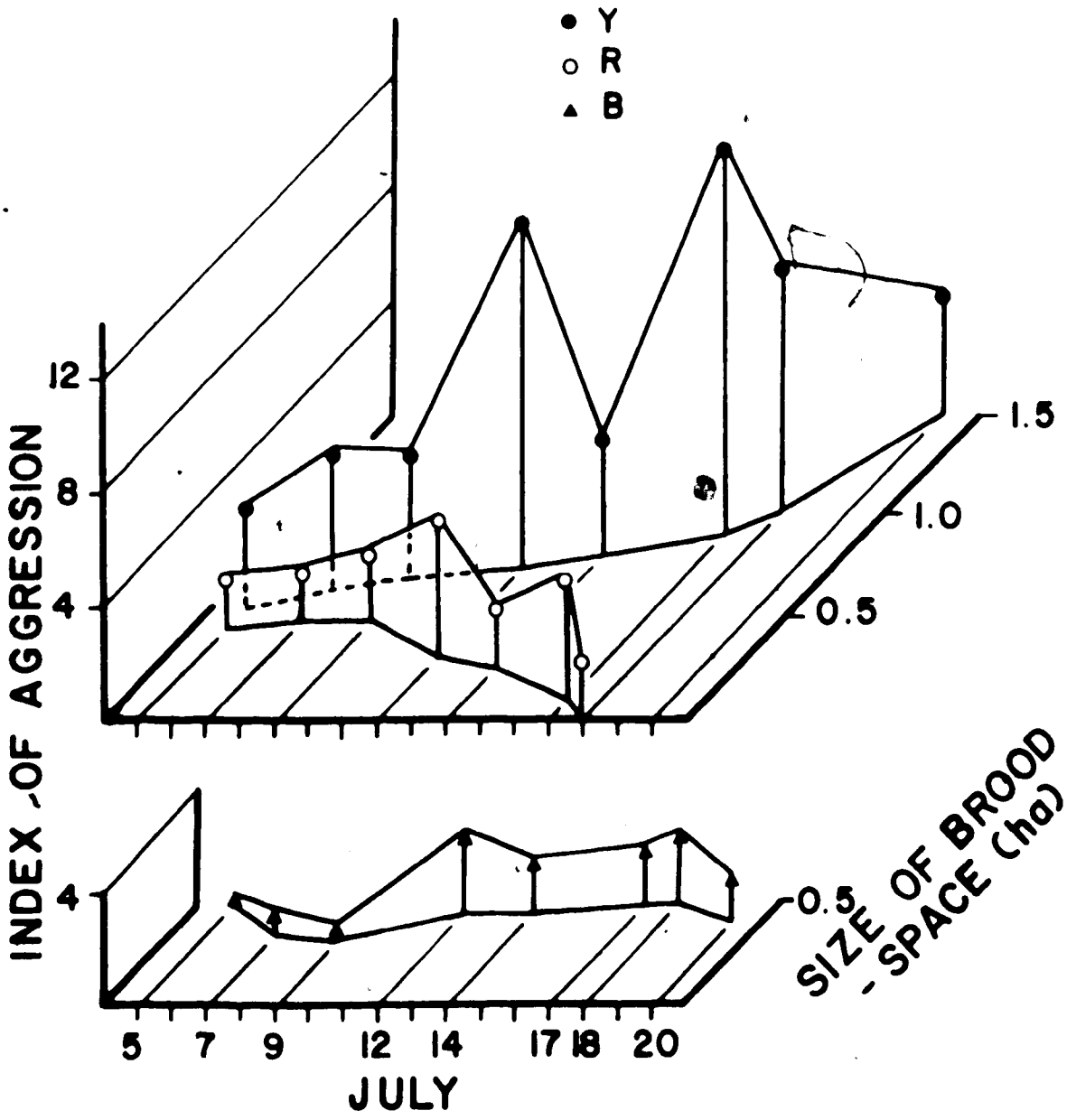


Figure 22. Relationship between aggression, size of brood-space and time for three colour-marked females with broods.

expanding brood-space suggests that all these variables may be interrelated. To investigate further these interrelationships it is desirable to analyze the effects of these variables independent of each other. Although this is best done with field experiments I consider at this stage the interrelationships between these variables using observed natural experiments.

Aggression and Size of Brood-space

The relationship between these factors, independent of brood size but not age of brood, was evident in one situation where sizes of broods were the same but ages of broods differed. On Pond J in 1973 R and B each had two ducklings yet B held a brood-space one third larger than that of R (Fig. 20 - Map 1). In 16 encounters between B and R, B won 9, lost 5 and drew 2 (Fig. 21). Blue initiated 10 encounters and won 6 of them and R initiated 3 and won 1. Therefore in terms of both the total number of encounters won, and those initiated, B with the larger space was clearly more aggressive than R. Blue's brood was 8 days younger than that of R's. Regardless of the extent to which age of brood or individual differences between the females contributed to B's greater aggression, size of brood-space was apparently determined by level of aggression.

Evidence presented in Figure 22 suggests that Y's larger brood-space resulted from her greater aggression. Again on Pond J in 1974 B held a larger brood-space than F Or (Orange) and won all fights against Or, again suggesting that the more aggressive female maintained a larger brood-space. Because aggression apparently determines size of brood-space the next question is: What external factors determine level of aggression?

Aggression and Brood Size

It is difficult to measure aggression objectively for comparing the aggressiveness of different individuals in different years and ponds. Comparisons must be made in the same year at the same pond. Rather than attempt to measure aggression it seems best to determine the relationship between brood size and size of brood-space and then relate this to aggression.

The number of bufflehead broods on a pond appears to depend on their density in relation to pond size and the number and density of competitors for space, especially red-necked grebes, and possibly other species of ducks. On ponds with only one bufflehead brood their brood-space encompasses the entire pond. To clearly interpret brood size in relation to size of brood-space only data from those ponds occupied by more than one bufflehead brood and no red-necked grebes were used. Only the 1972 data for Pond H and the 1972 to 1974 data for Pond J met these criteria. On Pond J in 1973 the number of broods, size of brood-space and brood size changed over time. In this situation when three broods occupied the pond, the averages of the two variables were plotted separately from when two broods occupied the pond.

Figure 23 shows a significant correlation (Spearman's correlation coefficient 0.7896, $P<.01$) between size of brood-space and brood size for 13 samples. Further evidence that size of brood-space of an individual female is a response to her brood size is provided by the relationship between these variables for B in successive years. Blue's mean size of brood-space and brood size was 0.5 ha and 2, respectively in 1973 and 1.0 ha and 6 in 1974. Furthermore the shape of B's brood-space in successive years in relation to topography of the pond (compare

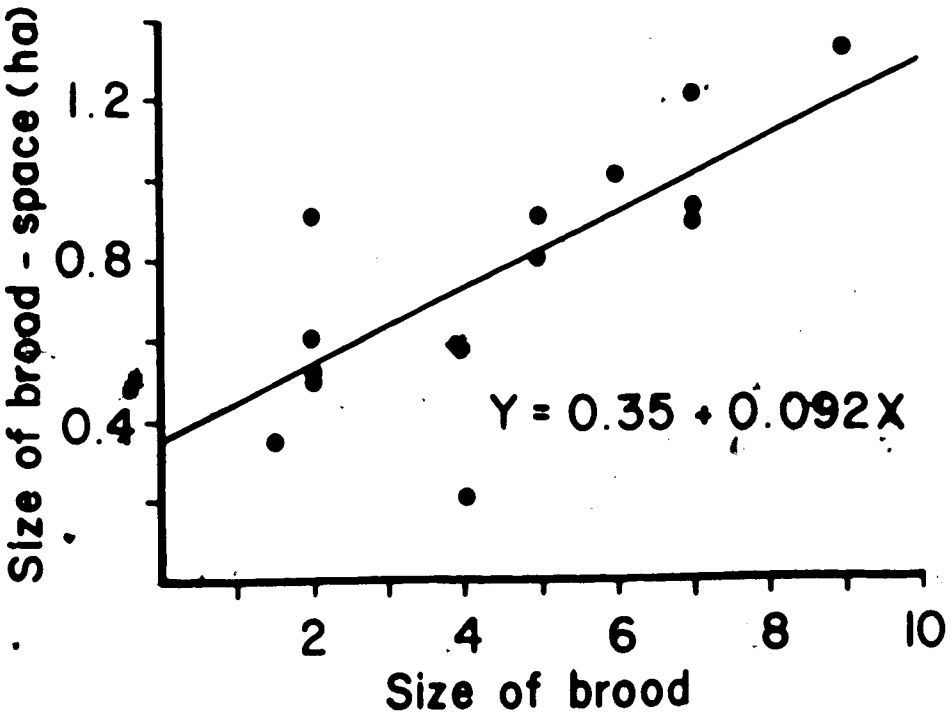


Figure 23. Relationship between size of brood-space and size of brood.

Fig. 20 - Maps 2 to 8 with Fig. 24a) indicate that B's size of brood-space was a response to her brood size, as well as neighbouring females with broods, independent of pond topography. In one situation at Pond J in 1972 where ages of broods were the same, the more aggressive female with the larger brood held the largest brood-space. Females with a larger brood-space have larger broods and are more aggressive suggesting that brood size is linked to aggression which in turn determines size of brood-space. If brood size determines level of aggression then the next question is: What is the effect of age of brood on level of aggression?

Aggression, Age of Brood and Brood Size

The interrelationships between these variables, especially the effect of age of brood on aggression, was investigated in situations where brood size was constant. Before the arrival of Y at Pond J in 1973, the two resident females each had a brood size of 2, but as mentioned earlier the more aggressive B with the larger brood-space had a brood 8 days younger. Thus females with younger broods appeared to be more aggressive than those with older broods. Furthermore, at Pond H on July 28, 1973 F R-W with a brood retreated from, and avoided the attacks of an intruding unmarked female with a brood (later F Bk-W). By July 31 F R-W had abandoned her brood. Both females had equal sized broods of seven but F R-W's brood was 33 days old (class IIc) and that of the unmarked female 10 days of age (class Ib), an age difference of 23 days. In 1972 again on Pond H brood size was similar for three of four females with broods, but two females with younger broods each held longer shorelines but area of brood-space was similar for all females (Fig. 16). Thus females with younger broods tended to be more

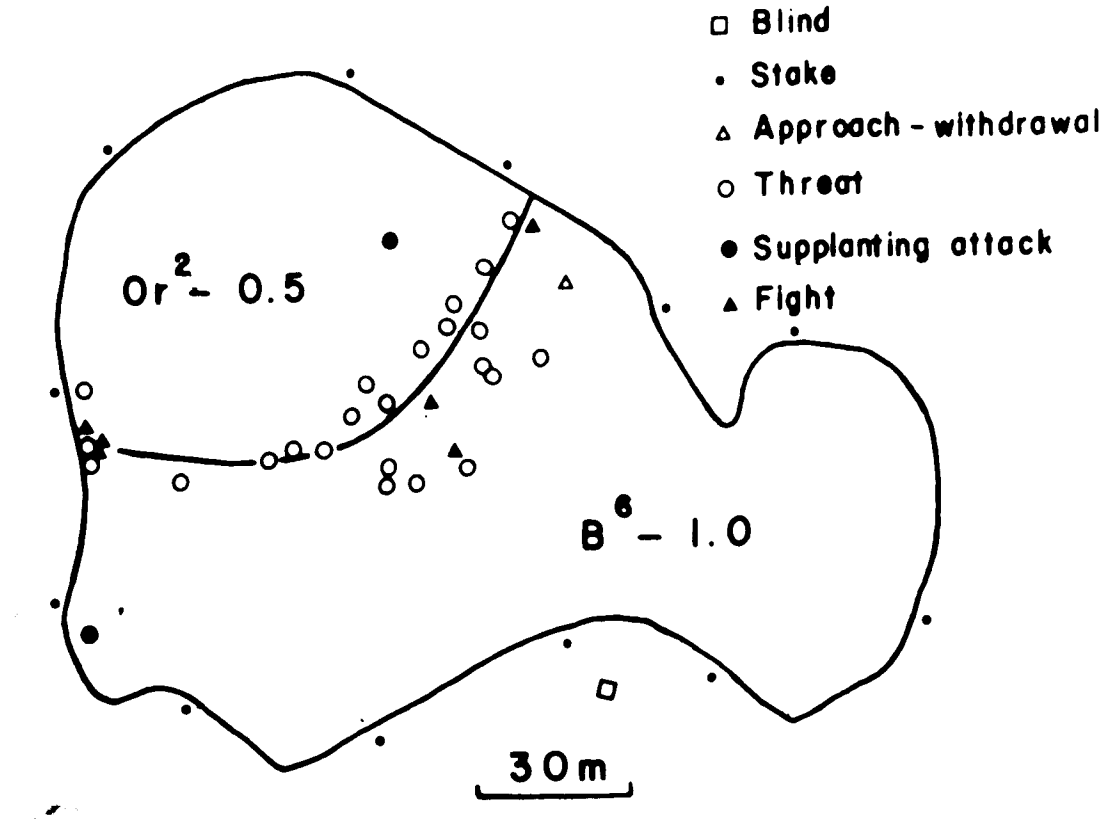
Figure 24a. Spatial relationships between two colour-marked females with broods on Pond J between July 10 and 15, 1974.

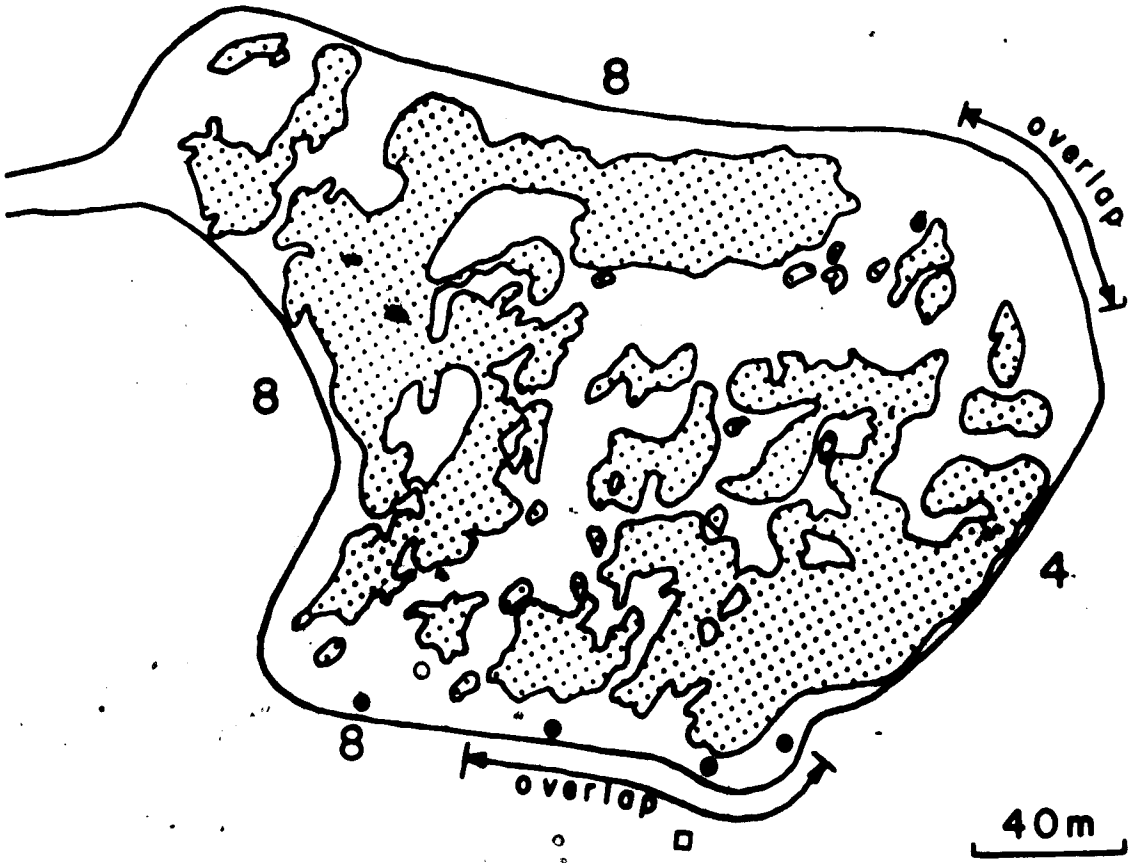
Or indicates a female marked with an orange nasal saddle.

See Figure 20 for explanation of numbers, the letter B and solid lines.

Figure 24b. Spatial relationships between two unmarked females with broods on Pond L on July 19, 1973.

Numbers and their positions outside the map of Pond L indicate the respective brood size of the two females, and the extent of shoreline foraged by each female with a brood. Stippled areas represent pond-lilies.


Blind
Stake
Approach - withdrawal
Threat
Supplanting attack
Fight
Or² - 0.5
B⁶ - 1.0
30m


8
overlap
8
4
8
overlap
40m

aggressive than those with older broods of the same size.

On Pond J in 1973 the larger brood of the more aggressive Y was 12 days younger than that of B's and 20 days younger than that of R's but the effect of age of brood on aggression was probably accentuated by brood size.

On Pond J in 1974 the less aggressive Or with a smaller space had a brood of two about 2 weeks younger than B's brood of 6 (Fig. 24a). This suggests that a larger brood overrides age of brood in determining level of aggression and size of brood-space.

On Pond L in 1973 F 8 with a larger, older brood and longer shoreline encroached upon F 4's space and was attacked and chased (Fig. 24b). It seems simpler to interpret this behaviour as a response to intrusion whereby F 8's position within her opponent's space released the aggression. Female 4 was more aggressive in this context yet she had a brood of 4 ducklings whereas her neighbour had a brood of 8, but 4's brood were 6 to 9 days younger than that of 8's. Brood-spaces overlapped at the boundary zones in time and space and interactions were too few to establish dominance or aggressiveness in other contexts.

Overall then brood size and age of brood were linked to aggression but brood size appeared to be a much more important determinant of aggression which in turn determines size of brood-space.

Interspecific Hostility

1. Female Buffleheads with Broods and Other Ducks

Female bufflehead with broods often attacked and chased other species of diving ducks, especially lesser scaup and common goldeneye, but also ring-necked duck and once a white-winged scoter (*Melanitta deglandi*). Occasionally dabbling ducks such as blue-winged and

green-winged teal were attacked and chased. On Pond J in 1973 lesser scaups were the only common resident diving duck. Congeneric common goldeneyes attempting to settle on the pond were vigorously attacked and chased off. The agonistic behaviour patterns involved are similar to those described for males.

Interspecific encounters occurred on all ponds but only those on Pond J in 1973 were suitable for quantitative analysis. At Pond J in 1973 the number and intensity of interspecific encounters were inversely proportional to the dominance of individual female buffleheads with broods (Tables 13 and 14). For example, lesser scaups were attacked more often by R than B, and more often by B than Y (Table 13). Furthermore there were proportionately more attacks of higher intensity (aerial attack and pursuit) by R than by B, and proportionately more attacks by B than Y (Table 14).

After losing encounters with Y, R often launched aerial attacks at lesser scaups and mostly pursued them from her brood-space. This suggests that the subordinate R was greatly threatened by the more aggressive, encroaching Y and redirected aggression at lesser scaups. By contrast, the dominant Y spent more time in intraspecific encounters interacting with both R and B, and as a result possibly attacked fewer scaups with less intensity even though most scaups sought refuge in Y's space. Blue sooner or later excluded all scaups from her brood-space suggesting that interspecific hostility can be partly explained by redirected aggression and partly by the scaup's position in space, which released B's aggression.

2. Female Buffleheads with Broods and Grebes

At the close approach of a red-necked grebe in Low threat, a

Table 13. Number of interspecific agonistic encounters recorded among female buffleheads with broods and other ducks without broods at Pond J during six observation days between July 5 and 17, 1973.

Colour-marked female buffleheads	Lesser scaup	Common goldeneye	Other diving ducks	Dabbling ducks (teal)	Totals
R	63	6	1	4	74
B	52	4	1	1	58
Y	28	9	0	0	37
Totals	143	19	2	5	169
	(85%)	(11%)	(1%)	(3%)	(100%)

Table 14. Number of interspecific agonistic encounters recorded between female buffleheads with broods and other ducks without broods at Pond J during six observation days between July 5 and 17, 1973.

Colour-marked female buffleheads	Nature and intensity of attack by buffleheads				
	Approach	Attack on the water	Aerial attack	Aerial pursuit	Totals
R	18	9	22	25	74
B	11	19	17	11	58
Y	21	5	6	5	37
Totals	50	33	45	41	169
	(30%)	(19%)	(27%)	(24%)	(100%)

bufflehead brood forms a compact group behind their mother or scampers to the shoreline. A female bufflehead may retreat with her brood, stay alert in front of her brood and face the grebe, or often respond with an approach flight and patter on the water surface over the submersed grebe in a manner similar to that described for males. On several occasions a threatening grebe, at the approach and patter flight of a female bufflehead, responded by rotating on the water so that it continually faced the bufflehead pattering around it. When the grebe submerged the female bufflehead made a retreat flight away from her brood, landed, then assumed an upright posture and waited. Upon the grebe's withdrawal the female bufflehead swam to her brood.

Bufflehead broods and breeding red-necked grebes coexisted on the same pond but at times, probably the grebe's presence and aggressive behaviour prevented bufflehead broods from settling. For instance, at Pond J on June 17, 1972 the first bufflehead brood arrived at the west end near the nest site of a pair of red-necked grebes. At the approach of a threatening grebe this female bufflehead and her newly hatched brood retreated into the shoreline vegetation and subsequently occupied an adjacent peripheral pond for the next few weeks. Presumably the buffleheads left Pond J because of the presence and hostility of this pair of grebes. A second bufflehead brood settled on June 18 in the smaller east-end bay of Pond J farthest away from the grebe's nest. These buffleheads shared this space with the grebe[redacted]he next few weeks, but were excluded by the grebes from the l[redacted] west-end bay. In mid-July shortly before the grebes left, the bufflehead brood that settled on a peripheral pond was able to reoccupy Pond J presumably because the grebe's hostility waned following five unsuccessful attempts

at nesting.

Further observations of settlement of bufflehead broods and possible interactions with red-necked grebes were obtained at Pond H in 1973. Four bufflehead broods occupied Pond H in 1972 in the absence of red-necked grebes. In 1973 a pair of red-necked grebes occupied the south-west half of Pond H when the first bufflehead female (F R-W) and her brood arrived on June 27 and settled in the north-east half. On July 2 a second, class Ia bufflehead brood (F unmarked) was seen within the grebe's half of the pond but had moved by July 10, when a Ib bufflehead brood of the same size was seen in the nearest bay of an adjacent lake. Later these grebes left. Another class Ia bufflehead brood arrived between July 19 and 21, and in the absence of grebes settled within the grebe's former space. These observations suggest that when a pond is divided between a bufflehead brood, and a pair of breeding red-necked grebes other bufflehead broods were deterred from settling.

HABITAT SELECTION AND INTERSPECIFIC RELATIONS

Female buffleheads with broods used ponds of different habitats (different nature of aquatic and shoreline vegetation) as well as ponds of various sizes. However, some ponds were not occupied (Table 15). This suggests that females make certain choices in selecting habitats for raising their ducklings.

Habitat selection is behaviour manifested through the choice of a specific habitat in response to environmental stimuli. This need not imply that habitat selected is optimal or that it is preferred, simply that a choice is made. A habitat may be optimal to a species in terms of survival and reproduction only in the absence of a competitor. Breeding success of a species may be reduced if it occupies this habitat together with its competitor, but enhanced if the competitor is absent. If the optimal habitat of a species is occupied by competitors, then another habitat where competition is absent or reduced may be selected by the species and this may become the preferred one (Hildén, 1965).

Selection of preferred habitat for bufflehead broods that may or may not be optimal habitat, probably depends on many factors such as number and habitat type of ponds available, distance from nest site to a pond, pond size in relation to spatial requirements of the brood, and the presence and density of conspecifics and other species.

The data presented in Table 15 and subsequent tables have several limitations as they are based on a small sample of 20 ponds, most of which were only visited once in one year. However, distribution of pond size and habitat type is probably representative as it is similar to that of a larger sample in the general area (Donaghey, 1974). The data provide some insight into habitat selection and interspecific relations

Table 15. Use of habitat by bufflehead broods in relation to pond size.

Pond Size (ha)	Habitat type: Bog		Cattail		Sedge		Pond-lily		Totals	
	No. censused	No. used	No. censused	No. used	No. censused	No. used	No. censused	No. used	No. censused	No. used
0.1-2.0	9	5	1	1	-	-	-	-	10	6
2.1-4.0	-	-	3	2	1	0	4	1	8	3
4.1-6.0	-	-	1	0	-	-	-	-	1	0
6.1-8.0	-	-	1	0	-	-	-	-	1	0
Totals	9	5	6	3	1	0	4	1	20	9

so are worth analyzing.

Table 15 shows that among all types of ponds, those less than 4 ha, were the most common; furthermore bog and cattail type ponds were more available than the other habitat types. In proportion to the number of ponds available bufflehead broods used nearly twice as many smaller ponds (0.1 to 2.0 ha) as larger ones (2.1 to 4.0 ha). Female buffleheads would appear to prefer smaller ponds, however all bog ponds sampled were less than 2.0 ha. Thus pond size and habitat are interrelated and it is difficult to determine if there was any clear preference for smaller ponds in general, or bog ponds in particular or both. Further, there appeared to be no clear preference for either bog or cattail ponds (Tables 15 and 16). Two cattail ponds more than 4.0 ha (Table 15), and three of four bog ponds 0.3 to 0.5 ha (Table 16) were not used. This suggests that bog and cattail ponds 0.5 to 4.0 ha were most attractive for bufflehead broods and that pond size may be more important than habitat type. Before examining why bufflehead broods were absent from the other 11 ponds in the sample, it is appropriate to present evidence of other factors that female buffleheads might use in selecting a habitat for raising their brood.

Apparently, the presence and density of conspecifics is [illegible] environmental cue that females use before permanently settling on a pond. For example at Pond J in 1973 two female buffleheads each had only two ducklings at the time Y and her brood of 7 settled [illegible] ages of the three broods differed considerably. In 197[illegible] [illegible] resident females [illegible] broods in the Pond J area. [illegible] June 19. White's clutch of eight eggs and [illegible]

Table 16. Size of bog ponds used by bufflehead broods.

Pond size (ha)	No. ponds censused	No. ponds with broods
0.3-0.5	4	1
0.6-1.0	2	1
1.1-1.5	3	3
Total	9	5

hatched, yet surprisingly neither W nor Y settled on Pond J with their broods. Instead Or and her brood of three, which I estimated to have hatched a few days after Y's brood, settled on Pond J. They did not settle on Pond C closer to her nest site presumably because it was occupied by a pair of red-necked grebes and possibly another bufflehead brood at the time her brood hatched. A thorough search revealed no broods of Y or W on any nearby ponds, so presumably both these females took them to a nearby lake. The spatial requirements of bufflehead broods (see Fig. 23) indicate that Pond J was probably too small to accommodate two large broods of similar age. White and Y were last seen at Pond J on June 20 and June 26 respectively; about the time their respective clutches were due to hatch. I suggest that during visits to the pond about the time of hatching, both these females assessed the density of B and her brood, presumably using visual cues such as brood size (large or small) and possibly the aggression of B. Both these females avoided settling on Pond J apparently because of limited space and the likelihood of engaging in a high level of aggression. In common goldeneyes in Finland, Sirén (1952) reported that before a brood left its nest site the female made reconnaissance flights in the same direction in which the brood was subsequently led. Presumably during these flights the female assessed the state of the habitat so as to lead her brood to that which was most suitable.

[redacted]

had a female bufflehead and a brood of 3 (class III) in 1973, but no broods in 1974; Pond B (0.3 ha) had a breeding pair of buffleheads in each of 2 years censused, while Pond P was only censused in 1974. Bog Pond M (0.7 ha) had a lesser scaup brood in 1974, but was occupied by breeding pairs of buffleheads in 1972 to 1974, and bufflehead broods of 5 and 2 respectively in 1972 and 1973. Bog Pond V (0.4 ha) had a bufflehead brood of 3 but no sign of a female in 1974. Thus small bog ponds (0.3 to 0.5 ha) are probably suitable for breeding pairs of buffleheads in almost all years, but may be suitable only for small broods with perhaps a maximum of three surviving ducklings.

Breeding red-necked grebes occupied 6 of the remaining 7 ponds with no bufflehead broods, and the largest pond (7.9 ha) had a pair of common loons (*Gavia immer*) with two young and no grebes. It is now appropriate to examine the interspecific association of bufflehead broods and breeding red-necked grebes (Tables 17 and 18). They are largely segregated by pond size which is related to habitat. Two thirds of ponds with bufflehead broods were less than 2.0 ha, and two thirds of these were bog ponds (0.4 to 1.5 ha) with no grebes (Table 18). By comparison, two thirds of ponds with breeding red-necked grebes were larger, 2.1 to 4.0 ha, and half of these were lily ponds with no bufflehead broods (Table 18).

Bufflehead broods and breeding red-necked grebes have overlapping [illegible]. Minimum size of brood-space for buffleheads [illegible] with [illegible] (Fig. [illegible]), but 1.0 to 1.5 ha [illegible] adequate [illegible] A [illegible] of red-necked [illegible] 1974 [illegible] pairs of [illegible]

Table 17. Interspecific association of bufflehead broods (B) and breeding red-necked grebes (A) in relation to pond size.

Pond size (ha)	Number of ponds with A+B	A	B	neither A nor B	Totals
0.1-2.0	2	0	4	4	10
2.1-4.0	1	5	2	0	8
4.1-6.0	0	1	0	0	1
6.1-8.0	0	0	0	1	1
Totals	3	6	6	5	20

Table 18. Interspecific association of bufflehead broods (B) and breeding red-necked grebes (A) in relation to habitat type and pond size.

I) Bog ponds (N=9)

Pond size (ha)	Number of ponds with A+B	A	B	neither A nor B	Totals
0.3-0.5	0	0	1	3	4
0.6-1.0	0	0	1	1	2
1.1-1.5	1	0	2	0	3
Totals	1	0	4	4	9

II) Cattail ponds (N=6)

Pond size (ha)	Number of ponds with A+B	A	B	neither A nor B	Totals
0.1-2.0	1	0	0	0	1
2.1-4.0	1	1	1	0	3
4.1-6.0	0	1	0	0	1
6.1-8.0	0	0	0	1	1
Totals	2	2	1	1	6

III) Pond-lily ponds (N=4)

Pond size (ha)	Number of ponds with A+B	A	B	neither A nor B	Totals
2.1-4.0	0	3	1	0	4

IV) Sedge ponds (N=1)

Pond size (ha)	Number of ponds with A+B	A	B	neither A nor B	Totals
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	1

whereas a 2.4 ha pond (A) had two pairs in 1973, one of which reared young, and one pair in 1974. Thus the spatial requirements of a bufflehead brood and a pair of grebes completely overlap on 1.5 ha ponds (for example, Pond J in 1972), and probably overlap to some extent on larger ponds depending on pond size relative to numbers of grebes and number and size of bufflehead broods.

Bufflehead broods and breeding red-necked grebes largely occupy separate ponds, but can coexist on the same pond (Tables 17 and 18) (see below). There was no clear tendency for the settling of female buffleheads with broods to be precisely adjusted relative to environmental cues such as pond size, brood size, and number of grebes. For instance, Pond J (1.5 ha) in 1972 had one pair of grebes and a class I bufflehead brood of 12; whereas in 1974 cattail Pond C (1.7 ha) and bog Pond R (1.5 ha) each had a pair of grebes and class I bufflehead broods of two and one respectively.

Breeding red-necked grebes apparently prefer lily ponds (Table 18). To determine whether these ponds are their optimal habitat it is best to compare their breeding success in different habitats. Breeding success of ten pairs of grebes based on one census in 1974 was apparently much higher on lily Ponds F and L (three of four pairs each [illegible] three young) than on cattail Ponds C, T, U and W (two of four [illegible] two and one young [illegible] two pairs [illegible] sedge Pond A one pair [illegible] young [illegible] Pond J [illegible] young [illegible] ful [illegible] of red-[illegible]

because food fed to young (leeches) and foraging habitat (pond-lilies) is superior. Perhaps breeding success is intermediate on cattail ponds and sedge ponds, but lowest on bog ponds possibly because of less nest site cover and increased predation on eggs. These few data suggest that lily ponds are both the optimal and preferred habitat of breeding red-necked grebes, while bog ponds are marginal habitat. The later dates of their arrival at bog ponds provides further evidence that they are marginal habitat for grebes. For example at three ponds studied, the first grebes arrived at two cattail ponds from April 30 to May 3 in 2 years, whereas on bog Pond J in 1973 the first grebe arrived on May 11, and in 1974 one grebe arrived by May 5 but had departed by May 6, and the next grebes (a pair) arrived on May 15.

In summary, competitive exclusion appears to be operating through displacement of bufflehead broods to smaller ponds, but it is not complete possibly because of limiting amount of suitable habitat for bufflehead broods, and overlapping spatial [illegible] broods and breeding red-necked grebes use all available pond habitats, but apparently lily ponds are the optimal and preferred habitat of grebes. Bog ponds are probably [illegible] habitat for bufflehead broods, though it is possible that [illegible] grebes [illegible] optimal.

DISCUSSION

Spacing Systems - Concepts and Problems

Before evaluating the contribution that my data make to understanding the nature of spacing system(s) in buffleheads, I want to introduce the concepts of home range and territory and the problems associated with studying them. Home range is an area within which an individual normally restricts its movements (Burt, 1943). Home ranges may overlap and have territories within them that are defended (Burt, 1943).

The concept of territory first emphasized in birds by Howard (1920) has been defined mainly as a behavioural phenomenon. In describing territory as "any defended area" Noble (1939) stressed the idea of defence, whereas Pitelka (1959) defined it in an ecological sense to mean "an exclusive area, not merely a 'defended' one" in terms of use of resources. He emphasized the [illegible] of the ecological consequence(s) of territory, not [illegible] for achieving [illegible]veness.

The variety of spacing mechanisms [illegible] with [illegible] of territoriality, but no defence, led [illegible] (1971) [illegible] the validity [illegible] definition [illegible] described [illegible] [illegible] defence.

temporal frame of reference". Emlen (1957) and Willis (1967) preferred the idea of dominance to that of defence. They defined territory as the area within which an individual dominates conspecific rivals, and that dominance between neighbours reverses across a boundary between them.

As pointed out by Wiley (1973) Noble's definition poses further problems. For instance, defence does not specify whether intruders are actively expelled, or whether an exclusive area is maintained passively by avoidance. Some of these difficulties were resolved by Brown and Orians (1970). First they interpreted defence widely to include not only attacking, chasing, and threatening but also vocalizations, displays and scent markings. Then they defined territory as a fixed area which the possessor, by acts of defence, keeps exclusive with respect to rivals. Tinbergen (1957) considered that territory is the result of two distinct forms of behaviour, namely site attachment and hostility.

The above comments are particularly [illegible] spacing systems in birds, because [illegible] range, and behaviour patterns [illegible] territorial. However, Howard's (1948) concept of territory [illegible] by territorial defence [illegible]

Species of diving ducks of the genera *Aythya* and *Melanitta* have not been reported to be territorial in the classical sense. Instead, an area around a paired female that is defended by her mate and moves with the pair, has been described in the velvet scoter (*Melanitta fusca*) (Koskimies and Routamo, 1953), canvasback and redhead (Dzubin, 1955), ring-necked duck (Mendall, 1958) and lesser scaup (pers. obs.). Conder (1949) and Koskimies and Routamo (1953) described this phenomenon as "mated-female distance" (no topographical reference), whereas Dzubin (1955) termed it a "moving territory".

Territory in ducks has been used to refer to: 1) an area of isolation, required by a pair of ring-necked ducks, that is not defended but is possibly maintained by avoidance (Mendall, 1958); 2) a feeding area exclusively occupied by a pair of common shelduck (*Tadorna tadorna*) not necessarily actively defended (Young, 1970); 3) occupied areas from which conspecific intruders are expelled; for example in the northern shoveler, blue-winged teal (Dzubin, 1955; McKinney, 1970; Seymour, 1974) and in the mallard (Dzubin, 1955). However, Hori (1963) considers that neither the mallard nor the shoveler have territories. Core areas or activity centres from which conspecific intruders are expelled have been described for the gadwall (*Anas strepera*) (Gates, 1962; Dwyer, 1974) and shoveler (Poston, 1974).

Another difficulty in understanding spacing systems in ducks concerns the nature of aerial pursuits, particularly those in species of the genus *Anas*. Two types can be distinguished, three-bird flights and attempted rape flights (McKinney, 1965). Dzubin (1955) found that a mallard pair used several potholes at different times, and from any one of these potholes the paired male occupant chased off approaching

mallard pairs by attacking and pursuing the female of the pair (three-bird flight). In turn, this attacking male and his mate were chased off potholes, if they were occupied by another pair or a paired male. Three-bird flights have also been noted in blue-winged teal (Dzubin, 1955), shoveler (Hori, 1963; McKinney, 1965; Poston, 1974), gadwall (Gates, 1962; Dwyer, 1974) and American wigeon (pers. obs.). Lebret (1961) reported similar flights during spring migration in the mallard, pintail and Eurasian green-winged teal.

As the breeding cycle advances and the pair bond of ducks weakens, attempted rape flights occur more often and they are sometimes not easy to distinguish from three-bird flights (McKinney, 1965). Thus difficulties arise in interpreting these two types of flights because they could indicate expulsion of intruders, defence of an area and/or a mate, or a rape tendency. Thus these flights "could be motivated by either attack tendency, rape tendency, or a combination of the two" (McKinney, 1965).

The degree of male attachment to a site is another problem associated with interpreting spacing behaviour in ducks. Use of a specific area by a paired male could result from, either attachment to that site, or from being paired with a female that is herself attached to that area for nesting, or a combination of both factors. McKinney (1965) believes that the hostility of paired males regularly using certain areas is "primarily an expression of the male's attachment to his mate".

Home ranges of ducks overlap in space, and different pairs use the same areas at different times, thus resources are shared between pairs (Sowls, 1955; Dzubin, 1955). For example, a shoveler pair spends most

of their time on a core area, but in their absence it could be occupied by other pairs. Some ponds are often shared between pairs, the first occupants dominating any other pairs attempting to settle (Poston, 1974).

All ducks studied so far have a home range on the breeding grounds. Buffleheads are no exception. In this study, however, I studied spacing behaviour of buffleheads only on that part of their home range where they spent almost all their time. Their behaviour at this site suggests territoriality, therefore, I now attempt to evaluate the observed spacing behaviour of buffleheads mainly in terms of the behavioural manifestations of territoriality. These include "active expulsion of intruders, agonistic boundary encounters, exclusive occupancy of an area, changes in dominance at different locations, and spatial restriction of movements or advertising behaviour" (Wiley, 1973).

Spacing Systems in Buffleheads

In buffleheads the pair bond breaks before the hatching of young, so I will consider the spacing system of breeding pairs separate from females with broods.

At high densities on a bog pond the resident breeding pairs totally divided the open water area among themselves, and excluded unpaired males from the pond. Fighting between neighbouring males during the prelaying period served to establish space for each pair with boundary zones between them. Males maintained the space, during the laying and incubation periods while the pair bond was intact, largely by threat encounters but also by fighting. As incubation advanced and the pair bond weakened there were proportionately more approach - withdrawal encounters, and less fighting.

Almost all agonistic encounters between males occurred within a boundary zone. These encounters mostly involved threat, fighting and approach - withdrawal.' The visual stimulus of a male or a pair of conspecifics and their behaviour patterns at a boundary zone prompted a neighbouring male to initiate an agonistic boundary encounter.

Within his own space each male actively and usually quickly expelled virtually all conspecific intruders such as unpaired males, neighbouring paired males, neighbouring and strange pairs, and lone females. Strange females that were probably incubating were not always evicted from the space of resident males. The position in space of intruders and their behaviour patterns provided visual stimuli which usually released immediate aerial attack by the resident male to defend either his attacked mate and/or his pair-space.

The attack and escape movements of neighbouring males engaged in threat encounters and flap-paddle chases within their boundary zones indicated that dominance reverses across this zone. Within his own space a resident male was dominant over almost all intruding conspecifics.

At intermediate and low densities on a lily pond and a cattail pond respectively, the open water area and sometimes the shoreline was not completely divided among the resident pairs, and unpaired male bufflehead occupied a central, apparently neutral area of the pond. Spacing behaviour among bufflehead at lower densities in terms of eviction of intruders, agonistic boundary encounters, and dominance reversal, seemed to be essentially similar to that at high densities. The main differences were that at lower densities there were fewer agonistic interactions among neighbouring males, less fighting and less

intruding by males to attack neighbouring females. Boundary zones also appeared to be less distinct away from the shoreline toward the centre of the pond.

The spacing behaviour described above is consistent with territoriality. However, at high densities on a bog pond boundary zones between two pairs shifted markedly throughout the breeding cycle resulting in considerable expansion and concomitant contraction of their defended space. This is not in accord with Brown and Orians (1970) definition of territory as "a fixed area, which may change slightly over a period of time". However, a focal area, such as a bay or a certain length of shoreline, was retained within each pair-space throughout the breeding cycle. Furthermore, on any given day agonistic encounters between neighbouring males occurred within a relatively stable boundary zone and conspecific intruders were expelled from within the space held by each pair. Therefore I consider that on ponds spaces held by pairs of buffleheads are territories, and hereafter territory refers to a pair-space.

A territory was more or less exclusively occupied by a pair of buffleheads with the exception of strange, incubating females. Pairs were absent from their territories for short periods during the prelaying period when females presumably searched for and inspected nest sites and visited peripheral ponds but rarely absent during the laying and incubation periods while the pair bond was strong. When a pair was absent from their territory neighbours did not intrude into it, except for males which occasionally intruded to attack strangers but not to exploit resources. Strangers, however, did intrude into a vacant territory but were expelled on return of the resident male. Based on

all observation periods throughout the breeding cycle, two paired males spent about 98 percent of their time within their respective territories while the pair bond was strong. Thus virtually all activity such as feeding, preening, bathing, resting on the water, loafing on dry land and sexual activity occurs within the territory.

Two pieces of evidence suggest that in male buffleheads site attachment is independent of mate attachment. Firstly, paired males responded to each other's agonistic behaviour patterns and positions in space, within a boundary zone or within a territory, irrespective of the positions of their mates. This shows that males defend an area, not just a space around their mate. Further evidence of site attachment in males was obtained on a bog pond when unpaired males occupied smaller territories than paired males, successfully maintained these small territories for a few days by threats and fighting, even expelling an intruding strange pair.

On the basis of limited field removal experiments in common shelducks, in which either a territorial male or a female of a pair were shot, Young (1976) suggested that females have "a stronger attachment to the territory than the male". These experiments, however, could indicate that a male has no attachment to a territory per se, only to his mate on the territory.

Seymour (1974), on the other hand, demonstrated experimentally that site attachment occurs in male northern shovelers. One male established two different territories where the same female was present in a trap, formed a pair bond with this female, became dominant, and expelled male conspecifics from these sites, even in the absence of the female. When this paired female in the trap was placed at a different

site, out of sight from her mate, an unmated male established a territory there, and was dominant over, and expelled all other males, even the mate of the female. Therefore Seymour (1974) concluded that "a site *per se*, and not just the female, may provide a basis for attachment and apparent defensive behavior" and "that the mere presence of the mate does not ensure that the male will be dominant at a given site".

Aggressive responses of territorial, unpaired male buffleheads at the onset of the breeding season indicate that male aggression in buffleheads is at least partly determined by state of the gonads and not solely by the presence of the female. Furthermore, in the absence of their mates, male buffleheads occupy and maintain their territories by agonistic boundary encounters and actively expel conspecific intruders. However, in one instance, a strange pair resisted expulsion by a territorial male in the absence of his mate, but were evicted only after her return. On this occasion the aggression of the territorial male increased markedly in response to the external stimuli of his mate. This suggests that in buffleheads male hostility "is primarily an expression of the male's attachment to [illegible] ([illegible], [illegible]). In buffleheads the possible link between [illegible], male aggressiveness and phases of the female [illegible] suggests that level of male aggression is the result of complex interactions involving the state of the gonads and the external stimuli of their mates primarily, and also other males. Increased male aggression in the presence of the female has been noted in blue-winged teal ([illegible], 1955), [illegible] shoveler ([illegible], [illegible]) and [illegible] ([illegible]).

In buffleheads [illegible] territorial male

do not seem to be motivated by any sexual tendency, unlike those in the pintail (Smith, 1968). I never saw any attempted rape flights in buffleheads. For instance, persistent aerial attacks and pursuits directed by a territorial male almost solely toward the female of a strange intruding pair occurred both in the presence and absence of his mate. Aggression by this territorial male seemed to be clearly motivated solely by an attack tendency with the intention of expelling the strange pair. The energy expended by a territorial male in expelling a strange pair is likely to be less if attacks are directed solely at the female, because a female shows greater site tenacity than a male, and once she is evicted her mate soon follows her. Therefore, in buffleheads three-bird flights do not appear to result "from conflict between the pursuing male's tendency to chase the female of a strange pair (with intent to rape and/or possibly attack her) and his tendency to remain near his mate" as suggested by McKinney (1965) for species of ducks of the genus *Anas*. Siegfried [illegible] interpreted three-bird flights in the southern black duck (*Anas* [illegible]) as aggression, as I do for buffleheads.

Before evaluating the spacing system of female buffleheads with broods I will try to identify behavioural mechanisms that could assist in producing a spread in hatching dates of bufflehead broods by hastening or delaying the onset of laying. Among individual females of known breeding experience (probably 3 years of age and older), migrational homing to a specific pond, early arrival, nest-site tenacity and successful establishment of a territory all tended to produce early laying. [illegible] stimuli that [illegible] the date of clutch [illegible] of a territory that provides suitable [illegible]

nest cavity.

The aggressive behaviour of males, mated to females of known breeding success, enabled them to compete for space successfully on a bog pond, even when these pairs arrived later than other pairs which were unsuccessful in establishing space there. These latter pairs of no known breeding experience probably either moved elsewhere or became peripheral breeders. Aggressive behaviour of territorial males is thus one mechanism that disperses pairs and probably delays their reproductive cycle until they occupy a space suitable for breeding.

Aggression by a resident male bufflehead towards a female conspecific, engaged in nest-searching flights and/or inspecting a nearby nest cavity, is a behavioural mechanism that appeared to delay the onset of laying in the attacked female. Because most female buffleheads used nest sites that were not visible from the study ponds, their approach flights to the nest entrance did not release aggression by males on the ponds. Thus this male behaviour is not likely to cause much staggering in hatching dates of broods.

Female buffleheads breeding for the first time probably have to search for a nest cavity, whereas older birds that have bred successfully tend to use the same nest site as in previous years. Time involved in finding a suitable nest cavity could be one of the most important factors in delaying clutch initiation, not only among females breeding for the first time, but also among females with breeding experience that have to find new nest sites.

In this study no marked females were of known age. [illegible] broods of resident [illegible] those of peripheral females. Possibly peripheral females were breeding for the first time, probably

at 2 years of age, possibly later. Erskine (1972:84) did not demonstrate that most 2-year old females started laying later than older birds, because too few birds were of known age. However, he found three 2-year old females nesting and all of these "started laying relatively late".

In a large sample of female wood ducks of known age Grice and Rogers (1965) clearly showed that most adult females started nesting early in the first half of the season, thus causing the first peak in "nest-initiation", whereas most yearlings breeding for the first time nested later in the second half of the season, causing a second peak. Grice and Rogers (1965) found that at least some yearlings arrived on the breeding grounds much earlier than any yearlings nested. Therefore they suggested (p. 35) that the later nestings of yearlings was not entirely the result of their late arrival, but may have been due in part to "competition for nest sites or slightly later development of the gonads". Furthermore, Grice and Rogers (1965) found that when the wood duck population was increasing and the number of nest boxes were limited, proportionately fewer yearlings nested and proportionately more 2-year olds were found nesting for the first time; this they attributed to unsuccessful competition with older females for [illegible] sites. Returning now to [illegible], possibly most staggering [illegible] hatching [illegible] results from the later nesting of most 2-year [illegible] breeding for the first [illegible] because they are less successful at competing for [illegible], and [illegible] and possibly competing for [illegible], than older birds with [illegible].

I shall now evaluate the [illegible] behaviour of female buffleheads with breeds [illegible] to [illegible] manifestations

of territoriality. The spacing system of females with broods was essentially similar to that of pairs in terms of the behaviour patterns involved in establishing and maintaining space, site attachment, location of agonistic encounters, expulsion of intruders, stimuli that released aggression, dominance reversal and exclusive occupation of an area.

At high densities females with broods totally divided among themselves the open water area and shoreline of a bog pond and a cattail pond. Space was established by aggressive behaviour such as fighting, and maintained largely by threat encounters but also by fighting. In situations where females were expanding their space, aerial attacks and pursuits were frequent.

Most agonistic encounters occurred within a boundary zone, particularly in situations where size of brood-space was relatively stable, but also where space of a female was expanding. In both these situations the visual stimuli of a female encroaching within a boundary zone and her behaviour patterns prompted a neighbouring female to leave her brood and launch a long distance aerial attack at her opponent, sometimes initiating fighting at the boundary. Agonistic boundary encounters occurred on the open water area and near the shoreline of a bog pond, but only near the shoreline of [illegible] cattail pond. However, on the cattail pond females and their [illegible] restricted their activity to particular open water spaces, [illegible] maintained mainly by passive [illegible].

All [illegible] females with broods, intruders within a brood-space were usually actively expelled by the [illegible] female, except in situations [illegible]

intruder was dominant and expanding her space. When size of space maintained was relatively constant, neighbouring females with broods within their own space were dominant over all conspecific intruders. Female dominance within their own space reversed across a boundary zone with their neighbours.

At lower densities on a lily pond and the cattail pond female buffleheads with broods divided the shoreline, but not the open water area, among themselves. The behavioural manifestations of territoriality in these females at lower densities seemed to be essentially similar to that at high densities, but fighting and threat encounters were much less frequent. However, at lower densities conspecific intruders sometimes elicited no response from a resident female on the lily pond. Intrusions by a neighbouring female with a larger brood, along the shoreline of this pond beyond her boundary zones, resulted in overlap in use of space, whereby females shared space at different times of day.

Size of home-space maintained by individual neighbouring females was relatively [illegible] and female expanded her space at [illegible]

All [illegible] of female buffleheads with [illegible] by [illegible]

shortly before a female abandoned her brood, there was overlap in use of space and intrusions by neighbouring females.

The main difference between the stable territorial system of female buffleheads with broods and that of pairs, is that pairs usually arrive at ponds over a period of a few days and maintain a space for at least 4 weeks, whereas the staggered hatching of broods and the abandonment of older broods may result in neighbouring females maintaining space for only a week or two.

A relationship between aggression and family size (Boyd, 1953; Raveling, 1970) and aggression and territory size (Watson, 1964) has been demonstrated, but I am not aware of any studies that show the interrelationships of all three variables, namely aggression, territory size and number of young.

Male red grouse that held larger territories were more aggressive in terms of their frequency and outcome of agonistic encounters (Watson, 1964). Watson (1970) demonstrated that androgen controlled aggression since androgen implants resulted in territorial males extending their territory and pairing with more females, and in two non-territorial males establishing territories.

[redacted]

Raveling (1970) found that larger families of Canada geese dominated smaller ones and won proportionately more aggressive encounters. Raveling (1970) suggested that numbers in a brood affected the outcome of aggressive encounters. Furthermore immediate changes in dominance and success of a family following separation and reunification of family members suggested that numbers in a brood determined the outcome of encounters.

Territory size of kookaburras (*Dacelo gigas*) was correlated with the number of individuals defending it but the amount of space per bird was constant (Parry, 1973). Similarly in the Tasmanian native hen (*Tribonyx mortierii*) Ridpath (1972b) found that trios held larger territories than pairs (see Schoener, 1968 for further examples). However, in buffleheads only one female defended a brood-territory and territory size was correlated with the number of young.

To my knowledge, the spacing system in *Bucephala albeola* and its congeners, *B. clangula* and *B. islandica* has not been described and quantified; thus there are no data on species of *Bucephala* suitable for comparing with mine. Bengston (1972:54) stated, without evidence, that Barrow's goldeneye in Iceland "defends a territory prior to and during egg-laying". Erskine (1972:1[illegible]) reported interspecific hostility between a male bufflehead and a male Barrow's goldeneye. Thus it seems likely that breeding pairs of Barrow's goldeneyes are territorial and compete for space among themselves and perhaps [illegible] pairs of bufflehead.

Bengston [illegible] considered that in Iceland Barrow's goldeneye holds a [illegible] on the basis of its high degree of site [illegible] of [illegible] from the vicinity of its brood, but

provided no data that it defends an area. Female Barrow's goldeneyes with broods have been reported to be hostile towards other conspecifics with broods (Erskine, 1972:185), female buffleheads with broods (Robertson and Stelfox, 1969; Erskine, 1972:184, 185), a female lesser scaup and her brood (Sugden, 1960), and a female blue-winged teal and her brood (Robertson and Stelfox, 1969). Thus it seems highly likely that female Barrow's goldeneyes with broods are territorial and compete for space among themselves, and perhaps among female buffleheads with broods.

Adaptive Significance of Spacing Behaviour in Buffleheads

Why have buffleheads evolved a territorial system? Brown (1964) advanced the hypothesis that territoriality has evolved through natural selection primarily as a behavioural response to competition for the ecological, defendable requisites for reproduction. The approach used in this study to try to explain the evolution of territorial behaviour of buffleheads is to "ask about the factors which might select for increased or decreased individual aggressiveness with respect to space" (Brown and Orians, 1970). Ultimate factors such as the nest site, cover and food, that could favour selection for territoriality in bufflehead pairs are each discussed in turn.

A comparison between hole-nesting ducks and a typical hole-nesting passerine may be useful in assessing whether the nest cavity is likely to be a major selective force in the evolution of territoriality of bufflehead pairs. The male pied flycatcher (*Ficedula hypoleuca*) restricts its activity to near the nest site, both to advertise it to females, and defend it from other males. Territorial fighting is concentrated on the nest hole, unlike open-nesting passerines which

mainly fight near boundaries (von Haartman, 1956).

By comparison, in the wood duck the lack of a defended territory and a marked increase in the density of a local population, through the use of nesting boxes, led Grice and Rogers (1965) to deduce that cavity nesters may be less likely to evolve territoriality. They speculated that reduced aggressiveness in wood ducks has survival value since nest sites, concentrated in specific areas, can be more fully exploited. However, Jones and Leopold (1967) found that in a dense population of wood ducks with insufficient number of nest boxes, lack of defence of the nest site resulted in nesting interference, nest desertion, and reduced production per pair.

Of 30 species of Anatidae that regularly nest in holes, 26 are in the tribes Tadornini, Cairinini and Mergini (Lack, 1968). It is useful to compare the association between territoriality and hole nesting in Australian Anatidae because the high proportion of hole-nesting ducks there could suggest that nest holes are readily available and that competition for them has not been a major factor in the evolution of territoriality among these ducks. Possibly there has been heavy selection for hole-nesting in Australian Anatidae because of the number and diversity of ground-nest predators (for example, snakes). Thus competition for these nest sites among birds and mammals may now be important. Of 13 species of ducks native to Australia in the tribes Tadornini, Anatini and Cairinini, both species of shelducks, three of five species of dabblers, and all three species of perching ducks, nest solely or most commonly in holes in trees (Frith, 1967). Of these eight species, a territory is defended by the shelducks, probably two species of perching ducks, possibly the third, but none of the three

species of dabbling ducks (Frith, 1967). Thus territoriality among hole-nesting ducks appears to be associated more with taxonomic groups than the nest site and there was no clear tendency for hole-nesters to be either territorial or non-territorial.

In buffleheads the nest cavity is located outside the territory and is not actively defended. Occupation of the cavity by the female during laying could have some role in its passive defence since there are only a few records of two or more females laying in the same cavity (Erskine, 1972:83), whereas in wood ducks "dump nesting" is relatively common (Grice and Rogers, 1965). However, passive defence during the laying period is probably insignificant because the cavity is apparently not occupied on days when eggs are not laid. Furthermore, most unsuccessful nests were deserted before incubation mainly as a result of disturbance by other female buffleheads (Erskine, 1972:95). A pair did not restrict their activity to near the nest site. Moreover peripheral breeding pairs, that failed to establish a territory on a larger pond, successfully nested. Thus there was no evidence that competition for nest sites or space prevented females from breeding, nor that nest sites limited numbers of breeding buffleheads. Evidence that sufficient nest sites were available and the lack of defence centred on the nest hole suggests that in buffleheads the nest cavity is not a major selective force for territorial behaviour at the pond.

Cover is another factor which could favour selection for dispersion. Familiarity with cover by adults could reduce predation upon them (thereby increasing survival) and cover could also reduce predation upon nests (thus increasing the reproduction of individuals) (Orians, 1971). McKinney's (1965) suggestion that spacing of nests in

ground-nesting ducks "has survival value as an anti-predator device" does not apply to cavity-nesting bufflehead. Eggs of bufflehead are relatively safe from predators as indicated by a high nest success of 75 to 80 percent (Erskine, 1972:94).

Territorial male bufflehead are conspicuous on open water, yet no predation of adults was apparent in this study. Erskine (1972:187) mentions predation on bufflehead by avian predators, but considered predation on adults to be unimportant. Thus predation is most likely an insignificant selective pressure in the evolution of territoriality in pairs of bufflehead, both in terms of individual survival and reproduction.

Brown and Orians (1970) considered that in birds "the temporal and spatial distribution of food resources is the most important single factor which has influenced the advantages and disadvantages accruing to individuals from space-related agonistic behavior". Thus the distribution and availability of food is a factor that could give a selective advantage to a female bufflehead within a territory in terms of its survival and reproduction during two phases of the nesting period, laying and incubation.

Perrins (1970) pointed out that in "those species which lay many eggs, most of the biomass of the clutch cannot be stored in advance of laying, since the increase in weight of the female before laying is not nearly so much as the weight of her clutch". A female bufflehead on the average lays a clutch of eggs virtually equivalent to her own body weight; assuming a female weighs 340g, an egg weighs 37.5g and an average clutch of eggs is 9 (Lack, 1968:350; Erskine, 1972:82, 206). This fact plus evidence that female bufflehead lay eggs on alternate

days, or on average an egg every 35 to 40 hours, suggests there are heavy demands on the laying female to find enough food on the breeding grounds to form eggs.

Recent studies of feeding ecology of ducks (Swanson and Meyer, 1973; Krapu, 1974; Swanson, Meyer and Serie, 1974) demonstrate that breeding female ducks consume and apparently select a diet higher in aquatic invertebrates during the prelaying and laying periods, than during postlaying. Moreover a greater proportion and amount of invertebrates consumed by females than males suggests that breeding females require a diet higher in animal protein to provide nutrients for forming eggs (Swanson and Meyer, 1973).

Comparable studies of feeding ecology of breeding bufflehead are lacking. Bufflehead feed mainly on invertebrates throughout the year. In spring the diet consists of aquatic insects, chiefly larvae of chironomids, nymphs of mayflies, and dragonflies in that order of importance (Erskine, 1972:152, 153). I observed female bufflehead feeding on what I believe were chironomid larvae and dragonfly nymphs during the laying period and females appeared to feed more frequently than males. Presumably female bufflehead apparently also select a diet higher in animal protein during laying.

Dwyer (1974) postulated that chasing and dancing behaviour in gadwalls functions primarily "to protect the food supply and secondarily to provide for undisturbed feeding time". He assumed that food is the most important factor in the evolution and maintenance of territorial behaviour of bufflehead pairs it is necessary to provide evidence that differences in the distribution and availability of food within foraging areas are correlated also differences in fitness of

individuals that use these areas. Differences in breeding success have been demonstrated, for example, when less aggressive individuals are prevented from obtaining a territory and breeding (see Brown and Orians, 1970 for examples). In this study no data were gathered on foods available to, and consumed by breeding buffleheads. Thus other evidence is presented to evaluate the importance of food in the evolution of their territoriality.

Peripheral breeding pairs of buffleheads were unsuccessful in competing for space on a bog pond and occupied much smaller peripheral ponds. However, the females of peripheral pairs successfully reared offspring on the larger bog pond. More aggressive resident pairs must have a greater fitness than less aggressive individuals if increased aggressiveness and territorial behaviour is maintained in a population. Food available in peripheral ponds was sufficient for one of three peripheral females to have a clutch similar in size to those of the two resident females. Watson and Moss (1971) postulated that female red grouse that consume highly nutritious heather form high quality eggs which produce better surviving young. Possibly resident female buffleheads lay eggs of a higher quality, than those of peripheral females, and produce ducklings that have a higher survival rate and subsequently rear more offspring. However, there was insufficient evidence to validate this hypothesis. Clutch size of the other two peripheral females was intermediate but their broods were smaller than resident females. These few data suggest that on average peripheral females lay smaller clutches, perhaps in response to the proximate factor of less available food (Lack, 1954) in peripheral ponds in most years.

Differences in breeding success (number of surviving young) between resident and peripheral breeding buffleheads was not clearly established. A resident female reared more ducklings on a bog pond than a peripheral female in 1 year, but breeding success of the two other resident females was not known. In another year peripheral females reared more offspring than resident females, but both the latter were disturbed at the nest site, and one of them deserted its clutch. At a cattail pond a similar number of ducklings was reared by early and late arriving females with broods.

Territorial behaviour of bufflehead pairs may have evolved in response to food requirements of the laying female. However, the successful breeding of peripheral females and the lack of sufficient evidence of differences in breeding success makes it difficult to rigorously evaluate this hypothesis. Nevertheless peripheral females may have had a lower fitness.

Distribution and availability of food to the female bufflehead during incubation could also favour selection for territoriality if survival of females is thereby increased. Krapu (1974) found that female pintails declined in body weight throughout the nesting period, fat reserves were depleted during incubation but females during post-laying compensated for this by consuming more high energy foods. Individual female blue grouse (*Dendragapus obscurus*) declined in body weight throughout incubation (Redfield, 1973). Body weights of female buffleheads decline throughout the nesting period ([illegible], 1972, [illegible]) but changes in body weight of individual [illegible] in relation to stage of breeding cycle [illegible].

[illegible] of [illegible] among paired

males was higher during the first 2 weeks of incubation than later. Furthermore the daily occurrence of copulations between members of a pair at least during the first 2 weeks of incubation suggests this behaviour functions to maintain the pair bond, and assist in the maintenance of territories by males. Thus females can have access to a food supply and feed undisturbed during early incubation, and perhaps reduce the rate of depletion of their fat reserves.

Strange females, that were probably incubating, exploited food within the territories of resident pairs. This behaviour could weaken the argument that territorial behaviour of males evolved as a consequence of competition for food by females since we might expect competitors for food to be expelled from territories. However, it is unlikely that strange females had a significant affect on the food supply and there was no evidence that strange females exploited food during the laying period. Thus exploitation of food, within the territories of resident pairs, by strange females indicates that the territorial system of pairs is not perfect, and that this phenomenon is insignificant in evaluating the importance of food on the evolution of territoriality.

The nest site and cover appear to be insignificant ultimate factors in the evolution and maintenance of territoriality of bufflehead pairs. Despite the lack of sufficient evidence to rigorously evaluate the importance of all ultimate factors, the evidence presented suggests that food is the more likely major factor that has favoured selection for territorial behaviour. Thus I consider that space held by males evolved as a consequence of competition for food by females. The selective [illegible] that space might give to individuals by [illegible]

adaptive significance of territorial behaviour in bufflehead pairs appears to be primarily to provide females with a foraging space and a guaranteed food supply during the prelaying and laying periods in general, but also during early incubation, and thus allows them to feed relatively free of interference from competitors.

The correlation between size of brood-territory and brood size suggests that either competition for food or space for ducklings may be the major factor favouring selection for the evolution of territorial behaviour in female buffleheads with broods. Dispersion could reduce predation on ducklings. However, Erskine (1972:187,188) found little evidence that predation is significant, except possibly by pike (*Esox lucius*) in some areas. Thus it appears unlikely that territorial behaviour evolved primarily as a means of dispersing individuals to reduce predation, but possibly this was a secondary factor.

Competition for food by ducklings appears to be the major factor favouring selection for territoriality in females with broods. However, no evidence was obtained that food is the critical resource. Defence and more or less exclusive use of a foraging space guarantees individuals a food supply that can be exploited efficiently, and yet not depleted through over-exploitation. Several aspects of spacing behaviour of female buffleheads with broods suggest that foraging space is a more likely critical resource than food *per se*. Some females with broods do not return to the pond where they were resident as a breeding pair, but move elsewhere, possibly to marginal habitat, because all space on a pond is held by conspecifics or other competitors. Competition for space among female buffleheads with broods, and between the latter and breeding red-necked grebes suggests that suitable foraging

space is a scarce resource. Female buffleheads with broods have several adaptations to efficiently use this resource. Staggering of hatching dates of broods, waning of female aggression with increasing age of broods, abandonment of broods and the greater aggression of later arriving females with younger broods of similar size to those already present on a pond, plus other interrelationships among size of brood-territory, size of brood, aggression and age of brood, all appear to be adaptations that result in the maximum number of buffleheads being reared on a particular habitat.

The adaptive significance of aggression and territorial behaviour of female buffleheads with broods appears to be primarily to provide a sufficient, familiar and exclusive foraging space for ducklings so that they can more efficiently exploit food resources. Possibly a secondary selective advantage of territoriality of females with broods is reduced predation upon broods resulting from their dispersion to different habitats and familiarity with cover within their territory.

In the remainder of this discussion I try to explain differences in pair-bond tenure at two different ponds, then discuss the evolution of polygyny in buffleheads.

Buffleheads competed more vigorously for space on a bog pond than on a larger cattail pond as indicated by the earlier arrival of pairs, the higher density of pairs, the exclusion of unpaired male(s) and other pairs and the higher number of agonistic encounters on the bog pond. Available nest sites in the bog Pond J area in excess of the number of resident pairs on Pond J, and the scarcity of alternative suitable ponds apparently resulted in greater competition for space on Pond J than on other ponds. Maintenance of space on this pond during

the first 3 weeks of incubation apparently served to expel competitors from the area and allowed females to feed undisturbed. The greater influx of bufflehead (presumably subadults and surplus males) on a bog pond than on a cattail pond following the break in the pair bond and the departure of resident males, suggests that the pair bond lasted longer on the bog pond to reduce competition for food and space. This hypothesis is further strengthened by the water chemistry of these ponds and the findings of Jeglum (1973) that bog and muskeg stands have a lower nutrient status than emergent fens (cattail was only dominant in emergent fen stands). These data suggest that cattail ponds have a higher nutrient status than bog ponds and thus are more likely to have a greater abundance and diversity of intertebrates. Thus competition for food is likely to be more intense on the bog pond.

Verner and Willson (1966) suggest that polygyny in passerine birds is more likely to evolve in habitats like marshes and prairies where food is concentrated into a narrow vertical zone and availability of food among territories differs substantially. Resident male bufflehead copulated with and formed a simultaneous pair bond with their respective mates and a strange female on a bog pond, but apparently not on a cattail and a lily pond. However, the latter ponds were not studied as intensively. Almost all species of ducks are monogamous, except for a few, chiefly of warmer regions, that are promiscuous (Lack, 1968:122-123). Polygyny in bufflehead appears to be unusual and may be an adaptation to a local situation. Assuming that strange females seeked mates, the only ponds in the vicinity available for feeding were [illegible] by a pair of red-necked grebes, the bog pond with the resident bufflehead, and the small peripheral ponds. [illegible]

suitable foraging space appeared to be limited. Presumably a strange female that copulates with resident territorial males benefits by feeding within the male's territory and in addition a female is closely attended by a male and can feed undisturbed without being harassed by grebes or unpaired male bufflehead. The local scarcity of suitable foraging space appears to be the major factor that has favoured the evolution of a polygynous mating system among incubating females and resident territorial males on a bog pond.

In conclusion, breeding pairs of bufflehead and female bufflehead with broods both have a territorial system on ponds in a southern boreal forest region. Territoriality of paired male bufflehead appears to have evolved as a consequence of competition for food by laying females. Food and foraging space for ducklings seem to be the major factors that have favoured the selection for territorial behaviour of female bufflehead

LITERATURE CITED

Addy, C.E., ed. 1956. Guide to waterfowl banding. Unpublished report. U.S. Fish and Wildl. Serv., Laurel, Maryland.

Bengtson, S.-A. 1971a. Habitat selection of duck broods in Lake Mývatn area, north-east Iceland. Ornis Scand. 2:17-26.

_____. 1971b. Variations in clutch-size in ducks in relation to the food supply. Ibis 113:523-526.

_____. 1972. Reproduction and fluctuations in the size of duck populations at Lake Mývatn, Iceland. Oikos 23:35-58.

Bishop, R.A., and R. Barratt. 1969. Capturing waterfowl in Iowa by night-lighting. J. Wildl. Manage. 33:956-960.

Boyd, H. 1953. On encounters between wild white-fronted geese in winter flocks. Behaviour 5:85-129.

Brown, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.

Brown, J.L., and G.H. Orians. 1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst. 1:239-262.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346-352.

Caldwell, P.J., and A.E. Snart. 1974. A photographic index for aging mallard embryos. J. Wildl. Manage. 38:298-301.

Carpenter, C.R. 1958. Territoriality: A review of concepts and problems. Pages 224-250 in A. Roe and G.G. Simpson, eds. Behavior and Evolution. Yale Univ. Press, New Haven. 557 pp.

Conder, P.J. 1949. Individual distance. Ibis 91:649-655.

Cooper, J.A., and [illegible]. 1972. Criteria for aging giant Canada [illegible]. J. Wildl. Manage. 36:[illegible]

[illegible]

Donaghey, R.H. 1974. Waterfowl use of boreal forest waterbodies near Utikuma Lake, northern Alberta. Unpublished Final Report, Ducks Unlimited (Canada). 97 pp.

Drury, W.H., B. Dane, M.T. Myres and A.J. Erskine. MS. On the bufflehead, for the Handbook of North American Birds.

Dwyer, T.J. 1974. Social behavior of breeding gadwalls in North Dakota. Auk 91:375-386.

Dzubin, A. 1955. Some evidences of home range in waterfowl. Trans. N. Am. Wildl. Conf. 20:278-298.

Emlen, J.T., Jr. 1957. Defended area? - A critique of the territory concept and of conventional thinking. Ibis 99:352.

Erskine, A.J. 1959. A method for opening nest holes. Bird-Banding 30: 181-182.

_____. 1961. Nest-site tenacity and homing in the bufflehead. Auk 78:389-396.

_____. 1972. Buffleheads. Can. Wildl. Serv. Monogr. Ser. No. 4. 240 pp.

Fjeldsa, J. 1973. Antagonistic and heterosexual behaviour of the horned grebe, *Podiceps auritus*. Sterna 12:161-217.

Frith, H.J. 1967. Waterfowl in Australia. Angus and Robertson, Sydney. 328 pp.

Gates, J.M. 1962. Breeding biology of the gadwall in northern Utah. Wilson Bull. 74:43-67.

Gilmer, D.S. 1971. Home range and habitat use of breeding mallards (*Anas platyrhynchos*) and wood ducks (*Aix sponsa*) in north-central Minnesota as determined by radio tracking. Unpublished Ph.D. Thesis, Univ. Minnesota. 142 pp.

Gollop, J.B., and W.H. Marshall. 1954. A guide for aging duck broods in the field. Mississippi Flyway Council Tech. Sect. 14 pp. Mimeo.

Grice, D., and J.P. Rogers. 1965. The wood duck in Massachusetts. Mass. Div. Fisheries and Game. Proj. No. W-19-[illegible], 56 pp.

[illegible], W.G., ed. [illegible]. Alberta: A Natural History, M.G. Hurtig, [illegible]. [illegible] pp.

[illegible]. Breeding season and clutch size in the European [illegible], and the tufted duck, *A. fuligula*, in [illegible] Zool. Listy [illegible]:175-[illegible].

Hilden, O. 1964. Ecology of duck populations in the island group of Valassaaret, Gulf of Bothnia. Ann. Zool. Fenn. 1:153-279.

_____. 1965. Habitat selection in birds. A review. Ann. Zool. Fenn. 2:53-75.

Hinde, R.A. 1952. The behaviour of the great tit (*Parus major*) and some other related species. Behaviour, Suppl. 2:1-201.

_____. 1956. The biological significance of the territories of birds. Ibis 98:340-369.

Hochbaum, H.A. 1944. The Canvasback on a Prairie Marsh. Am. Wildl. Inst., Washington, D.C. 201 pp.

Hori, J. 1963. Three-bird flights in the mallard. Wildfowl Trust Annu. Rep. 14:124-132.

Howard, H.E. 1920. Territory in Bird Life. Murray, London. 308 pp.

Jeglum, J.K. 1972. Boreal forest wetlands near Candle Lake, central Saskatchewan. I. Vegetation. Musk-Ox 11:41-58.

_____. 1973. Boreal forest wetlands near Candle Lake, central Saskatchewan. Part II - Relationships of vegetational variation to major environmental gradients. Musk-Ox 12:32-48.

Johnsgard, P.A. 1965. Handbook of Waterfowl Behavior. Cornell Univ. Press, Ithaca, New York. 378 pp.

Jones, R.E., and A.S. Leopold. 1967. Nesting interference in a dense population of wood ducks. J. Wildl. Manage. 31:221-228.

Kaufmann, J.H. 1971. Is territoriality definable? Pages 36-40 *in* A.H. Esser, ed. Behavior and Environment. The use of space by animals and men. Plenum Press, New York. 411 pp.

Kevan, C.L. 1970. An ecological study of red-necked grebes on Astotin Lake, Alberta. Unpublished M.Sc. Thesis, Univ. Alberta, Edmonton. 80 pp.

Kilham, L. 1954. Repeated territorial attacks of pied-billed grebe on ring-necked duck. Wilson Bull. 66:265-267.

Klomp, H. 1970. The determination of clutch-size in birds. A review. Ardea 58:1-124.

_____. 1972. Regulation of the size of bird populations by means of territorial behaviour. Neth. J. Zool. 22:456-488.

Koskimies, J., and E. Routamo. 1953. Zur Fortpflanzungsbiologie der Samtente *Melanitta f. fusca* (L.). I. Allgemeine Nistökologie. Riistatiet. Julkaisuja 10:1-105.

Krapu, G.L. 1974. Feeding ecology of pintail hens during reproduction. Auk 91:278-290.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London, 409 pp.

Lebret, T. 1961. The pair formation in the annual cycle of the mallard, *Anas platyrhynchos* L. Ardea 49:97-158.

Lindmeier, J.P., and R.L. Jessen. 1961. Results of capturing waterfowl in Minnesota by spotlighting. J. Wildl. Manage. 25: 430-431.

Lorenz, K. 1951. Comparative studies on the behaviour of Anatinae. Avicult. Mag. 57:157-182.

_____. 1952. Comparative studies on the behaviour of Anatinae. Avicult. Mag. 58:8-17, 61-72, 86-94, 172-184.

_____. 1953. Comparative studies on the behaviour of Anatinae. Avicult. Mag. 59:24-34, 80-91.

McKinney, F. 1961. An analysis of the displays of the European eider *Somateria mollissima mollissima* (Linnaeus) and the Pacific eider *Somateria mollissima v. nigra* Bonaparte. Behaviour, Suppl. 7: 1-124.

_____. 1965. Spacing and chasing in breeding ducks. Wildfowl Trust Annu. Rep. 16:92-106.

_____. 1967. Breeding behaviour of captive shovelers. Wildfowl Trust Annu. Rep. 18:108-121.

_____. 1970. Displays of four species of blue-winged ducks. Living Bird 9:29-64.

Marler, P. 1956. Behaviour of the chaffinch (*Fringilla coelebs*). Behaviour, Suppl. 5:1-184.

Mendall, H.L. 1958. The Ring-necked Duck in the Northeast. Univ. of Maine Studies, Second Ser. No. 73, 317 pp.

Moynihan, M. 1958. Notes on the behavior of some North American gulls. III. Pairing behavior. Behaviour 13:112-130.

Munro, J.A. 1942. Studies of waterfowl in British Columbia. Buffle-head. Can. J. Res., Sec. D 20:133-160.

Myres, M.T. 1959a. The behaviour of the sea-ducks. Unpublished Ph.D. Thesis, Univ. British Columbia, Vancouver. 506 pp.

_____. 1959b. Display behavior of buffleheads, scoters and goldeneyes at copulation. Wilson Bull. 71:159-168.

Noble, G.K. 1939. The role of dominance in the social life of birds. Auk 56:263-273.

Orians, G. 1971. Ecological aspects of behavior. Pages 513-546 *in* D.S. Farner and R.J. King, eds. Avian Biology, Vol. 1. Academic Press, New York. 586 pp.

Parry, V. 1973. The auxiliary social system and its effect on territory and breeding in kookaburras. Emu 73:81-100.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Pitelka, F.A. 1959. Numbers, breeding schedule, and territoriality in pectoral sandpipers of northern Alaska. Condor 61:233-264.

Poston, H.J. 1974. Home range and breeding biology of the shoveler. Can. Wildl. Serv. Rep. Ser. No. 25. 48 pp.

Raitasuo, K. 1964. Social behaviour of the mallard, *Anas platyrhynchos*, in the course of the annual cycle. Riistatiet. Julkaisuja 24: 72 pp.

Raveling, D.G. 1970. Dominance relationships and agonistic behavior of Canada geese in winter. Behaviour 37:291-319.

Redfield, J.A. 1973. Variations in weight of blue grouse (*Dendragapus obscurus*). Condor 75:312-321.

Ricklefs, R.E. 1973. Fecundity, mortality and avian demography. Pages 366-435 *in* D.S. Farner, ed. Breeding Biology of Birds. Natl. Acad. Sci. Washington, D.C. 515 pp.

Ridpath, M.G. 1972a. The Tasmanian native hen, *Tribonyx mortierii*. I. Patterns of behaviour. CSIRO Wildl. Res. 17:1-51.

_____. 1972b. The Tasmanian native hen, *Tribonyx mortierii*. II. The individual, the group, and the population. CSIRO Wildl. Res. 17:53-90.

Robertson, I., and H. Stelfox. 1969. Some interspecific intolerance between Barrow's goldeneye and other duck species during brood-rearing. Can. Field-Nat. 83:407-408.

Rogers, J.P. 1964. A decoy-trap for male lesser scaups. J. Wildl. Manage. 28:408-410.

Rowe, J.S. 1959. Forest regions of Canada. Can. Dep. North. Aff. and Nat. Resour., For. Branch Bull. 123:1-71.

Schierbaum, D., and E. Talmage. 1954. A successful diving duck trap. N.Y. Fish and Game J. 1:116-117.

Schoener, T.W. 1968. Sizes of feeding territories among birds. Ecology 49:123-141.

Seymour, N.R. 1974. Site attachment in the northern shoveler. Auk 91: 423-427.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York, 312 pp.

Siegfried, W.R. 1968. The black duck in the south-western Cape. Ostrich 39:61-75.

Sirén, M. 1952. Undersökningar över knipans, *Bucephala clangula*, fortplantningsbiologi. (Summary: Studies on the breeding biology of the goldeneye, *Bucephala clangula*.). Riistatiet. Julkaisuja 8:101-111.

Smith, R.I. 1968. The social aspects of reproductive behavior in the pintail. Auk 85:381-396.

Sowls, L.K. 1955. Prairie Ducks. Wildl. Manage. Inst., Washington, D.C. 193 pp.

Stansell, S.S.6. 1909. Birds of central Alberta. Auk 26:390-400.

Stewart, R.E., and H.A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish and Wildl. Serv. Resour. Publ. 92. 57 pp.

Sugden, L.G. 1960. An observation of interspecific strife between Barrow's goldeneye and lesser scaup. Can. Field-Nat. 74:163.

Sugden, L.G., and H.J. Poston. 1968. A nasal marker for ducks. J. Wildl. Manage. 32:984-986.

Swanson, G.A., and M.I. Meyer. 1973. The role of invertebrates in the feeding ecology of Anatinae during the breeding season. Pages 143-185 *in* Waterfowl Habitat Manage. Symp., Spec. Publ. Wildl. Manage. Inst. 306 pp.

Swanson, G.A., M.I. Meyer and J.R. Serie. 1974. Feeding ecology of breeding blue-winged teals. J. Wildl. Manage. 38:396-407.

Thornsberry, W.H., and L.M. Cowardin. 1971. A floating bail trap for capturing individual ducks in spring. J. Wildl. Manage. 35: 837-839.

Tinbergen, N. 1957. The functions of territory. Bird Study 4:14-27.

_____. 1959. Comparative studies of the behaviour of gulls (Laridae): A progress report. Behaviour 15:1-70.

Trauger, D.L. 1971. Population ecology of lesser scaup (*Aythya affinis*) in subarctic taiga. Unpublished Ph.D. Thesis, Iowa State Univ., Ames. 118 pp.

Verner, J., and M.F. Willson. 1966. The influence of habitat on mating systems of North American passerine birds. Ecology 47: 143-147.

von Haartman, L. 1956. Territory in the pied flycatcher *Muscicapa hypoleuca*. Ibis 98:460-475.

Watson, A. 1964. Aggression and population regulation in red grouse. Nature (Lond.) 202:506-507.

_____. 1970. Territorial and reproductive behaviour of red grouse. J. Reprod. Fert., Suppl. 11:3-14.

Watson, A., and R. Moss. 1971. Spacing as affected by territorial behavior, habitat and nutrition in red grouse (*Lagopus l. scoticus*). Pages 92-111 *in* A.H. Esser, ed., Behavior and Environment. The use of space by animals and men. Plenum Press, New York. 411 pp.

Wiley, R.H. 1973. Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*. Anim. Behav. Monogr. 6:87-169.

Willis, E.O. 1967. The behavior of bicolored antbirds. Univ. Calif. Publ. Zool. 79:1-127.

Young, C.M. 1970. Territoriality in the common shelduck *Tadorna tadorna*. Ibis 112:330-335.