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Some aspects of the behavior and ecology of harlequin ducks breeding in Glacier National Park Montana

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SOME ASPECTS OF THE BEHAVIOR AND ECOLOGY OF HARLEQUIN DUCKS BREEDING IN GLACIER NATIONAL PARK, MONTANA

By

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The behavior and ecology of Harlequin Ducks (Histrionicus histrionicus) on McDonald Creek in Glacier National Park, Montana, were studied during the 1973-1976 breeding seasons. Pairs were formed prior to arrival on the breeding grounds in early May. Harlequins confined nearly all activities to swiftly running waters, but also used stretches of abandoned stream-channel. Pairs were not territorial; home ranges were linear and consisted of approximately 1 to 2 km of stream habitat. Considerable overlap of home ranges occurred, especially at favored feeding sites. Density was approximately one pair per 1.1 to 1.5 km of stream. Males comprised 64 percent of the breeding population. Resightings of marked ducks during successive breeding seasons indicated a high degree of breeding site fidelity among females, and that females breeding for the first time returned to their natal breeding grounds. Most eggs were laid between 18 May and 8 June, and hatching occurred during the first week of July. Previously undocumented copulatory behaviors indicated possible phylogenetic affinities with the Goldeneyes (Bucephala sp.). During years when late runoff and high water levels imperiled newly hatched juveniles, still waters were used almost exclusively during the first month after hatching. Females with broods avoided all areas frequented by humans. During the final 2 weeks of the 55-day preflight period, broods shifted all activities to running waters. Productivity was closely correlated with the timing and intensity of spring runoff. Survival to fledging of known juveniles was 83 percent in 1973, 40 percent in 1974, and 18 percent in 1975. Mean brood size and the number of broods hatching declined similarly during the 3 years. High juvenile survival in 1973 was attributed to a relatively snow-free winter and an early spring runoff. During both 1974 and 1975, flooding occurred. Floods affected production through nest washout and increased mortality of juveniles. Management suggestions stressed recreating pristine conditions by restricting human access to vital habitats and allowing the stream's natural aging process to create new habitats.

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

Harlequin Ducks (Histrionicus histrionicus) are members of the tribe Mergini, the sea-ducks (Delacour and Mayr 1945). Wintering populations occupy northern coastal waters of both the Atlantic and Pacific oceans. With the approach of spring, sexually mature birds migrate inland where small, isolated breeding populations inhabit turbulent montane streams.

Two distinct and widely separated populations comprise the species' North American distribution. A small northeastern population winters along the North Atlantic coast from southern Labrador to New Jersey and breeds in subarctic habitats from southeastern Baffin Island southward as far as the Gulf of St. Lawrence. A substantially larger western population winters along rocky seacoasts from the Aleutian Islands south to central California. The breeding range of the western population extends from the Aleutian Islands down along the coast ranges through Oregon. It includes the inland mountains from northcentral Alaska as far south as the Cascade and Sierra Nevada ranges of central California (Johnsgard 1975, Palmer 1976). Sparse breeding populations also occur in the Rocky Mountains of British Columbia and Alberta, while south of the Canadian border, scattered breeding populations range as far inland as western Montana and Wyoming.

Throughout their western range, breeding Harlequins are restricted ecologically to swift, clear mountain streams. Bengtson (1966) concluded that Harlequins are more strictly confined to running water than any other waterfowl species breeding in the Northern Hemisphere. Though Harlequins are ecologically unique among northern ducks, they share their adaptation to swift waters with two genera of waterfowl which breed in the Southern Hemisphere. The rare Blue Duck (Hymenolaimus malacorhynchos), generally placed in the tribe Anatini, is confined to turbulent montane streams of New Zealand. Merganetta armata, the Torrent Duck of South America, occupies the rapids and falls of Andean streams as high as 4,500 m (Johnsgard 1966). Phylogenetic affinities of Torrent Ducks are also uncertain with various authors either including them among the dabbling ducks, Anatini (Delacour 1954), the perching ducks, Cairinini (Johnsgard 1966), or in a monotypic tribe, Merganettini (Delacour and Mayr 1945). Both species nest along torrential waters and feed primarily on aquatic insects, but unlike Harlequin Ducks, both species are monogamous and territorial and may maintain their territories throughout the year (Johnsgard 1966, Kear 1972). Ecological similarities among Blue Ducks, Torrent Ducks, and Harlequins are extensive (even plumage patterns of Harlequins and Torrent Ducks are strikingly similar). However, those similarities appear to be entirely the result of ecological convergence.

In western Montana, near the limit of the Harlequins' distribution, breeding populations are uncommon and localized. Although numerous streams appear superficially to provide suitable habitat, precise ecological requirements and extreme sensitivity to human intrusion limit breeding activities to remote, pristine areas. Recently, human population growth has created an increasing demand to develop pristine habitats both to exploit their energy potential and to provide recreational opportunities for the burgeoning human population. A thorough knowledge of the Harlequin Duck's breeding requirements is needed to enable assessment of the species' status and the potential impact of further human encroachment and habitat alteration. Thorough studies of Harlequin biology have been conducted only in Iceland (Bengtson 1966, 1972, Bengtson and Ulfstrand 1971). Those studies provide insights into basic ecological requirements, but extensive habitat differences limit their value in management of western populations.

As a senior thesis project, I began studying Harlequin Ducks on the Upper McDonald Creek in Glacier National Park, Montana, in May 1973. My primary objectives were to assess the size of the breeding population, become familiar with the species' habits and the study area, and determine the feasibility of continuing the project at the graduate level. The McDonald drainage provides optimal habitat in a comparatively unaltered state, and breeding Harlequins are relatively abundant. During 1973 I obtained only a small amount of data during the courtship and nesting period, but I was able to follow several broods from hatching until fall migration. I monitored production and survival of young, development of juveniles, and habitat use by broods. Continuing at the graduate level, I gathered ecological and behavioral data from April until September in 1974 and 1975, and during spring 1976.

Specific objectives of the study included the following:

1) determination of the chronology of breeding and brood-rearing activities;

2) observation of behaviors and those activities which may influence breeding density and habitat selection;

3) determination of population numbers, local distribution, and daily and seasonal movements;

4) evaluation of reproductive success and description of the development and survival of young;

5) identification of habitat requirements of Harlequins on McDonald Creek; and

6) provision of management suggestions.

CHAPTER II

DESCRIPTION OF THE STUDY AREA

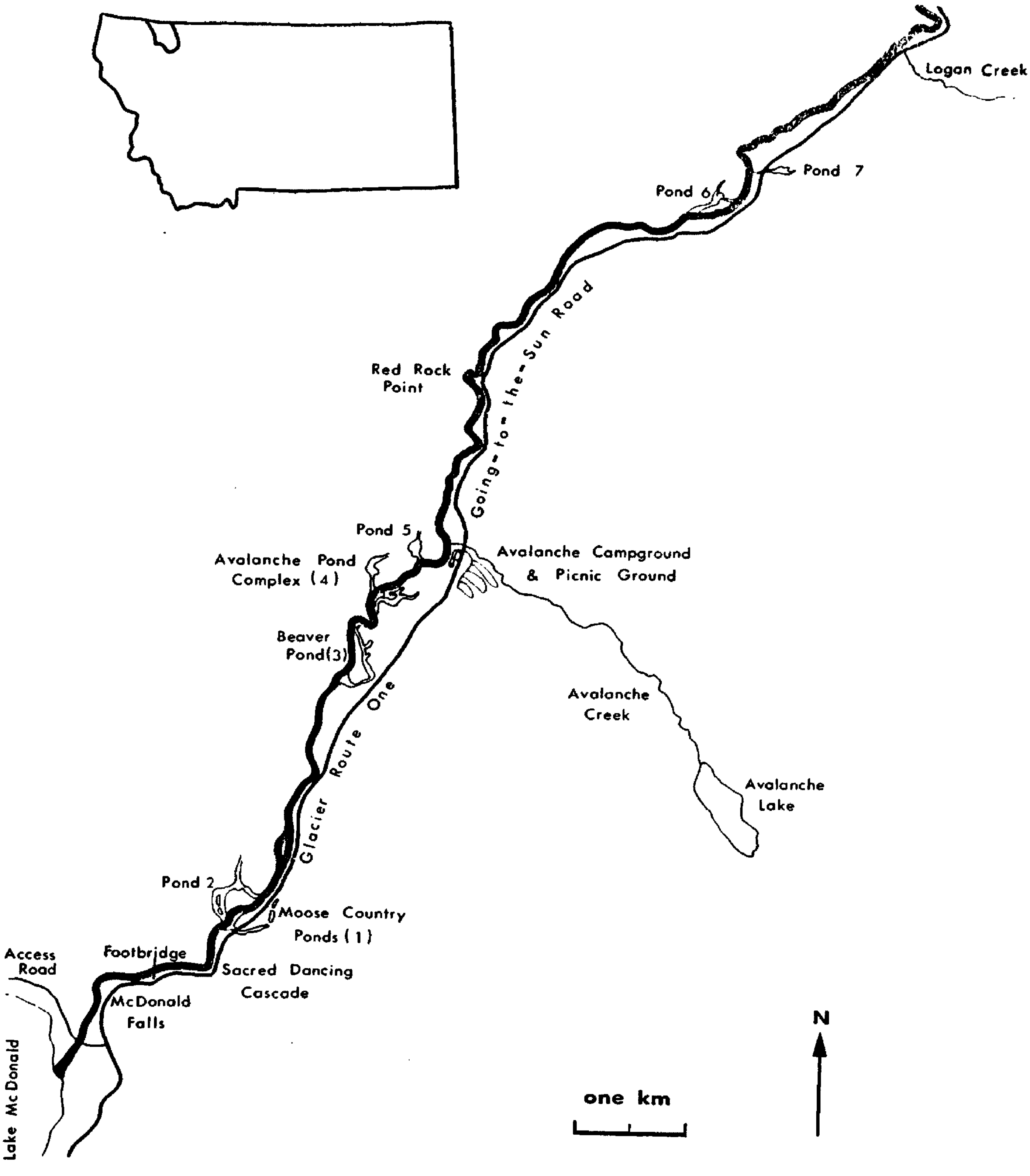
Location

During the breeding season, Harlequins inhabit a number of creeks in Glacier National Park, but few creeks contain sufficient habitat to support more than one or two breeding pairs. My study area (Fig. 1) consisted of a 16 km section of the Upper McDonald Valley extending southwest along McDonald Creek from its confluence with Logan Creek to its entrance into Lake McDonald. Breeding Harlequins were relatively abundant on the area and a major park road facilitated travel, providing access to many sections of the stream. Additional observations were made in other parts of the McDonald drainage and along other streams in the park.

Geology

The origin of McDonald Creek lies near the Continental Divide, southwest of West Flattop Mountain. From its headwaters at approximately 1,859 m, the creek drops 898 m in 35.4 km before emptying into Lake McDonald. The gradient is steepest in the upper reaches where the creek drops 773 m in 19.4 km, as it flows southeast toward its confluence with Logan Creek. From Logan

Fig. 1. Map of study area. Inset shows location of Glacier National Park in Montana.


Logan Creek
Pond 7
Pond 6
Going-to-the-Sun Road
Red Rock Point
Pond 5
Avalanche Pond Complex (4)
Avalanche Campground & Picnic Ground
Beaver Pond(3)
Avalanche Creek
Glacier Route One
Avalanche Lake
Pond 2
Moose Country Ponds (1)
Access Road
Footbridge
Sacred Dancing Cascade
McDonald Falls
Lake McDonald
one km
N

Creek at 1,086 m the creek trends southwest toward Lake McDonald, dropping 125 m in 16 km. Though the average gradient between Logan Creek and Lake McDonald is only 7.8 m/km, it is considerably steeper, up to 20 m/km, where the creek flows over exposed bedrock. Numerous small, snow-fed streams flowing from ridges and hanging valleys high above the McDonald Valley supply water to the creek.

On the study area, McDonald Creek cuts through a steep-walled valley which was deepened and straightened during the Pleistocene glaciation (Alden 1953). Less than 10,000 years ago, the extensive ice cap which buried most of the park began to recede, leaving in the McDonald Valley thick deposits of glacial debris overlying Precambrian sediments (Alt and Hyndman 1973). Those deposits of glacial till and outwash comprise the substrate over which McDonald Creek presently runs. The creek meanders freely across the broad floodplain, except in several areas where glacial debris is interrupted by exposed bedrock from the Appekunny and Grinnell argillite formations (Ross and Rezak 1959).

Two distinct stream habitats occur. Where the creek flows over erosion-resistant bedrock, the channel is strictly confined, forming narrow gorges containing numerous waterfalls and rapids. Erosion proceeds slowly in the gorges since the stream carries very little sediment except during spring runoff in May and June. Emergent rocks, though occasionally present in riffles and pools, are most prevalent in these bedrock areas.

Where the substrate consists primarily of cobbles averaging 8 to 25 cm in diameter, the creek tends naturally to form regular series of alternating riffles and pools. Numerous unstable meander bends form as the stream wanders over easily erodible glacial deposits. The meanders move slowly downstream and continually grow in amplitude as the stream undercuts concave outer banks and deposits sediments slightly downstream where current is slack along the convex inner banks. Eventually sediment deposition chokes the channel with debris and the stream cuts across the necks of bends, isolating old sections of stream channel. This process is highly accelerated during seasonal spates when sediment loads are high. On the study area, several remnants of old stream channel still remain as shallow, oxbow-shaped ponds adjacent to the stream. Those still ponds have acquired mud bottoms and continue to fill with silt, particularly when high spring runoff links them with the creek. However, while the old ponds fill in and become swamps, new ponds are created as the stream constantly shifts its bed back and forth across the floodplain.

Climate

The rugged topography of Glacier Park exerts a marked influence on local climate. Lying west of the Continental Divide, the study area has a modified north Pacific coast type climate (Cordell 1971). However, topographic influences including valley-ridge configurations, elevation, aspect and exposure, combine to produce extreme variation in weather over short distances. The West Glacier townsite, elevation 961 m, lying approximately 18.5 km southwest of the study area, averages 76.2 cm of precipitation annually (Dightman 1961, see Table 1). But along the Continental Divide only 17 km southeast of the headwaters of McDonald Creek, gauges at Grinnell Glacier, elevation 1,950 m, indicate an annual average of nearly 305 cm (Cordell 1971).

Most of the area's precipitation occurs during two periods. At West Glacier approximately 41 percent of the average annual precipitation occurs as winter snowfall between November and February; nearly 25 percent occurs as spring rain during May, June, and July (Anon. 1967). Dightman (1961) estimated that the average winter snowfall on many mountain ridges exceeds 2,540 cm, and Soil Conservation Service figures indicate an average of 2,000 to 2,540 cm at high elevations in the Upper McDonald Valley (Anon. 1975a). Most of the winter snowpack near the origin of McDonald Creek accumulates between December and May. Although winters west of the Continental Divide are cold and some subzero temperatures usually occur, March and April typically bring warmer weather. Snowmelt begins in March though the water content of the high

Table 1. Climatological summary, West Glacier, Montana, for period 1937-1966.

U. S. DEPARTMENT OF COMMERCE, WEATHER BUREAU
IN COOPERATION WITH NATIONAL PARK SERVICE
CLIMATOGRAPHY OF THE UNITED STATES NO. 20 — 24

CLIMATOLOGICAL SUMMARY

LATITUDE 48° 30'
LONGITUDE 113° 59'
ELEV. (GROUND) 3154

STATION WEST GLACIER, MONTANA

MEANS AND EXTREMES FOR PERIOD 1931-1960

Month	Temperature (°F)							**	Precipitation Totals (Inches)								Mean number of days					Month
	Means			Extremes								# Snow, Sleet						Temperatures				
																		Max.		Min.		
	Daily maximum	Daily minimum	Monthly	Record highest	Year	Record lowest	Year	Mean degree days	Mean	Greatest daily	Year	Mean	Maximum monthly	Year	Greatest daily	Year	Precip. .10 inch or more	90° and above	32° and below	32° and below	0° and below	Month
(a)	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	
JAN	28.0	14.1	21.1	52	1931	-37	1937	1360	3.13	1.24	1951+	36.4	74.5	1954	19.0	1954+	10	0	17	30	6	JAN
FEB	32.9	15.8	24.3	58	1950	-40	1933	1140	2.42	2.09	1951	26.5	57.5	1937	16.0	1957	7	0	11	27	4	FEB
MAR	41.3	21.4	31.4	64	1941	-30	1960	1040	1.81	0.95	1947	16.2	35.5	1951	15.0	1954+	6	0	4	28	2	MAR
APR	54.2	29.4	41.8	80	1939	-8	1936+	700	1.87	1.29	1951	4.3	24.0	1948	8.5	1953	6	0	*	21	*	APR
MAY	64.9	37.2	51.1	91	1936	13	1954	430	2.36	1.22	1938	0.4	5.0	1956+	5.0	1951	7	*	0	7	0	MAY
JUN	70.3	43.6	57.0	92	1941+	24	1959	260	3.02	1.87	1947	T	T	1955+	T	1952+	8	*	0	1	0	JUN
JUL	80.6	47.3	64.0	101	1934	34	1959+	80	1.27	1.22	1932	T	T	1954+	T	1952+	4	3	0	0	0	JUL
AUG	78.5	45.5	62.0	95	1941	31	1937+	120	1.33	2.08	1947	0.0	0.0		0.0		3	1	0	*	0	AUG
SEP	67.2	39.4	53.3	88	1944+	16	1934	350	1.89	1.59	1952	T	1.0	1949	1.0	1949	5	0	0	5	0	SEP
OCT	53.6	32.5	43.1	79	1942	-9	1935	680	2.64	1.76	1955	2.3	28.0	1951	12.0	1951	7	0	*	17	*	OCT
NOV	37.6	24.2	30.9	67	1948	-29	1959	1020	3.06	1.50	1932	15.8	58.3	1959	12.0	1959+	8	0	7	26	1	NOV
DEC	31.6	19.7	25.7	57	1931	-22	1932	1220	3.26	1.02	1937	31.4	74.2	1951	20.0	1938	10	0	15	29	2	DEC
Year	53.4	30.8	42.1	101	JUL 1934	-40	FEB 1933	8400	28.06	2.09	1951	133.3	74.5	JAN 1954	20.0	DEC 1938	81	4	54	191	15	Year

(a) Average length of record, years.

T Trace, an amount too small to measure.

** Base 65°F (estimated)

+ Also on earlier dates, months, or years.

* Less than one half.

Hail was included in these values from July 1948 through December 1955.

elevation snowpack generally increases through early April. Typically during the latter part of April the water content of the snowpack in the headwaters of McDonald Creek decreases by 30 percent as spring runoff begins (Farnes and Shafer 1975). Heavy discharge occurs during May and June and peak flow regularly occurs during early June. The snowpack deteriorates rapidly in early summer. However, any significant amounts of precipitation or unusually warm temperatures in early June constitute a serious flood threat.

Benthic Invertebrates

Abundance of benthic invertebrates indicates the stability and fertility of the habitat. Since silty meander ponds are unstable, they generally contain faunas which are both less abundant and less varied than more stable stream habitats (Hynes 1970). Streams, however, also vary in their ability to support a benthic fauna. In general, distribution patterns of stream organisms reflect the complexity of the habitat; as complexity increases faunal diversity shows a corresponding increase (Hynes 1970). Meandering streams contain a variety of habitats not present in a simple channel. As the current sorts the substrate, it deposits larger particles in the upper layers to form shallow riffles. Riffles provide a sanctuary for benthic animals since the coarse substrate is quite stable during average flows and the turbulence in those areas prevents silt accumulation. Faunas are locally less abundant in deep pools because such areas tend to collect more silt. Diversity is often highest where the substrate is composed of large cobbles (Pennak and VanGerpen 1947, Wene and Wickliff 1940). Bedrock areas also contain a diverse fauna since the substrate is extremely stable and the irregular bottom provides numerous refugia which are colonized by rooted plants and filamentous algae (Macan 1963). Percival and Whitehead (1929) found that mosses and rooted plants supported a greater abundance of organisms than bare rocks.

Several investigators have found that flooding has a marked influence on stream biota (Moffet 1936, Mottley et al. 1938). Streams in which seasonal spates regularly occur show corresponding fluctuations in faunal density and generally have poorer faunas (Nevin 1936 in Hynes 1970). Gaufin (1959) found that organisms were least abundant during and after spates, though effects are minimized on those substrates least susceptible to washout. On the study area habitat loss due to washout and siltation is generally confined to pools and small ponds during years of normal runoff. During flood years, however, considerable habitat alteration occurs in stony reaches and abandoned meanders as well. Bedrock habitats are probably least affected during floods.

Vegetation

Because of maritime climatic influences, a complex of cool and moist sites predominates on the study area. Southern reaches of the Upper McDonald Valley are dominated by the *Clintonia uniflora* phase of the *Tsuga heterophylla*/*Clintonia uniflora* (western hemlock/ queencup beadlily) habitat type (Pfister et al. 1974). Beginning north of Moose Country a mosaic of two types prevails: the *Tsuga heterophylla*/*Clintonia uniflora* type occupies more mesic sites while the *Thuja plicata*/*Oplopanax horridum* (western redcedar/devil's club) type dominates the wet bottoms. *Thuja plicata*/*Oplopanax horridum* assumes dominance approximately 2 km south of Avalanche Creek and continues for nearly 4 km. North of Red Rock Point the dominant habitat type is the *Clintonia uniflora* phase of the *Picea*/*Clintonia uniflora* (spruce/queencup beadlily) habitat type. That habitat type is interspersed on the east side of the creek with numerous avalanche slopes which extend to the creek bottom; the valley's steep west wall is sparsely vegetated, the result of a fire in 1967. In low-lying and poorly drained areas, as well as the avalanche slides, vegetation is typically riparian. In those areas, streambanks are lined with willows (*Salix*), alder (*Alnus*), wild rose (*Rosa*), Hawthorn (*Cretaegus douglasii*), and red-osier dogwood (*Cornus stolonifera*), frequently forming dense thickets. Because of the continual shifting of the stream channel, the remainder of the stream generally has steeply cut banks with coniferous vegetation, interspersed with some riparian growth, extending to the stream's edge.

Human Use

Park visitation is seasonal and most human activity occurs during summer. In late autumn heavy snows cause closure of Glacier Route One which runs through the Upper McDonald Valley and vehicular traffic is prohibited north of Lake McDonald until snowplow crews begin to clear the road in mid-April. With the exception of winter hiking and ski touring, nearly all human activities along the study area occur between 1 May and 5 September, coinciding with the Harlequin breeding season. During the summer, sightseeing, hiking, and fishing are the dominant human activities.

Glacier Route One, the principal road through the park, runs parallel to the creek on its east side. In several places where the road lies adjacent to the creek, small parking turnouts enable tourists to stop to view the scenery. Short footpaths radiating from the parking areas provide access to the creek; in those areas the creek receives heavy use by tourists. Most human activity is confined to the immediate vicinity of parking areas since dense vegetation and blowdowns discourage foot travel along the creek bottom. The National Park Service does not maintain trails along the east side of the creek.

Two bridges at the extreme southern end of the study area enable tourists to cross the creek. A local road providing access to cabins on the north shore of Lake McDonald crosses the creek 400 m above the lake; approximately 1 km further upstream a small bridge enables hikers and equestrians to cross the stream. No other bridges exist on Upper McDonald Creek. A hiking trail begins at the lake and parallels the creek on its west side for approximately 8 km. Trail crews maintain the hiking trail to its terminus several hundred meters south of Avalanche Creek. Since it intersects no other trails and camping is not allowed in this region, few hikers venture more than 2 km north of the footbridge. Several times daily during the tourist season a local concessionaire conducts guided horse trips along the southern portion of the trail. Though some sections run adjacent to the creek, persons traversing the hiking trail are generally quite unobtrusive.

From 5 June until 15 October, the National Park Service permits sport fishing within Glacier Park. All of the Upper McDonald Creek except the lower 800 m between McDonald Falls and the lake is open to fishing without a license. After spring runoff subsides, at approximately the time Harlequin broods emerge, heavy use by anglers begins. Though most anglers congregate near auto access sites, a few determined fishermen reach even the most remote areas. Fish were formerly planted in the creek, but changes in management policies have precluded transplants since the late 1960's. The relative infertility of McDonald Creek creates notably poor fishing conditions and anglers' success is very low.

Most brood-rearing habitat is buffered from human intrusion by distance and dense vegetation. With rare exceptions, remote ponds provide sanctuaries and human influences on juveniles are negligible in most parts of the study area. However, the number of park visitors rose from 1,398,958 in 1973 to 1,571,393 in 1975 (Glacier Park records). As park visitation continues to increase by approximately 4 to 5 percent annually, human activities increasingly penetrate pristine areas.

CHAPTER III

METHODS AND MATERIALS

To expedite analysis and presentation of data, I separated the Harlequin breeding season chronologically into two distinct periods. During the courtship and nesting period, occurring between 14 April and 30 June, I collected data on activities, interactions, and habitat use by breeding adults. During the brood-rearing phase, lasting from 1 July through early September, I recorded observations of activities, development, survival, and habitat use by broods.

Observations

Habits of breeding Harlequins facilitated observation and censusing; while on the breeding grounds adult ducks confined nearly all activities to running water habitats. Once established in a suitable area, pairs were quite stationary while bachelor males moved greater distances along the stream (see Figs. 4, 5, Appendix VII). Although they seldom flew, Harlequins in flight always followed the stream channel precisely, typically within 2 m of the water's surface. No Harlequins were ever seen flying over land and I did not detect any movements between drainages. Bengtson (1972) reported that in Iceland no marked Harlequins moved overland to neighboring streams.

Most ducks on a section of creek were easily located by walking along the bank, and the majority of my data were collected while traversing the area on foot. However, when I needed to reach widely separated sections of the study area quickly, particularly during spring when snow depths inhibited walking, I traveled by automobile between access points and walked to areas not visible from those points. Coverage of the study area was not as thorough when automobile travel was employed. Throughout the study I attempted to distribute my time equally throughout the study area. For close-range observations I used an 8x binocular; a tripod-mounted 20-45 variable power spotting scope enabled viewing at greater distances.

Each discrete sighting of a duck or group of ducks was considered a new observation. An observation was terminated when ducks being observed were lost from view or when I moved to a different part of the study area. Relocations of ducks were considered distinct observations only when separated temporally or spatially from previous observations. Occasionally individual ducks were included in several observations during a single day. For each observation I recorded the following data: individual identity (when possible), date, time, location, group composition, movement, major activities, and social behaviors. I also described a number of features of the habitat being used. Habitat data were later used in conjunction with an extensive habitat inventory to evaluate preferences and requirements.

I plotted on maps the locations of known ducks to document movements, site tenacity and extent of seasonal home ranges.

Censusing

During 1974 and 1975 I censused the population weekly during both the courtship and nesting season and the brood-rearing period. Censuses conducted prior to 1 July provided direct information on the size of the breeding population and indirect data on the timing of arrival, incubation, and male departure. Later censuses revealed total production, mortality of juveniles, and timing of migration. During censusing I attempted to obtain an absolute count, beginning at the lake and walking the length of the study area along the banks of the creek and its adjoining ponds. Typically as ducks detected my presence, they swam upstream for a short distance, then moved to midstream allowing the current to sweep them downstream past me. I counted only the birds which drifted or flew downstream past me and disregarded the few which flew upstream before I reached them. Occasionally ducks, usually the less sedentary unpaired males, flew up past me, moving from a censused to an uncensused stretch of creek; I deleted any suspected duplications from the total count.

Except in early spring when snow depths hindered foot travel, censuses required only one day. When high water prevented movement near the creek in some regions, a combination of automobile and foot travel was necessary. At each access point I walked to provide visual coverage of inaccessible stretches. Unless I saw them fly between two different areas I assumed that ducks located at each point were different.

Deliberate attempts to eliminate duplicate counts, combined with my inability to locate every duck on the area, gave my estimates a conservative bias. A higher degree of accuracy was possible in 1975 since nearly half the pairs and one fourth of all the ducks comprising the population were banded. However, in 1974 occasional attempts to verify accuracy by censusing on consecutive days provided consistent approximations.

Censusing broods in July was difficult because females with young broods were extremely secretive and tended to hide in backwaters. Brood censuses required two people, one remaining near a pond outlet to detect ducks entering or leaving, and one to travel the perimeter attempting to flush any groups which retreated into side ponds. A search of the creek between pond complexes insured inclusion of nearly all broods. Brood counts were consistent since movements of flightless young were restricted, and even with unmarked females, the number of young and stage of development generally enabled positive identification of broods.

Capture and Marking

The Harlequins' habit of flying low following the creek made them relatively easy to capture in mist nets. However, using mist nets over running water required some deviation from the traditional techniques described by Low (1957). With minor modifications the method described by Bakus (1957) for capturing Dippers (*Cinclus mexicanus*) provided good results. Since the coarse substrate of McDonald Creek made conventional aluminum poles unsuitable, I constructed heavy steel poles which were driven into the substrate using a post-pounder. Two-ply mist nets with an 11 cm stretched mesh were used. The fine mesh was rarely detected by Harlequins and strength was generally adequate to hold them once they flew into the net.

Although I captured seven ducks while working alone, trapping success was higher when three to five persons assisted. When assistance was available, several people moved upstream to locate ducks and drive them downstream toward the net. Two persons remained near the net, one approximately 20 m upstream. As soon as ducks moved past the person upstream from the net, he rushed toward the ducks to flush them into the net. One person always remained near the net to prevent captured ducks from submerging and possibly drowning.

Trapping flightless broods in mist nets required considerable modification of usual techniques. The net was erected downstream from a brood, preferably in a pond outlet or narrow stream channel. The top half of the net was suspended on vertical poles with the middle horizontal support string at water level. The lower half was submerged and stretched horizontally upstream with the corners held loosely by wooden stakes. Split-shot attached to the lowest horizontal support string kept the net submerged. Ropes fastened to the lower corners and running through pulleys tied to the vertical poles permitted the horizontal section to be raised quickly in the manner of a drawbridge. Trapping broods required from three to five persons. One or two persons drove the brood slowly downstream by walking along the bank. The ducks were chased the final 10 m, causing them to rush toward the net. When they struck the net, the horizontal section was quickly raised by persons controlling the ropes; the ducks were suspended above the water in the loose net bag which was formed.

When capturing broods or pairs, I attempted to minimize disruption of social bonds by releasing the ducks simultaneously.

For all captured ducks I recorded weight and several other measurements (Baldwin et al. 1931, see Appendix III). Each duck then received an aluminum U.S. Fish and Wildlife Service band, size 6, as well as a combination of colored plastic leg bands (National Band and Tag Company) to enable individual identification. I used only red, blue, and yellow bands since they were highly visible and could often be seen through the water as the ducks swam. Blue bands tended to fade badly during winter when the birds inhabited salt water.

To obtain food samples without sacrificing ducks, I administered an emetic to three bachelor males. Each received 2.5 cc of 1 percent antimony potassium tartrate in solution administered by means of a 5 cc disposable syringe and a length of flexible plastic tubing with an external diameter of 2 mm (Prŷs-Jones et al. 1974). After administration of the emetic, ducks were held in a dark container to minimize the trauma of handling. After 30 minutes the ducks were released regardless of whether emesis had occurred.

Behaviors

For each observation I recorded basic data on maintenance and social behaviors, paying particular attention to agonistic behaviors, courtship patterns, and the copulatory sequence. Though most data were gathered by means of a stopwatch, portable cassette recorder, pencil and notebook, occasional use of a super 8 movie camera provided more accurate and detailed data for some behaviors. During the brood-rearing period I recorded interactions within and among broods.

Habitat

Data on habitat selection provided insights into ecological requirements of Harlequins. I recorded the following information for each observation:

1) general characteristics of the site used (bank type, bottom type, streamside vegetation);

2) distance of ducks from nearest loafing site and characteristics of loafing sites which were used;

3) frequency of use of abandoned meanders; and

4) proximity to areas of human activities.

To enable assessment of ecological requirements and habitat preferences of Harlequins, I prepared a composite map locating major habitat features and classifying habitats in terms of human accessibility. Data for the habitat map were collected at 200 m intervals and supplemented with information recorded during observations of ducks. At each sampling site I separated habitats into two broad categories: running or standing water.

Running water habitats were further classified in terms of the following habitat features:

1) Channel type
    a. meander
    b. reticulate
    c. bedrock canyon
2) Bank types
    a. vertical ($\geq 45°$ from horizontal)
    b. horizontal ($< 45°$ from horizontal)

3) Bank composition
   a. vegetation
   b. snags
   c. rip-rap
   d. bedrock
   e. cobbles

4) Distance in meters from water's edge to vision-obscuring vegetation.

5) Substrate type
   a. bedrock
   b. mud
   c. sand
   d. pebbles (16 to 64 mm diameter)
   e. cobbles (64 to 256 mm diameter)
   f. boulders (> 256 mm diameter)

6) Availability of midstream loafing sites
   a. none/10 m
   b. 1 to 3/10 m
   c. > 3/10 m

7) Human accessibility
   a. adjacent: established area of human activity maintained within 10 m of the creek

b. near: established area of human activity maintained > 10 m and < 50 m from the creek

c. away, accessible: area which, though > 50 m from an area of human activity, is made accessible by a maintained trail

d. away, inaccessible: area which is > 50 m from an area of human use and not accessible by a maintained trail

Pond habitats were considered separately to facilitate analysis of preferences for various habitat factors present in those areas. Each standing water area was categorized in terms of the following habitat components:

1) Origin of pond
   a. abandoned stream channel
   b. beaver pond
   c. enlarged areas around springs or small streams which empty into McDonald Creek
2) Source
   a. ground water
   b. small streams
   c. creek overflow
   d. hyporheal flow
3) Approximate age: estimated by using aerial photographs

and USGS topographic maps.

4) Approximate area during mid-May: calculated within broad limits from topographical maps.

5) Depth in mid-May: measured during early spring runoff

   a. < 1 m

   b. 1 to 3 m

   c. > 3 m

6) Bank type

   a. vertical and undercut ($\geq 45°$ from horizontal)

   b. horizontal ($< 45°$ from horizontal)

7) Persistence: estimated by comparing depth and approximate area on 15 July with that of 15 May.

8) Description of bankside vegetation.

9) Human accessibility

   a. adjacent: established area of human activity maintained within 10 m of the pond

   b. near: established area of human activity maintained > 10 m and < 50 m from the pond

   c. away, accessible: area which, though > 50 m from an area of human activity, is made accessible by a maintained trail

   d. away, inaccessible: area which is > 50 m from an area of human use and not accessible by a maintained trail

10) Human use during summer

   a. heavy: > 10 persons visit area each day

   b. moderate: > 5 persons visit area each week

   c. little: 2 to 5 persons visit area each week

   d. none: < 5 persons visit area each month

11) Use by Harlequin Ducks during courtship and nesting season

   a. heavy: > 10 observations each week

   b. moderate: 2 to 10 observations each week

   c. little: ≤ 2 observations each week

   d. none: < 5 observations each breeding season

12) Use by Harlequin Ducks during brood-rearing season

   a. heavy: > 10 observations each week

   b. moderate: 2 to 10 observations each week

   c. little: ≤ 2 observations each week

   d. none: < 5 observations each breeding season

In an effort to detect temporal changes in requirements, locations of all ducks observed during weekly intervals were plotted on maps delineating major habitat features.

Preference or avoidance of available habitats was evaluated for both running and standing water habitats using chi-square and Bonferroni z tests, as described by Neu et al. (1974). The null hypothesis for chi-square tests was that various habitat features were used in proportion to their occurrence on the study area. Habitat selection during the courtship and nesting period was considered separately from habitat selection during the brood-rearing season; results appear under appropriate subheadings.

Stream Measurement

In evaluating the influence of runoff patterns on breeding activities and reproductive success, I depended primarily on daily stream measurement data from gauges on the Middle Fork of the Flathead River (Anon. 1973d, 1974e, 1976). Since the Middle Fork originates in a region similar to the headwaters of McDonald Creek, those measurements provided a fairly reliable index of runoff on the study area. A gauge at Apgar Bridge on Lower McDonald Creek also provided information (Anon. 1973c, 1974d, 1975e). Though Lower McDonald Creek is the only stream flowing from Lake McDonald, measurement of that stream yielded less valuable information since the gauge was read irregularly at approximate weekly intervals. During 1975 I measured the streamflow on Upper McDonald Creek using a modification of the technique described by Robins and Crawford (1954). For my measurements I timed oranges (Hynes 1970) floating through a 10 m interval.

Benthic Collections

To provide a qualitative index of food potentially available to Harlequins, I collected samples of aquatic insects during autumn 1974 and at monthly intervals during the 1975 breeding season. Collecting sites included three distinct habitats:

1) riffle areas with cobble substrates;
2) rapids with bedrock bottoms; and
3) silt-laden ponds connected to the creek.

I was able to make regular collections from riffle areas, but high water often precluded sampling in ponds and bedrock areas. For stream collections I used a kick net with approximately 8 meshes/cm; a dredge was used to sample pond biota. Collected materials were preserved in 70 percent ethanol.

CHAPTER IV

RESULTS

Trapping and Banding

Twenty-seven birds were captured and marked during the study (Appendix VI). Mensural data appear in Appendix III. Only three adults, all females, were trapped during 1974. During 1975 nine additional adults were banded, three each of unpaired males, paired males, and paired females. Both members of a pair were marked in only two cases; in one instance the male was the only pair member marked. Eight adults were banded in 1976, four single males and two pairs. During 1974 five juveniles were marked, and in 1975 the only two young surviving on the study area until migration were also banded.

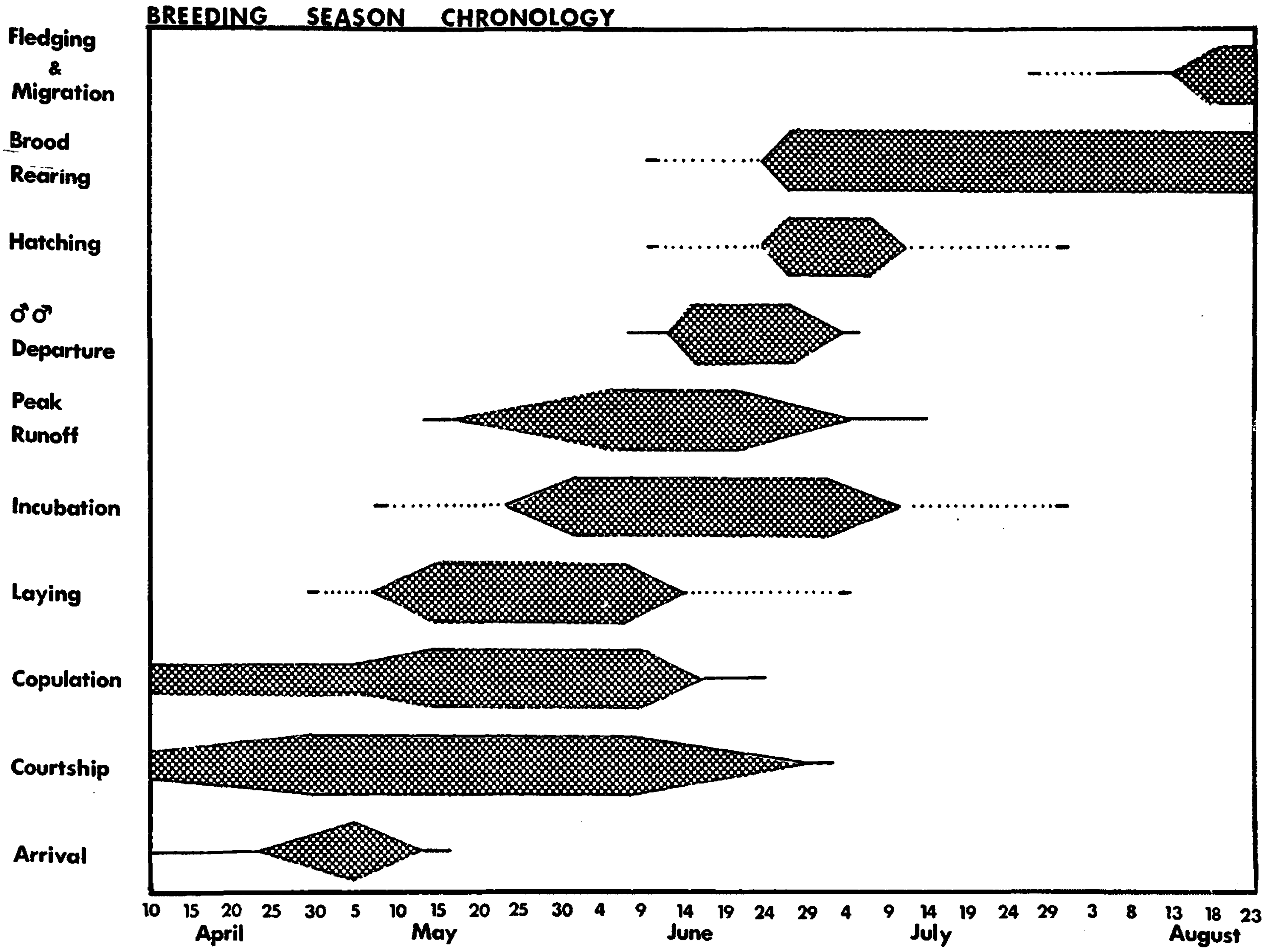
All of the three adult females captured in 1974 returned to the study area in both 1975 and 1976. In 1976, 10 banded ducks (4 males and 6 females) returned to the creek. Of the four returning males, one was unpaired in both 1975 and 1976. Another male, which was unpaired in 1975, returned with a female in 1976. The other two males were paired each year. One marked male was paired with the same marked female during both years. The other paired male, though he accompanied an unmarked female during both seasons, occupied the same 600 m section of creek and used the same loafing and feeding sites in 1975 and 1976 (Appendix VIIc).

Two of the five ducks banded as juveniles during 1974 returned to the study area in 1976; both were females and were paired with unbanded males. Both known 2-year-old females arrived on the study area on approximately 22 May, 2 to 3 weeks later than most pairs arrived. Each established a seasonal home range with 2 km of its natal home range.

Courtship and Nesting Season

Chronology. Fig. 2 depicts the breeding chronology of Harlequin Ducks on McDonald Creek. Each spring one or more nonbreeding males arrived on the study area in mid-April, preceding the majority of the population by 2 to 3 weeks (Table 2). The earliest record of a Harlequin near Glacier Park was that of an unpaired male seen on 4 April 1970, on the Middle Fork of the Flathead River (Glacier National Park Files). After reaching the study area, early arrivals confined their activities to the upper end of Lake McDonald and the southern 3 km of Upper McDonald Creek (see Fig. 3). In both 1974 and 1975 I estimated that fewer than five Harlequins, all single males, were present before 27 April when the first pairs were located. Numbers increased gradually until the third week of May

Fig. 2. Chronology of breeding activities on Upper McDonald Creek, 1973-1975.


BREEDING SEASON CHRONOLOGY
Fledging & Migration
Brood Rearing
Hatching
♂♂ Departure
Peak Runoff
Incubation
Laying
Copulation
Courtship
Arrival
10 15 20 25 30
April
5 10 15 20 25 30
May
4 9 14 19 24 29
June
4 9 14 19 24 29
July
3 8 13 18 23
August

when the majority of the population was present. All females observed were paired upon arrival, and no unescorted females were seen before 13 May. On 13 May 1975, a banded female was observed feeding alone for 30 minutes. That female had been paired when captured on 10 May and was located with a mate on five subsequent occasions.

Table 2. Earliest arrival dates of spring migrants.

Year	Unpaired males	Pairs
1974	14 April	27 April
1975	12 April	27 April
1976	16 April	30 April

Courtship activities, though well underway upon arrival, continued through the middle of June. Observations of courtship behaviors typically involved interactions between bachelor males and pairs. Unpaired drakes maximized the potential for social encounter by traveling long distances along the creek. Whenever unpaired males encountered a female, courtship displays ensued. Pairs typically reacted aggressively to thwart any intruder; in all interactions where individual identification was possible, pairs succeeded in repelling bachelor males. During the latter part of May the frequency of courtship interactions declined and the intensity and duration of those interactions decreased. Toward the end of June, males displayed little sexual interest in females, even when the females were unattended.

Among pairs, copulation represented the culmination of courtship and pair-maintaining activities. Copulatory behavior probably begins preceding arrival on the study area, and the earliest copulation I observed was on 3 May. The frequency of copulations was highest during the latter half of May and first week of June; only one copulation was observed after 8 June.

I estimated dates for egg-laying, incubation, and hatching by backcounting from dates of brood emergence. In calculating approximate dates I allowed 13 days for completing an average clutch of six eggs (clutch size data from Bengtson 1972, D. E. Crouch pers. comm.), with the 28-day incubation period beginning after the last egg was laid (data from Bengtson 1972).

Most females in the population probably laid their eggs between 18 May and 8 June, though in 1973 the timing of two broods deviated considerably (see Fig. 6). Incubation lasted throughout June and in 1974 and 1975, coincided with the peak of runoff. With the onset of incubation, pair bonds began to disintegrate. By mid-June pair dissolution was complete and the males began departing from the study area. In 1974 and 1975 most males abandoned the breeding grounds at the height of spring runoff.

Of 15 known broods produced on or above the study area during the 3 years, 11 probably hatched between 30 June and 6 July. From early July until September, dependent broods accompanied by their mothers occupied the study area. During the first 4 weeks, broods typically spent little time outside the sanctuary of the backwaters. Thereafter movements became more extensive and home ranges were continually expanded in a downstream direction. Usually by the sixth week, broods abandoned their natal areas, moving downstream to an area of bedrock canyons less than 2 km above Lake McDonald. Members of only two broods remained on the creek until flight attainment; all other broods departed by the seventh or eighth week when the young, though not fully fledged, were able to flutter over the water for 30 m or more.

Population estimates. In 1974 and 1975 the breeding population increased steadily after the arrival of the first birds in April until the fourth week of May (Table 3). The highest population estimate in 1974 (11 pairs and 10 to 12 surplus males) was slightly less than the peak number in 1975 (13 pairs, 13 surplus males, and 2 unattended females). During 1974 censuses the greatest number of pairs was 11, observed on 24 May, while during 1975, 14 pairs were counted on 15 May. As early as the middle of May, I occasionally observed unescorted females. After 5 June the number of pairs

Table 3. Results of censuses of the breeding population.

	Census date												
	17 Apr.	24 Apr.	1 May	8 May	15 May	22 May	29 May	5 June	12 June	19 June	26 June	3 July	10 July
1974													
No. unpaired females	0	0	0	0	0	0	0	3	3	4	5	7	9
No. unpaired males	3	3	9	8	11	12	10	14	7	3	4	4	0
No. pairs	0	1	7	6	10	10	11	3	1	2	1	0	0
Sex ratio													
Males:females	3:0	4:1	16:7	14:6	21:10	22:10	21:11	17:6	8:4	5:6	5:6	4:7	0:9
(Percent males)	(100)	(80)	(70)	(70)	(68)	(69)	(66)	(74)	(67)	(45)	(45)	(36)	(0)
1975													
No. unpaired females	0	0	0	0	1	2	7	7	9	6	10	10	10
No. unpaired males	2	2	10	10	11	13	13	18	14	10	10	5	0
No. pairs	0	1	8	10	14	13	10	9	5	4	0	0	0
Sex ratio													
Males:females	2:0	3:1	18:8	20:10	25:15	26:15	23:17	27:16	19:14	14:10	10:10	5:10	0:10
(Percent males)	(100)	(75)	(69)	(67)	(63)	(63)	(62)	(63)	(58)	(58)	(50)	(33)	(0)

visible began to decline rapidly and single males increased slightly. Observations of unpaired males and females increased in mid-June and the frequency of observations of pairs dropped (Table 4). By late June only a small number of males remained, and unescorted females comprised an increasing proportion of the dwindling population.

Throughout the courtship and nesting season, there was a preponderance of nonbreeding males. All unpaired males appeared to have attained definitive plumage and were presumed to be adults which had been unsuccessful in obtaining mates. First year females are not distinguishable by plumage characters (Bengtson 1972, Palmer 1976), but based on behavioral criteria, all females in the population were considered sexually mature and potential breeders.

Distribution and movements. During April censuses all ducks were concentrated on the lower half of the study area and most occupied the southern 3 km (Fig. 3). By the middle of May, pairs were spaced quite regularly along the study area though few ducks inhabited the lower 2 km. Pairs, once established on a stretch of creek, tended to be rather sedentary and rarely ranged more than 1 or 2 km (Fig. 4, Appendix VII), while surplus males traveled extensively along the creek (Fig. 5, Appendix VII). Population estimates on 15 May 1974 revealed a density of one pair for every 1.5 km of stream habitat; on the same date in 1975 the density was

Table 4. Relative frequency of observations by sex and social status.

Week ending	No. observations	No. (percent) unpaired males	No. (percent) unpaired females	No. (percent) pairs
1974				
23 April	1	1 (100)	0 (0)	0 (0)
30 April	9	6 (67)	0 (0)	4 (44)
7 May	27	13 (48)	0 (0)	15 (56)
14 May	26	18 (69)	0 (0)	13 (50)
21 May	46	16 (35)	0 (0)	35 (76)
28 May	21	15 (71)	0 (0)	8 (38)
4 June	20	16 (80)	0 (0)	4 (20)
11 June	22	18 (82)	2 (9)	8 (36)
18 June	33	21 (64)	14 (42)	3 (9)
25 June	18	9 (50)	9 (50)	4 (22)
2 July	43	20 (47)	29 (67)	0 (0)
9 July	20	0 (0)	20 (100)	0 (0)
1975				
23 April	1	1 (100)	0 (0)	0 (0)
30 April	2	1 (50)	0 (0)	1 (50)
7 May	74	40 (54)	0 (0)	41 (55)
14 May	21	14 (67)	2 (10)	12 (57)
21 May	90	57 (63)	9 (10)	41 (46)
28 May	26	14 (54)	3 (12)	11 (42)
4 June	94	51 (54)	26 (28)	31 (33)
11 June	40	25 (63)	19 (48)	18 (45)
18 June	38	29 (76)	7 (18)	7 (18)
25 June	19	12 (63)	16 (84)	3 (16)
2 July	41	20 (49)	29 (71)	0 (0)
9 July	15	0 (0)	15 (100)	0 (0)

Fig. 3. Graphical representation of study area showing distribution of population during selected censuses.

△ = Single male.

● = Pair.

■ = Unescorted female.

X^1 = Superscript represents band number of known duck.

a and b were identifiable due to distinctive plumage features.

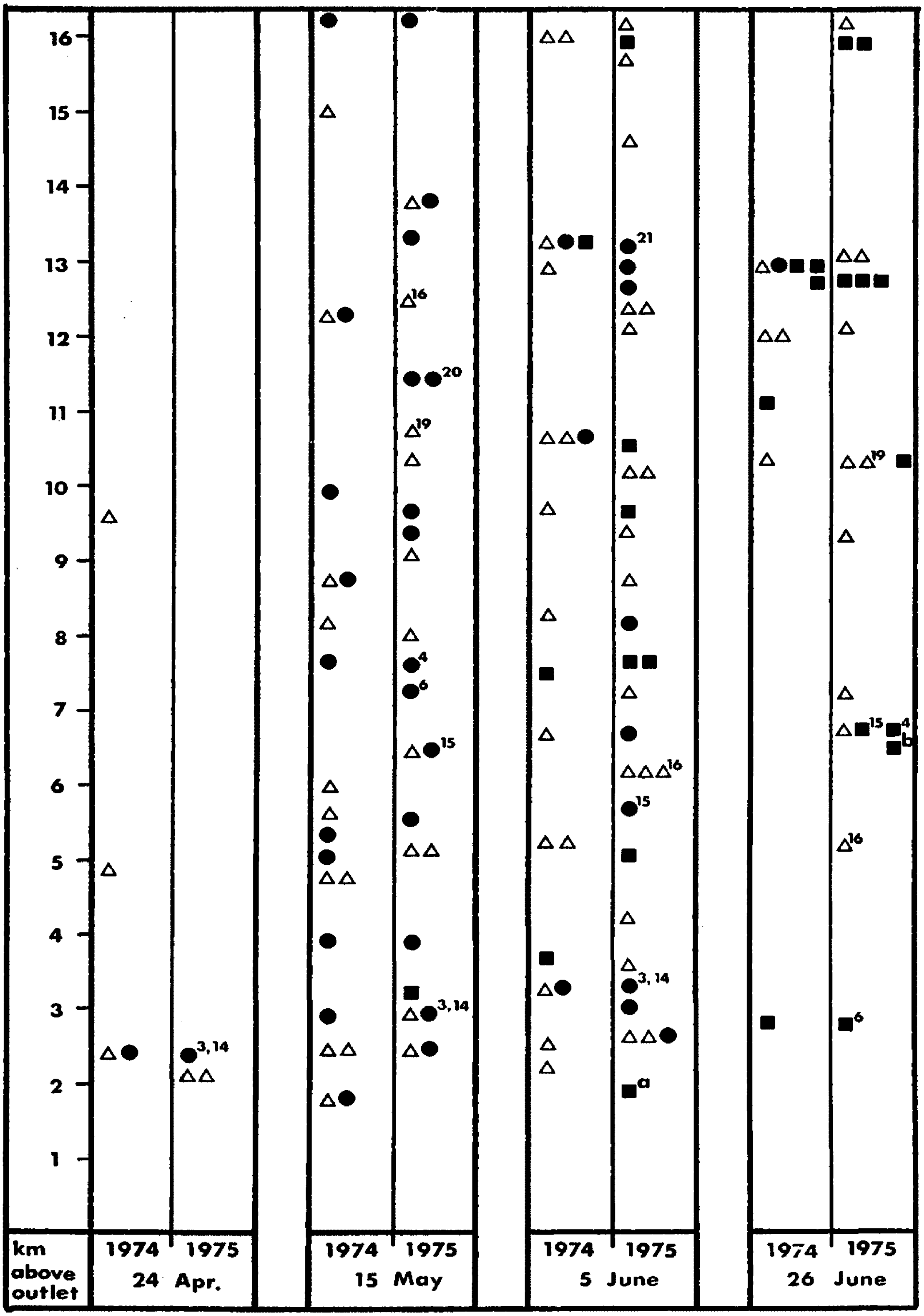

16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
km above outlet
1974
1975
24 Apr.
1974
1975
15 May
1974
1975
5 June
1974
1975
26 June
3, 14
16
20
19
4
6
15
21
a
b

Fig. 4. Locations and dates of observations of a pair (male 14 and female 3) during the 1975 and 1976 courtship and nesting seasons. In 1975 dissolution of the pair bond began on 4 June. In 1976 pair-bond dissolution began on 31 May. On 10 June 1975, female 3 was observed 2 km north of the pair's seasonal home range; she later reared a brood in the area of the 10 June location.

▲= Paired 1975.

△= Paired 1976.

■= Male only 1975.

□= Male only 1976.

●= Female only 1975.

◘= On 15 June, 14 and 3 arrived at the ponds separately and spent 2 hours feeding together before 3 departed flying upstream.

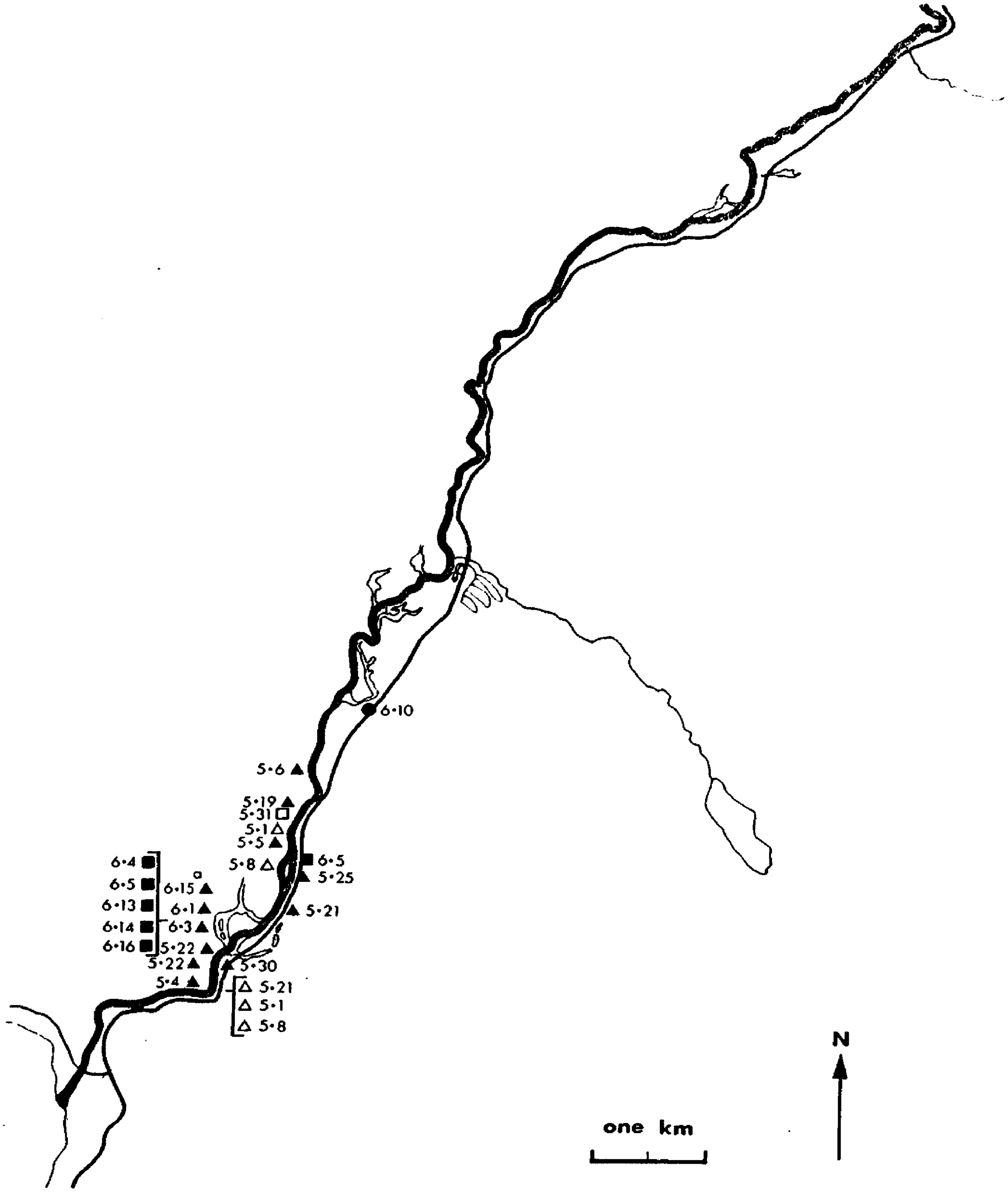
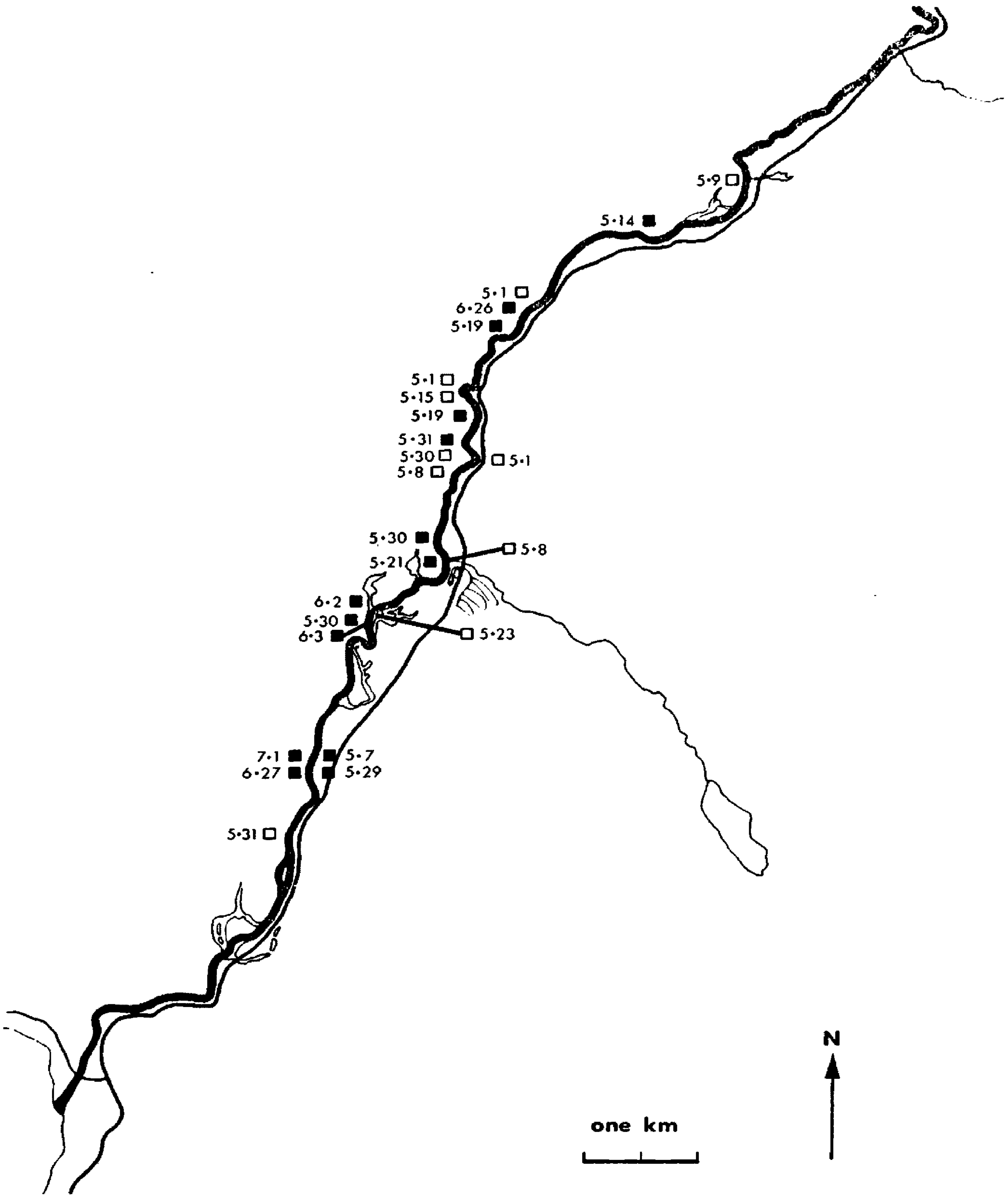

6·10
5·6
5·19
5·31
5·1
5·5
5·8
6·5
5·25
6·4
6·5
6·13
6·14
6·16
a
6·15
6·1
6·3
5·22
5·21
5·22
5·30
5·4
5·21
5·1
5·8
one km
N

Fig. 5. Locations and dates of observations of single male 16 during both the 1975 and 1976 courtship and nesting seasons.

■= 1975 observation.

□= 1976 observation.


5·9
5·14
5·1
6·26
5·19
5·1
5·15
5·19
5·31
5·30
5·8
5·1
5·30
5·21
5·8
6·2
5·30
6·3
5·23
7·1
6·27
5·7
5·29
5·31
one km
N

one pair per 1.1 km of stream. Appendix V compares estimates of breeding density on various creeks within the species' breeding range. On 5 June both pairs and single males seemed to concentrate activities in and near pond habitats. By 26 June the remaining ducks which were visible on the study area tended to be more gregarious than earlier in the breeding season (Fig. 3).

Behaviors. Throughout the courtship and nesting period, maintenance activities consumed the majority of the Harlequins' time. Long feeding bouts occurred throughout the day, but feeding was usually most intense during a 2- to 4-hour period beginning shortly after sunrise and again for several hours before sunset. Virtually all movements and feeding occurred during daylight and ducks typically selected a roosting site shortly after sunset.

Harlequins employed various foraging methods in response to stream depth and current. Where the water depth was 0.5 to 4.0 m, food was obtained by diving. When diving, ducks typically selected areas with turbulent current though they also frequented holes on the leeward side of rocks or deep pools. Often they fed in rapids which offered no sanctuary from strong currents, but eddies and pools, when available, served as temporary resting spots. Dives lasted up to 40 seconds and, during intense feeding, time underwater averaged slightly over 20 seconds with pauses between dives of 5 to 6 seconds.

While at the surface, ducks frequently dipped the bill and eyes in the water in the Looking-for-food posture (Myres 1959). Length of dives varied with depth, substrate type, and currents. Ducks generally oriented upstream when diving and moved against the current while submerged; often they surfaced slightly upstream from the point where the dive originated. Clear water frequently enabled me to observe the underwater actions of Harlequins. Though the wings were flicked open upon entry into the water, they were held loosely at the bird's sides and not used for propulsion while submerged. The alula were spread laterally, projecting outward from the wing. Both Bengtson (1966) and Michael and Michael (1922), felt that submerged Harlequin Ducks walk on the substrate like Dippers. At no time did I observe this behavior during diving; the feet were always extended postero-laterally and kicked continuously to propel the ducks as they probed among the rocks. When ascending, ducks ceased paddling momentarily and floated quickly to the surface.

More rarely, Harlequins used two other feeding methods. When moving upstream in shallow riffles or in shallow regions with slack current near the stream edge, the ducks often submerged only their bills or heads. While feeding in this manner, Harlequins either walked on the bottom or swam while probing the substrate. Less often, when feeding in areas of intermediate depth, they tipped up in the manner of dabbling ducks.

Between feeding bouts much time was spent either preening or sleeping on rocks and logs in midstream or at the stream's edge.

Harlequins were reluctant to fly and used flight primarily when moving long distances, particularly upstream. When swimming upstream they generally stayed near the stream edge where current strength was reduced. In more turbulent areas or when crossing the stream in heavy current, the ducks raised their bodies slightly out of the water and rushed short distances over the surface. Frequently they used their wings in a rowing motion to help propel them against strong current. When traveling downstream Harlequins almost always swam, depending on the current to provide most of the propulsion.

Flight was most common during spring arrival as the members of the population dispersed along the creek and preceding the departure of males and unproductive females. Bachelor males flew more often than pairs since they traveled greater distances along the study area. Incubating females also flew to reach preferred feeding areas during inattentive periods. Ducks typically signaled their intent to fly by displaying quick series of lateral bill shakes while extending the neck vertically and holding the head erect with the bill horizontal.

With few exceptions Harlequins rarely flew when threatened by potential predators; the escape reaction consisted of moving quickly to midstream and allowing the current to sweep them downstream until out of danger. Frightened ducks tended to fly more readily during the periods immediately following spring arrival and preceding the departure of males and unsuccessful females.

On the breeding grounds Harlequin Ducks were relatively nongregarious. Although there was no evidence of territoriality, pairs were generally intolerant of all other pairs, as well as bachelor males and unescorted females which violated their individual distance. Unescorted females were usually solitary, but they sometimes approached pairs and occasionally tolerated males in their presence. Bachelor males were most gregarious and occasionally as many as four unpaired males formed temporary associations, traveling and feeding together for several hours before separating. Data in Table 5 reflect the degree of sociability of pairs, single males, and unescorted females. Fewer than 10 percent of all observations involved pairs in social contact with other pairs, while slightly over 10 percent were pair-male interactions and about 5 percent involved pairs interacting with unescorted females. The frequency of social interactions involving single males resulted from their constant travel in search of potential mates. After 18 June, females which had failed to breed successfully tended to aggregate and many of them disappeared from the study area as the final males were leaving.

Even in social contexts, Harlequins possessed a meager repertoire of displays. The Head-nod (Myres 1959) was the primary

Table 5. Relative frequency of observations by social grouping. Expressed as number (percentage) of total observations from 1974 and 1975 combined.

Week ending	No. observations	Single male	> 1 male	Single female	> 1 female	Single pair	> 1 pair	Pair and single male	Pair and single female
23 April	2	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
30 April	11	6 (55)	1 (9)	0 (0)	0 (0)	4 (36)	1 (9)	1 (9)	0 (0)
7 May	101	36 (36)	17 (17)	0 (0)	0 (0)	51 (50)	5 (5)	8 (8)	0 (0)
14 May	47	28 (60)	4 (9)	2 (4)	0 (0)	19 (40)	6 (13)	12 (26)	0 (0)
21 May	136	60 (44)	13 (10)	8 (6)	1 (1)	72 (53)	4 (3)	18 (13)	2 (1)
28 May	47	26 (55)	3 (6)	2 (4)	1 (2)	17 (36)	2 (4)	3 (6)	1 (2)
4 June	114	51 (45)	16 (14)	25 (22)	1 (1)	31 (27)	4 (4)	7 (6)	2 (2)
11 June	62	32 (52)	11 (18)	21 (34)	0 (0)	24 (39)	2 (3)	10 (16)	2 (3)
18 June	71	39 (55)	11 (15)	18 (25)	3 (4)	9 (13)	1 (1)	6 (8)	1 (1)
25 June	37	18 (49)	3 (8)	17 (46)	8 (22)	7 (19)	0 (0)	1 (3)	4 (11)
2 July	84	30 (36)	10 (12)	41 (49)	17 (20)	0 (0)	0 (0)	0 (0)	0 (0)

social display. Both Bengtson (1966) and Myres (1957, 1959) felt that the form of the Head-nod display of Harlequins was similar to Rotary-pumping in Barrow's Goldeneye (Bucephala islandica). However, the Head-nod of Harlequins occurred in a variety of social contexts; it was a component of aggressive displays as well as courtship and pair-maintaining behaviors. Head-nodding, accompanied by vocalization, was particularly noticeable when ducks were alarmed or when pairs interacted aggressively with single males or other pairs (Table 6).

Harlequins also vocalized to signal alarm. The usual alarm or warning call consisted of a series of high-pitched squeaking notes uttered by the male; the female's call was slightly lower. Inciting behavior was often displayed by paired females during aggressive encounters with bachelor males. Bengtson (1966) discussed the similarity of Inciting in Harlequins and Goldeneyes (Bucephala sp.). Several components comprised the Inciting display. The female began with an exaggerated Head-nod which ended with the neck extended horizontally just above the water and the bill pointing at the intruder. The posture appeared to be a low-level chasing behavior and often led directly to the female rushing the interloper. The paired male typically responded by assuming the Threat posture and frequently chased the other male. Threat posture involved holding the body high in the water and thrusting the head forward horizontally on the surface with the bill open. Often vocalization was a component of the Threat.

Table 6. Frequency of behaviors displayed by at least one member of pair during aggressive interactions with intruders.

	Total number recorded	Percentage of total aggressive interactions
Type of display directed toward intruder		
Head-nod	91	95
Vocal threat	33	34
Threat posture	44	46
Chase	45	47
Fight	6	6
Inciting by female	31	32
Type of display directed toward pair member		
Pair maintaining behavior	96	100
Chase	10	10

Total number aggressive interactions = 96.

Threatening regularly led directly to chasing and occasionally resulted in fighting. Chasing consisted of holding the body in a horizontal attitude slightly above the water's surface and shooting over the surface toward the intruder. Those short rushes were always followed by quick movement back to the mate while Chin-lifting, Head-nodding, and vocalizing to affirm the pair bond. Generally Harlequins only assumed the Threat posture when an intruder was within 2 m and behaving aggressively.

Appeasement behaviors consisted of fleeing, feeding by diving, or false-sleeping. Bachelor males which assumed the Sleeping posture while floating or standing near a pair were often tolerated very near the pair. Diving was frequent during aggressive interactions. If an intruding male dived, the paired male, and often the female also, typically dived. All ducks surfaced almost simultaneously. If the female dived first, the paired male generally dived only if the surplus male also dived. Otherwise the paired male remained at the surface dipping his face in the Looking-for-food posture to remain aware of the female's position. A paired male anticipated his mate's ascent and moved to the spot where she would surface. While the female was at the surface, her mate always interposed himself between her and the intruding male. Often during or after aggressive interactions, paired males showed aggression toward their own mates by threatening or chasing.

During interactions with unpaired males, both pair members displayed aggression (Table 7). Mated males were particularly aggressive toward unescorted females, while paired females were quite tolerant and often expressed some interest in a lone female. Although both pair members were intolerant of other pairs and participated in agonistic interactions, paired males were generally more aggressive than their mates toward intruding pairs.

Intruding females were threatened and often chased by mated males, but were never attacked (Table 8). Though females of pairs threatened solicitous surplus males, their mates chased unpaired males more often; both pair members occasionally fought with bachelor males. During interactions between pairs, males were more aggressive and fights, though rare, involved only the males.

The ornithological literature provides an inadequate account of copulatory behaviors of Harlequins, and most authors feel there is little ritualized behavior. Observations of 19 copulatory sequences (6 partial, 13 complete) recorded during this study are summarized in Appendix IV. Successful copulations occurred only in calm stretches of the creek or in pond areas. Copulation was never attempted unless the pair was alone, and the appearance of an unpaired male disrupted the behavioral sequence. Aggressive elements were always present during copulatory behavior; often the precopulatory sequence was preceded by 10 to 15 minutes of low

Table 7. Frequency of involvement by pair members in aggressive encounters with intruding Harlequins. Expressed as number (percentage) of total interactions between pair and that class of intruder.

Class of intruder	Pair member displaying aggression			Total number of interactions recorded
	Male only	Female only	Both	
Unpaired female	6 (55)	1 (9)	4 (36)	11
Unpaired male	16 (24)	11 (17)	39 (59)	66
Pair	12 (55)	2 (9)	8 (36)	22
Total no. (%) interactions	34 (34)	14 (14)	51 (52)	99

Table 8. Frequency of aggressive behaviors displayed by pair members toward intruders. Expressed as number (percentage of total) interactions in which behavior was displayed.

Intruder (recipient of aggression)	Aggressor (pair member)						Number of interactions
	Threat		Chase		Fight		
	Male	Female	Male	Female	Male	Female	
Unpaired female	5 (45)	0 (0)	7 (64)	1 (9)	0 (0)	0 (0)	11
Unpaired male	19 (29)	23 (35)	23 (35)	12 (18)	3 (5)	2 (3)	66
Pair	9 (41)	3 (14)	8 (36)	3 (14)	2 (9)	0 (0)	22
Total	33 (33)	26 (26)	38 (38)	16 (16)	5 (5)	2 (2)	99

intensity aggression including some chasing by the male. Generally, however, preliminary displays lasted less than 5 minutes. Copulation was always preceded by vigorous Head-nods by the male and typically by both sexes. Precopulatory Head-nods were quite elliptical in form with the long axis parallel to the water's surface. Occasionally between Head-nods, the male assumed a Sentinel posture with the neck extended vertically and the tail pointed and elevated. Interspersed between Head-nods were Bill-dipping and occasional Lateral-bill-shaking. Also, between Head-nods, the male sometimes passed in front of the female displaying his brilliant plumage patterns. During most of the precopulatory sequence the male was beside or slightly behind the female with his body low in the water and quite prone. As display intensified, the male interspersed Head-nods with short rushes (15 to 30 cm) toward the female, ending each rush by striking and nibbling at her auricular patch. As the male's bill struck the female's cheek, the impact often turned her body and the male had to maneuver (zig-zag) to regain his position near his mate. Frequently between nibbles the male moved forward beside the female and displayed exaggerated Head-nods which ended with the bill deflected 30° below horizontal and pointing away from his mate. Occasionally Bill-dipping interspersed the Head-nod-nibble sequence. While the male repeated the Head-nod-nibble sequence 8 to 20 times, the female, if not already prone, lowered her body and extended her head and neck horizontally on the water's surface. Almost always, as copulation approached, the male performed one or more Upwards-stretches (occasionally Upwards-stretch with Wing-flap). On the final approach, the male moved deliberately to the rear of the female and mounted, pressing her body down in the water. Copulation lasted 2 to 8 seconds. On several occasions, I observed males flicking the wings and tail downward in one or two powerful thrusts immediately before dismounting. Also before dismounting, the male grasped the nape of the female and, maintaining his grip as he slipped back into the water, thrusted powerfully with his feet, causing both ducks to rotate 0.5 to 2 times. Postcopulatory displays were less stereotyped but regularly involved aggression by the male. Usually the male chased his mate one or more times as she scooted ahead 5 m or more. On two occasions the male assumed the Sentinel posture and vocalized before chasing the female. Preening and bathing seldom occurred. Always within 5 minutes both pair members began diving and foraging.

Habitat. Table 9 provides a habitat inventory summary. Running water habitats comprised approximately 90 percent of the area used by Harlequins. The remaining 10 percent, composed of abandoned meanders and other backwaters, served as a sanctuary during high water and as brood-rearing habitat. Habitat features of ponds which occur on the study area are summarized in Table 10.

Table 9. Habitat inventory summary, indicating relative abundance of general habitat features (expressed as percentage of total habitat).

General habitat type	
Running water	90
Standing water	10
Stream type	
Meander	80
Canyons and rapids	20
Substrate type	
Cobbles and boulders	74
Bedrock	26
Bank type[a]	
Vertical-vertical	44
Vertical-horizontal	51
Horizontal-horizontal	5
Composition of bank	
Vegetation	29
Snags	5
Rip-rap	6
Bedrock	17
Cobbles	25
Boulders	18
Availability of loafing sites in stream	
0/10 m	51
1 to 3/10 m	30
> 3/10 m	19
Accessibility to humans[b]	
Adjacent	35
Near	20
Away, accessible	12
Away, inaccessible	33

[a] Categories include both left and right banks; i.e., vertical-vertical signifies that both banks were vertical.

[b] Explanation of categories of human accessibility appears on pages 25-26.

Table 10. Characteristics of pond habitats found on study area (see Fig. 1 for pond locations).

Characteristic	Pond number						
	1	2	3	4	5	6	7
Type	Abandoned stream channel	Abandoned stream channel	Abandoned stream channel	Abandoned stream channel	Beaver pond on small stream	Abandoned stream channel	Spring-fed
Source	Ground water & small streams	Ground water & small streams	Ground water	Ground water	Small stream	McDonald Cr. hyporheal flow	Ground water & sm. streams
Approximate area	3,000 to 5,000 m^2	> 5,000 m^2	> 5,000 m^2	3,000 to 5,000 m^2	< 1,000 m^2	> 5,000 m^2	< 1,000 m^2
Depth	1 to 3 m	Mostly < 1 m	1 to 3 m	1 to 3 m	Mostly < 1 m	Mostly < 1 m	Mostly < 1 m
Bank type	Vertical, undercut	Mostly vertical	Vertical, undercut	Vertical, undercut	Horizontal	Mostly horizontal, some vertical	Vertical, undercut
Persistence	90%	Approx. 50%	90%	90%	50 to 90%	Approx. 50%	50 to 90%
Human use	Heavy	Moderate	Moderate	Little or none	None	None	None
Vegetation	Coniferous, riparian at pond edge	Coniferous, riparian at pond edge	Coniferous, riparian at pond edge	Coniferous, riparian at pond edge	Riparian	Riparian	Riparian
Approximate age	> 10 years	< 10 years	> 10 years	> 10 years	> 10 years	< 10 years	> 10 years
Use by Harlequins							
Courtship & nesting	None	Heavy	Moderate	Heavy	Moderate	Heavy	Moderate
Brood-rearing	None	Moderate	Heavy	Heavy	Little	Little	Little

A qualitative description of benthic food resources appears in Table 11; Appendix II provides a list of all insect species identified. In my benthic collections, larvae of mayflies (Ephemeroptera) exceeded those of other taxa in total number and number of species represented. Running-water species (i.e., Ephemerella doddsi and Rhithrogena sp.) predominated. Stonefly (Plecoptera) and caddis fly (Trichoptera) larvae, though less abundant, appeared in all but three samples. Large Dipterans of the family Tipulidae were absent only from bedrock areas. Dipterans of the family Chironomidae comprised a large proportion of the standing crop only on bedrock substrate.

Most insects collected in May and June were 10 to 20 mm in length, though many stonefly larvae (genus Arcynopteryx) and Tipulidae measured greater than 20 mm. Later collections contained some mayflies (genus Ephemerella) and Tipulidae which exceeded 13 mm, but the majority of larvae were under 10 mm in length.

Emesis did not occur in any of the three males which received the emetic. Since no food samples were obtained, I was unable to compare food habits with food availability.

Chi-square tests revealed that during the first week of May, Harlequins used running water habitats significantly more than backwaters ($x^2 = 11.44$, $p < .01$, DF 1). From 8 May until 11 June, use of the two habitats was proportional to their occurrence on the study area. However, between 12 June and 2 July, ducks showed a strong

Table 11. Results of collections of benthic invertebrates.

Date	Order	Collection site[a]								% frequency each size category		
		1	2	3	4	5	6	7	8	Size		
										S	M	L
Oct., Nov. 1974	Ephemeroptera		4			4	4	3	0			
	Plecoptera		6			2	1	1	0			
	Hemiptera		0			0	0	0	1			
	Megaloptera		0			0	0	0	1			
	Trichoptera		4			4	0	5	0			
	Coleoptera		1			0	0	0	0			
	Diptera		1			0	0	0	2			
	Total		16			10	5	9	4	65	23	12
20 May 1975	Ephemeroptera			6	5	5	5	4				
	Plecoptera			3	4	2	2	2				
	Trichoptera			1	1	1	2	1				
	Diptera			1	1	1	1	1				
	Total			11	11	9	10	8		48	34	18
10 June 1975	Ephemeroptera			6	5	6	4	4				
	Plecoptera			2	2	3	3	2				
	Trichoptera			1	2	1	0	0				
	Coleoptera			1	0	0	0	0				
	Diptera			1	3	3	2	1				
	Total			11	12	13	9	7		31	49	20
19 July 1975	Ephemeroptera			7	6	4	6	7				
	Plecoptera			2	3	3	3	3				
	Trichoptera			2	3	2	2	2				
	Diptera			1	1	2	2	2				
	Total			12	13	11	13	14		65	27	8
20 Aug. 1975	Ephemeroptera	4	6	4	5	4	5	4				
	Plecoptera	1	1	2	2	1	3	2				
	Hemiptera	0	0	0	0	0	0	0	1			
	Megaloptera	0	0	0	0	0	0	0	1			
	Trichoptera	1	3	2	2	1	1	2	1			
	Coleoptera	0	0	0	0	0	0	0	1			
	Diptera	1	2	1	1	1	1	2	3			
	Total	7	12	9	10	7	10	10	8	71	25	4

[a] See Appendix I for map locating collection sites and describing habitats of collection sites.

preference for standing water habitats ($x^2 = 229.76$, $p < 0.01$, DF 1). Bottom types were chosen randomly except between 8 and 14 May, when cobble substrates received a disproportionate amount of use ($x^2 = 5.85$, $p < 0.025$, DF 1). Use of stream types (i.e., meanders vs. bedrock rapids) showed no significant deviation from expected values with the exception of a 1-week period between 26 June and 2 July when canyons were selected ($x^2 = 6.89$, $p < 0.01$, DF 1). Throughout the season there was a strong preference for areas of the creek which provided abundant loafing sites away from the streambanks. Stretches with three or more available loafing sites per 10 m were favored ($x^2 = 44.32$, $p < 0.01$, DF 1). Table 12 illustrates relationships between use of areas by Harlequins and the ease of human access to those sites.

Brood-rearing Period

Chronology. Each year most broods hatched between 30 June and 4 July (Fig. 6). In 1973 hatching dates were slightly earlier than in the two subsequent seasons. There was also more variability, with one brood hatching before the middle of June and a second, probably a replacement clutch, around 2 August.

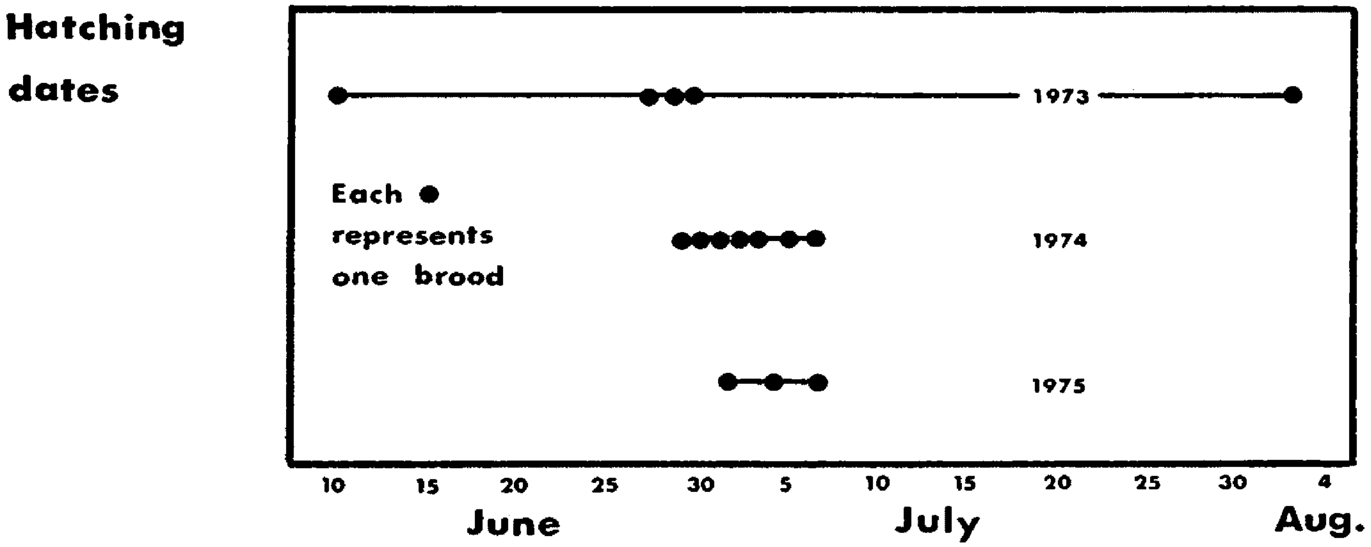
Within approximately 2 days following hatching, females led their broods to water. Though the newly hatched young were adept swimmers and were able to negotiate average stream currents, the

Table 12. A comparison of utilization by Harlequins with accessibility to humans during the 1974 and 1975 breeding seasons. "+" indicates preference of a particular category at the .95 level, "-" signifies avoidance, and "o" indicates neither preference nor avoidance (Neu et al. 1974).

Human accessibility	Percent of study area	Dates of interval sampled		
		5/1-5/21	5/22-6/11	6/12-7/2
Adjacent[a]	35	+	+	o
Near	20	o	o	o
Away, accessible	12	-	-	o
Away, inaccessible	33	-	-	o

[a] See pages 25-26 for definitions of categories used.

Fig. 6. Estimated hatching dates of broods observed during 1973, 1974, and 1975.



Hatching
dates
1973
Each ● represents one brood
1974
1975
10
15
20
25
30
5
10
15
20
25
30
4
June
July
Aug.

majority of activity during the early weeks was confined to the relative sanctuary of backwaters (Fig. 7). Juveniles dived infrequently until the third or fourth week. Until they became proficient divers, ducklings obtained most food by either skimming the surface along the pond edge and around fallen snags which were partially submerged or dipping their heads to probe the bottom in shallow areas. Since current was generally minimal, floating debris and adult insects were quite abundant on the surface of ponds. During feeding bouts lasting 30 to 45 minutes, juvenile ducks fed vigorously while females remained within a few meters, constantly alert for predators. Females accompanying broods fed rarely until the young were several weeks old. Though overhanging vegetation on the vertical banks provided shelter during feeding and escape cover when broods were alarmed, between feeding bouts, females brooded their young on rocks, logs, or sandbars away from shoreline vegetation. Attempts to escape detection by concealment under banks generally occurred only when broods were very young; usually females led their broods to open water to escape danger. Females were never observed performing distraction displays.

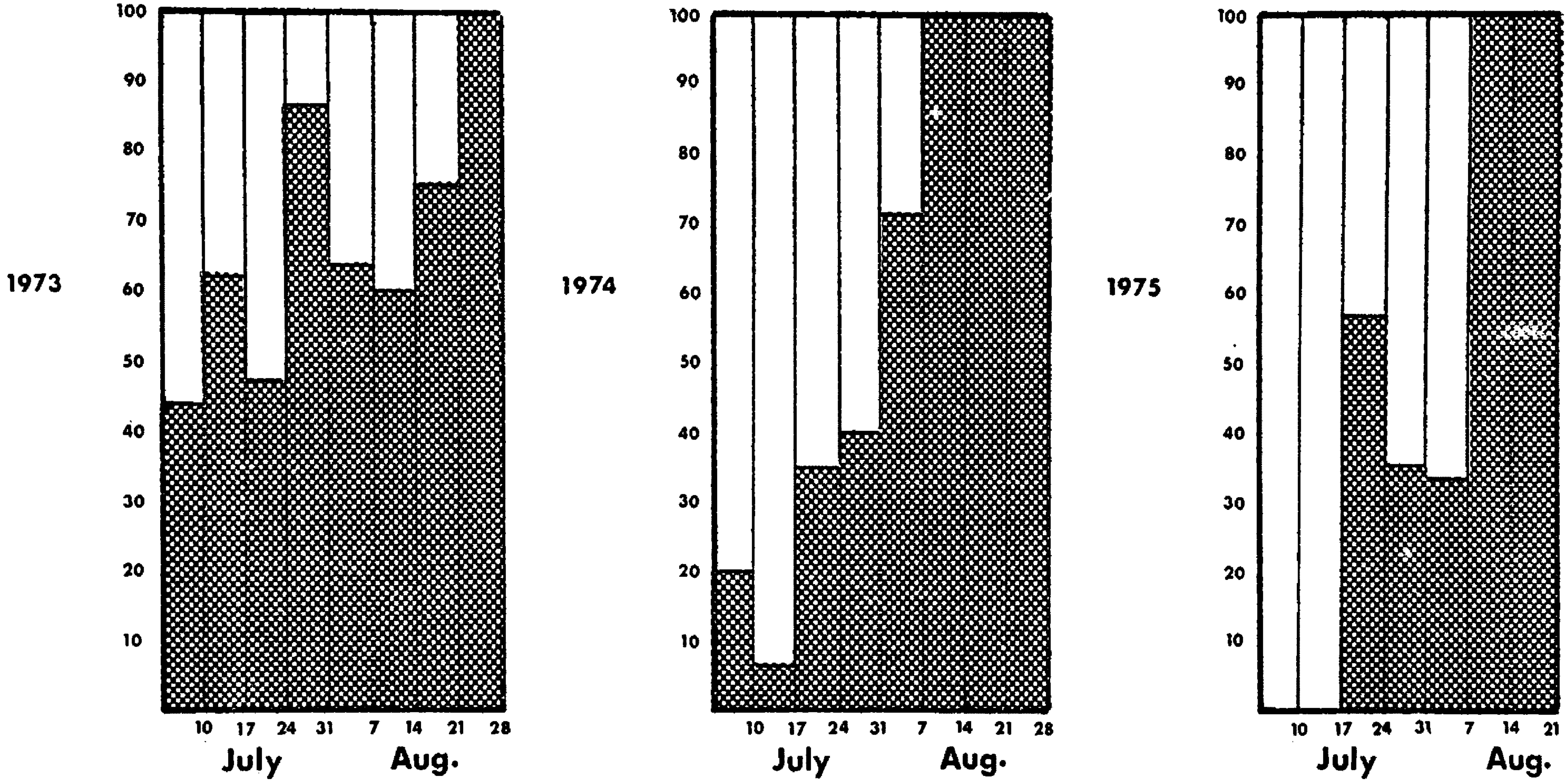
As juveniles acquired skill in both swimming and diving, an increasing proportion of time was spent in running water. During the study, 83 percent of brood activities observed during the second week occurred in backwaters and, of the remaining 17 percent, most creek

Fig. 7. Relative use of standing and running water habitats by broods from hatching until migration.

HABITAT USE BY BROODS

Expressed as percentage of weekly observations

Creek ▩ Backwaters ☐



use consisted of movement between pond habitats. By 4 weeks, broods used the creek 51 percent of the time and, by 6 weeks, visited pond areas only 8 percent of the time. After broods began using the creek, home ranges were continually expanded in a downstream direction (Fig. 8). Ultimately each brood abandoned its brood-rearing area, moving downstream as the group began the initial phase of their migration from the breeding grounds. After spending approximately 1 week in a region of bedrock and canyons near the lake, broods departed. In 1974 some broods moved downstream during the first 4 weeks, and several broods disappeared entirely from the study area within a few weeks after hatching.

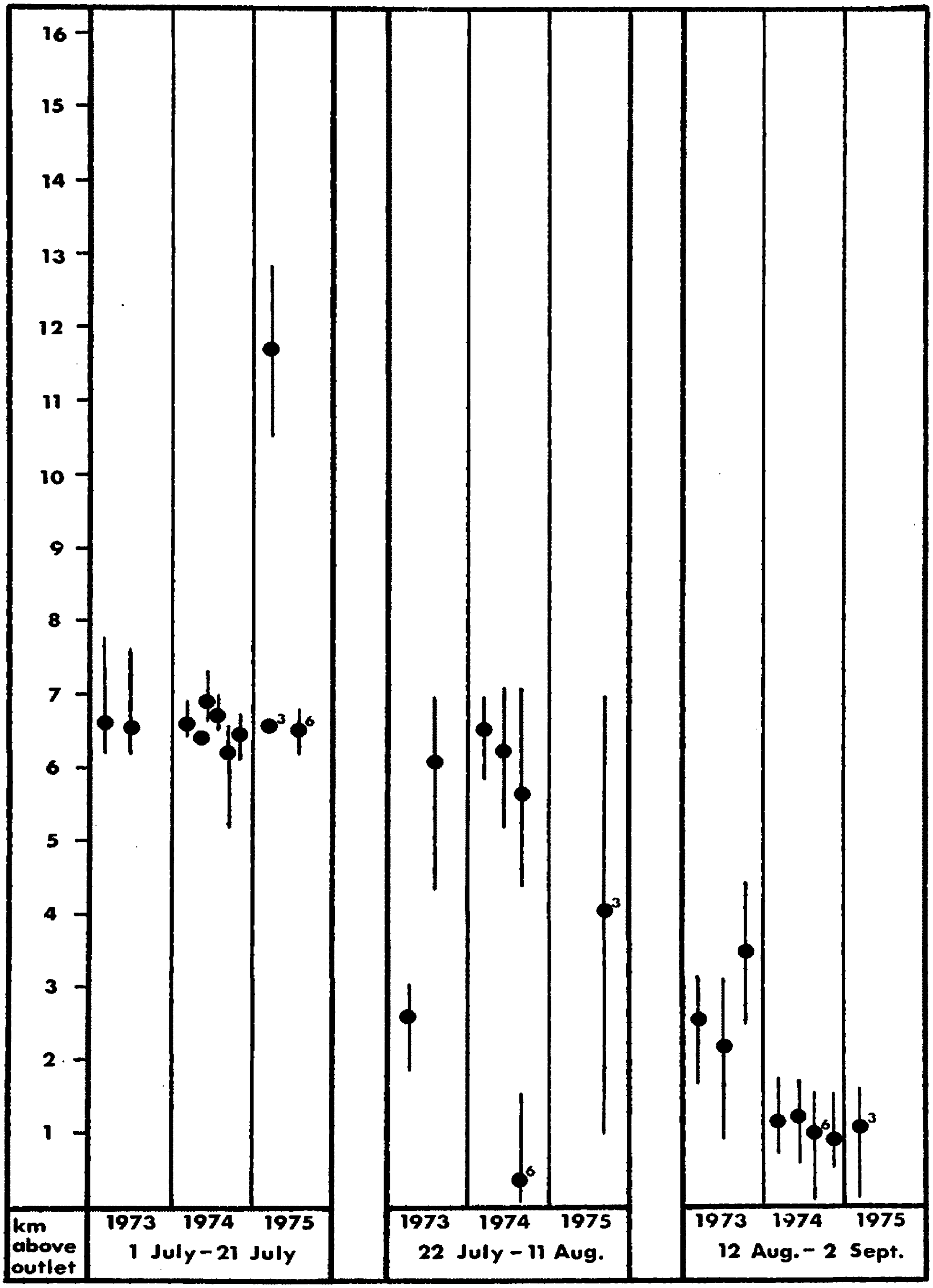
Behaviors. Females remained with their broods until departure from the breeding grounds. Broods were defended against conspecifics as well as against Goldeneyes and Mallards (*Anas platyrhynchos*). Harlequin females which had failed to breed successfully were not tolerated near broods, and when two broods of downy Harlequins encountered each other, females displayed aggression toward the other young as well as the female attending them. Several times when two broods mixed briefly, each female quickly departed with only her own young. Juveniles responded to the female's vocalizations and reinforced the social bond by vocalizing and performing Head-nods. There was no tendency to form creches, and females with

Fig. 8. Graphical representation of study area showing distribution of brood observations during 3-week intervals.

● = Central area of home range.

ɸ = Lines represent extremes of movement during interval.

$\bullet^1$ = Superscript represents band number of marked female accompanying brood.


16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
km above outlet
1973
1974
1975
1 July – 21 July
1973
1974
1975
22 July – 11 Aug.
1973
1974
1975
12 Aug. – 2 Sept.
3
6
3
6
3
6
3

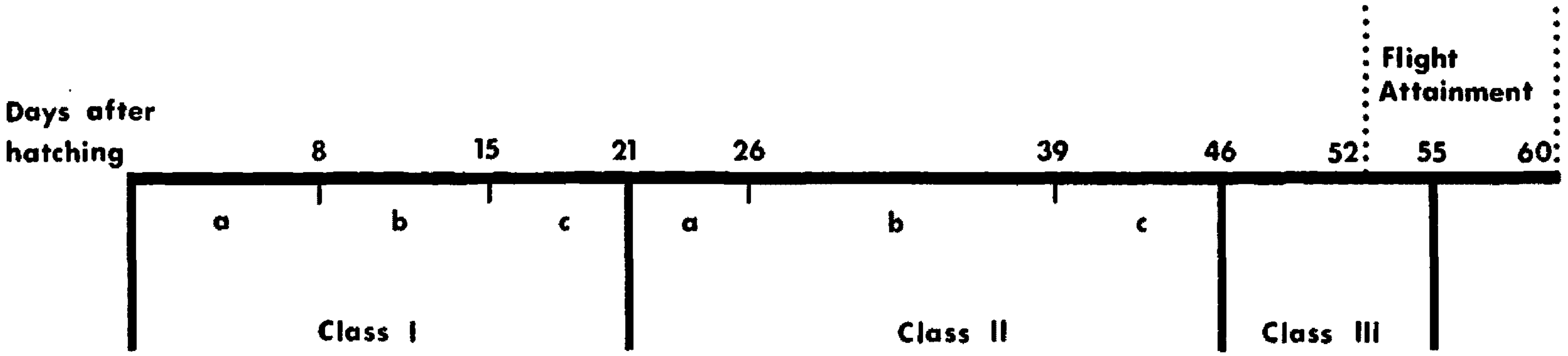
young did not accept juveniles from other broods.

Observations of the reactions of females, both with and without broods, toward an orphaned brood illustrated the nonsocial behavior of Harlequin females during the brood-rearing period. On 4 July when I first observed the brood which was later orphaned, the young were approximately 3 days old and were being attended by a female, presumably their mother. I relocated the female and her brood twice during the following 8 days. On 12 July I observed the brood in a backwater area for several hours during the late afternoon; the female escorted the juveniles, displaying typical maternal behavior and guarding the young as they fed. I left the area and returned 2 hours later to find only the seven young, swimming back and forth across the pond vocalizing. They were not feeding and were extremely wary. After more than 1 hour they swam from the pond and disappeared in the creek. I searched the perimeter of the pond but found no sign of the female and no evidence of a struggle; it appeared that the female had fallen prey to an aerial predator. The seven orphaned young returned to the pond the following day, and for several more days they frequented the same areas they had used when attended by their mother. Numerous times during their wanderings they encountered single females or females with young of approximately the same age; during each encounter the young approached the female, displaying Head-nods and vocalizing. Single females occasionally fed with them briefly, but more often avoided or ignored them. Females with broods were hostile toward the orphans and chased them if they approached closely. In every instance the orphaned juveniles were rejected and no female displayed maternal behavior toward them. During the week that they remained in the area, the orphans spent considerable time traveling and much less time feeding and loafing than broods accompanied by females. After a night of cold, hard rains, only one orphan remained in the area; the remainder either perished or abandoned the area.

Broodless females were never observed participating in the rearing of young Harlequins. Evidence of brood mixing was observed only twice, both times during 1974 in an area where six broods were concentrated due to high water levels.

Although the literature states that Harlequin young develop very rapidly, I found that development rates approximated those of other sea-ducks (Fig. 9). Except for small tufts of down about the head and rump, ducklings were fully feathered (juvenal plumage) at approximately 46 days. However, even after full feathering, young required nearly 2 more weeks before they were capable of flying. Young of only two broods remained on the study area until flight attainment; the preflight period in those juveniles was approximately 55 to 56 days.

Fig. 9. Chronology of plumage development in juvenile Harlequin Ducks (after Gollop and Marshall 1954).



Plumage Classes

Habitat use. During their first weeks, from 3 July until 6 August, broods frequented ponds significantly more than they used running water habitats ($x^2 = 459.6$, $p < 0.01$, DF 1). When they did use the creek, the broods selected cobble substrates until 23 July. Thereafter they used bedrock areas at a rate which was significantly higher than the expected value. During the final 3 weeks, preference for bedrock substrates was significant at the 0.01 level. Comparison of the frequency of use of bottom types during the period between 17 and 30 July to the use from 31 July to 13 August showed a significant change from cobbles to bedrock ($x^2 = 15.57$, $p < 0.01$, DF 1). Meanders were also preferred during the first 3 weeks and canyons and rapids thereafter. Again, there was a significant change in habitat use between the last 2 weeks in July and the first half of August ($x^2 = 6.14$, $p < 0.025$, DF 1). When using stream habitats, broods displayed a preference for reaches offering more than three midstream loafing sites per 10 m ($x^2 = 12.72$, $p < 0.01$, DF 1). The Bonferroni z test (Table 13) showed that during the first 4 weeks broods avoided areas near human use areas and selected only areas which were both distant and inaccessible. During the final 4 weeks broods still inhabited areas which were away from humans, though most were accessible by trail.

Table 13. A comparison of utilization by Harlequins with accessibility to humans during the 1974 and 1975 brood-rearing seasons. "++" indicates preference of a particular category at the .99 level, "-" signifies avoidance at the .95 level, and "o" indicates neither preference nor avoidance (Neu et al. 1974).

Human accessibility	Percent of study area	Dates of interval sampled	
		7/3-7/30	7/31-8/27
Adjacent[a]	35	-	o
Near	20	-	-
Away, accessible	12	-	++
Away, inaccessible	33	++	o

[a] See pages 25-26 for definitions of categories used.

Production

All ducks arriving on the study area were considered sexually mature and capable of breeding. Due to the difficulty of locating nests of Harlequins, no nests were found and the number of pairs actually breeding was unknown. In Iceland, Bengtson (1972) estimated a non-breeding frequency among females of 15-30 percent. He also reported an average hatching success of 87 percent for 89 known nests, with a mean of 5.3 eggs hatching in each successful nest. Using Bengtson's (1972) data, I calculated the minimum number of eggs which should have hatched on the study area in 1974 and 1975 (Table 14).

Table 14. Estimated number of eggs hatching on study area (calculated using data from Bengtson 1972).

Year	Total no. pairs	Minimum no. females breeding (0.7 x total pairs)	No. successful nests (0.87 x breeding pairs)	Total no. eggs hatched (5.3 x successful nests)
1974	11	8	7	37
1975	15	10	9	48

I obtained actual production estimates by combining numbers from brood censuses conducted during the first 2 weeks in July with any new broods subsequently located. Those estimates totaled 33 young in 1974 and 17 in 1975. Of the original number, 12 young

(36 percent) survived on the study area until migration in 1974 and 2 juveniles (12 percent) in 1975.

Table 15 indicates the mean number of ducklings per brood for each plumage class, considering only broods which I observed during that interval. Based on those data, the average number of young reared for each known successful nesting was nearly four.

Table 15. Mean brood size by plumage class based on all broods observed during plumage interval.

	1973	1974	1975	Mean
Class I				
no. young	16	27	11	
no. broods	3	6	2	
x brood size	5.33	4.5	5.5	4.9
Class II				
no. young	10	11	9	
no. broods	2	4	2	
x brood size	5	2.75	4.5	3.75
Class III				
no. young	17	12	2	
no. broods	4	3	1	
x brood size	4.25	4	2	3.88

The percentage of known young which survived from hatching until departure was substantially higher during 1973 than in the following 2 years (Fig. 10). In 1973, 83 percent of the young observed survived from their emergence on the study area until migration.

Forty percent successfully reached the nearly fledged stage in 1974 and only 18 percent in 1975. Each year mortality was greatest during the first 2 weeks, and after 3 weeks no additional young were lost. The average brood size of all known broods from shortly after hatching until nearly fledged, another way of comparing breeding success, revealed similar disparities among the three seasons (Fig. 11).

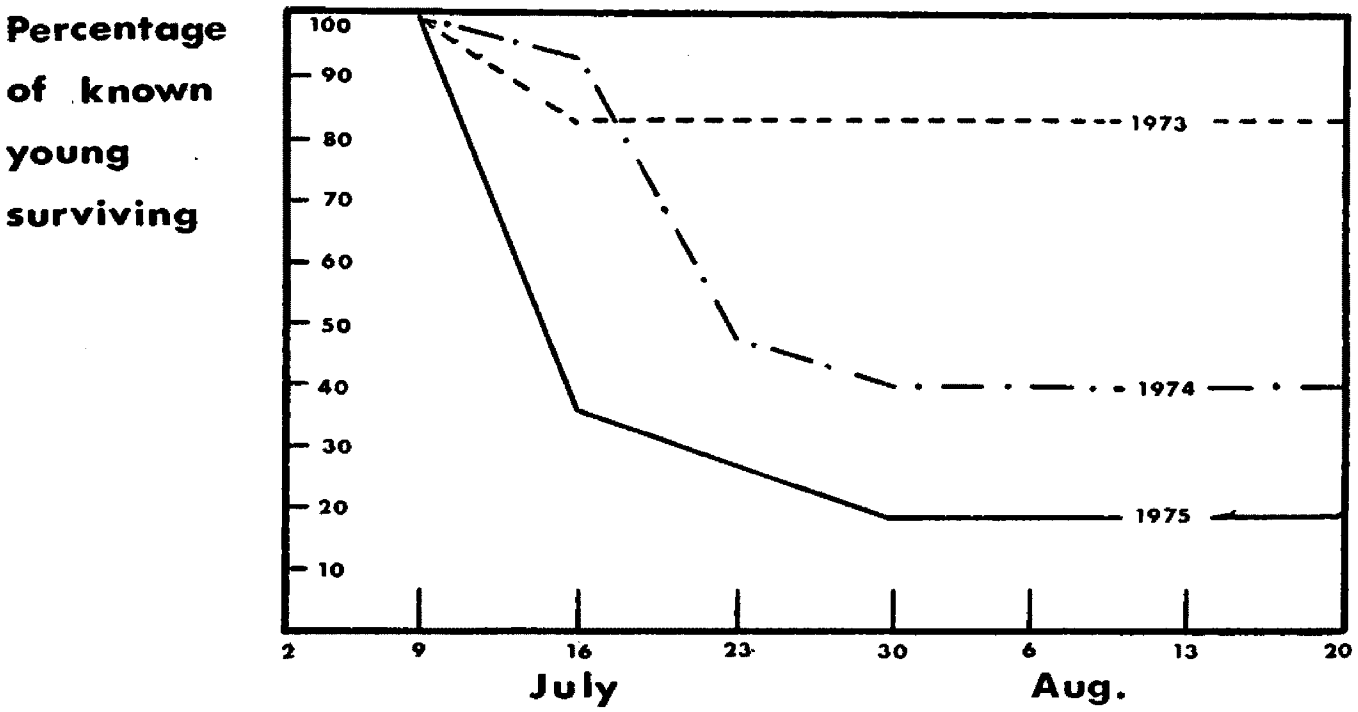
Factors Influencing Production

A number of environmental factors directly affected productivity and the subsequent survival of newly hatched young. Those climatic factors which influenced the timing, intensity, and duration of spring runoff were most important. Runoff depended ultimately on the accumulation of winter snowfall at middle and high elevations. Snowcourse surveys provided fairly reliable indicators of the potential runoff (Table 16).

Precipitation and temperature during winter and spring were the two principal variables controlling the accumulation and dissipation of snow. Except during December, winter and spring precipitation in 1973 was extremely low (Fig. 12). The snowpack was so deficient that the National Weather Service, which compiles runoff forecasts, predicted the lowest runoff in 29 years (Anon. 1973e). Winter precipitation during 1974 was far above average. On 1 April snow

Fig. 10. Comparison of survival of known broods during 1973, 1974, and 1975.

Fig. 11. Comparison of average brood sizes of known broods during 1973, 1974, and 1975.


Percentage of known young surviving
100
90
80
70
60
50
40
30
20
10
1973
1974
1975
2
9
16
23
30
6
13
20
July
Aug.

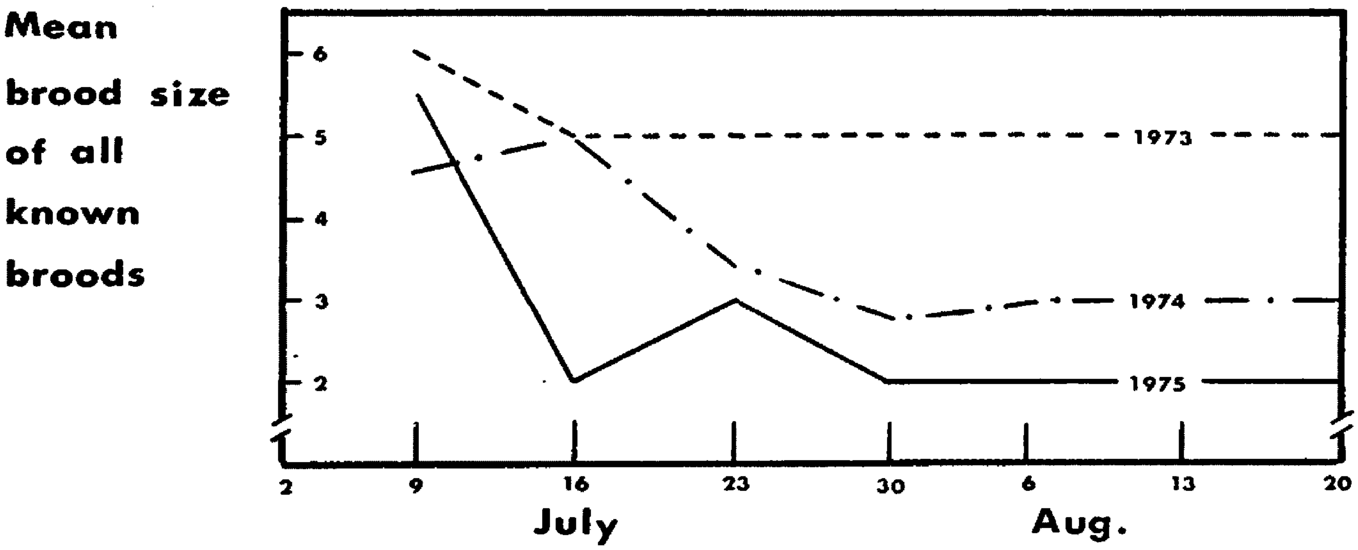

Mean brood size of all known broods
6
5
4
3
2
1973
1974
1975
2
9
16
23
30
6
13
20
July
Aug.

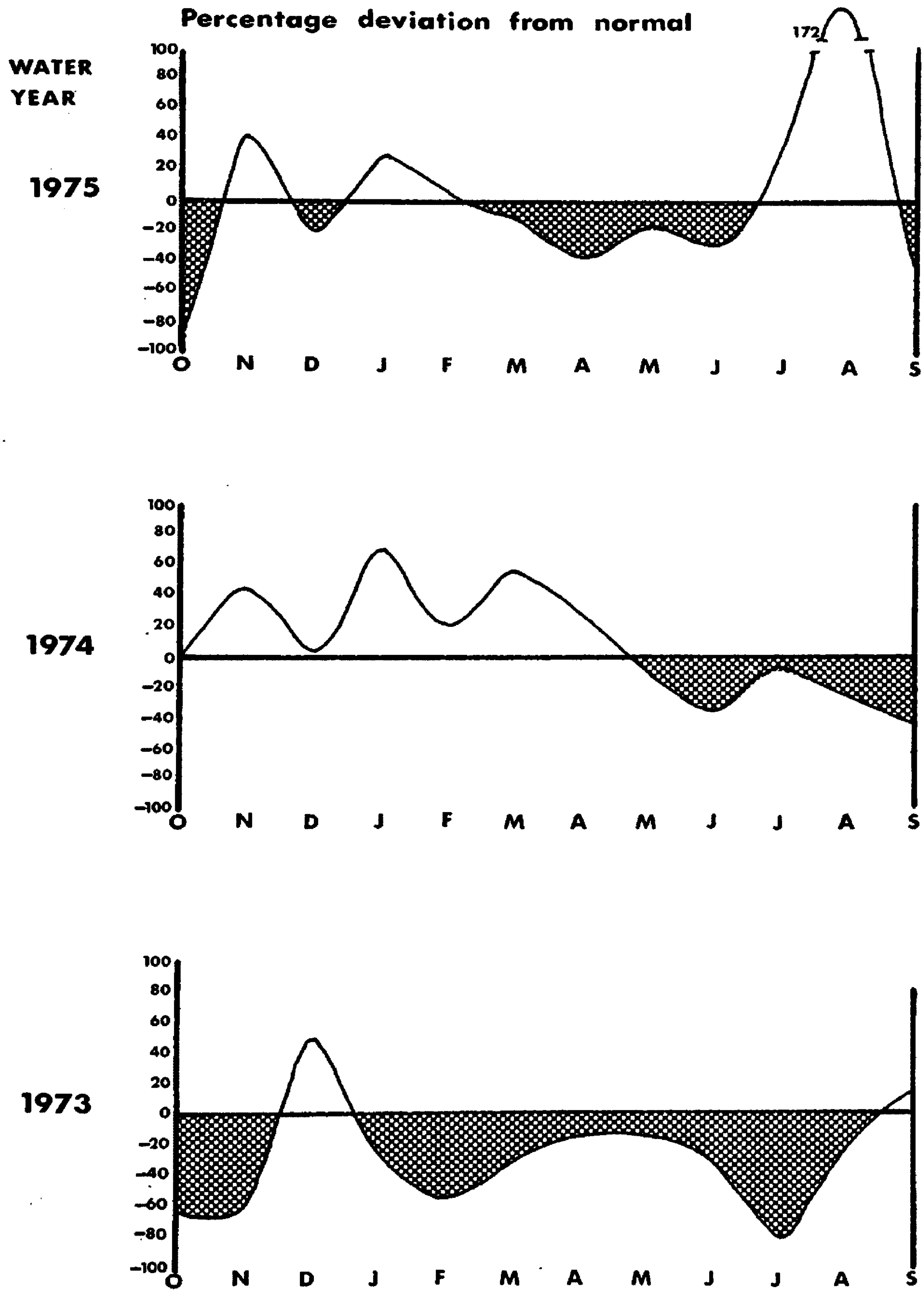
Table 16. Summary of snowcourse survey data, Mineral Creek snowcourse (from Anon. 1975f, Farnes and Shafer 1975).

Year	1 March			1 April			1 May		
	Snow depth (cm)	Water equiv. (cm)	% 15-year average	Snow depth (cm)	Water equiv. (cm)	% 15-year average	Snow depth (cm)	Water equiv. (cm)	% 15-year average
1973	88.9	29.72	64	88.9	30.23	60	38.1	13.72	38
1974	213.3	61.98	133	182.9	58.42	115	127.0	52.6	147
1975	149.9	48.3	103	182.9	54.6	108	114.1	44.45	124

Fig. 12. Comparison of monthly precipitation, West Glacier, MT, for 1973, 1974, and 1975. Expressed as percentage deviation from normal. (From Anon. 1973b, 1974c, 1975d.)

MONTHLY PRECIPITATION

Percentage deviation from normal



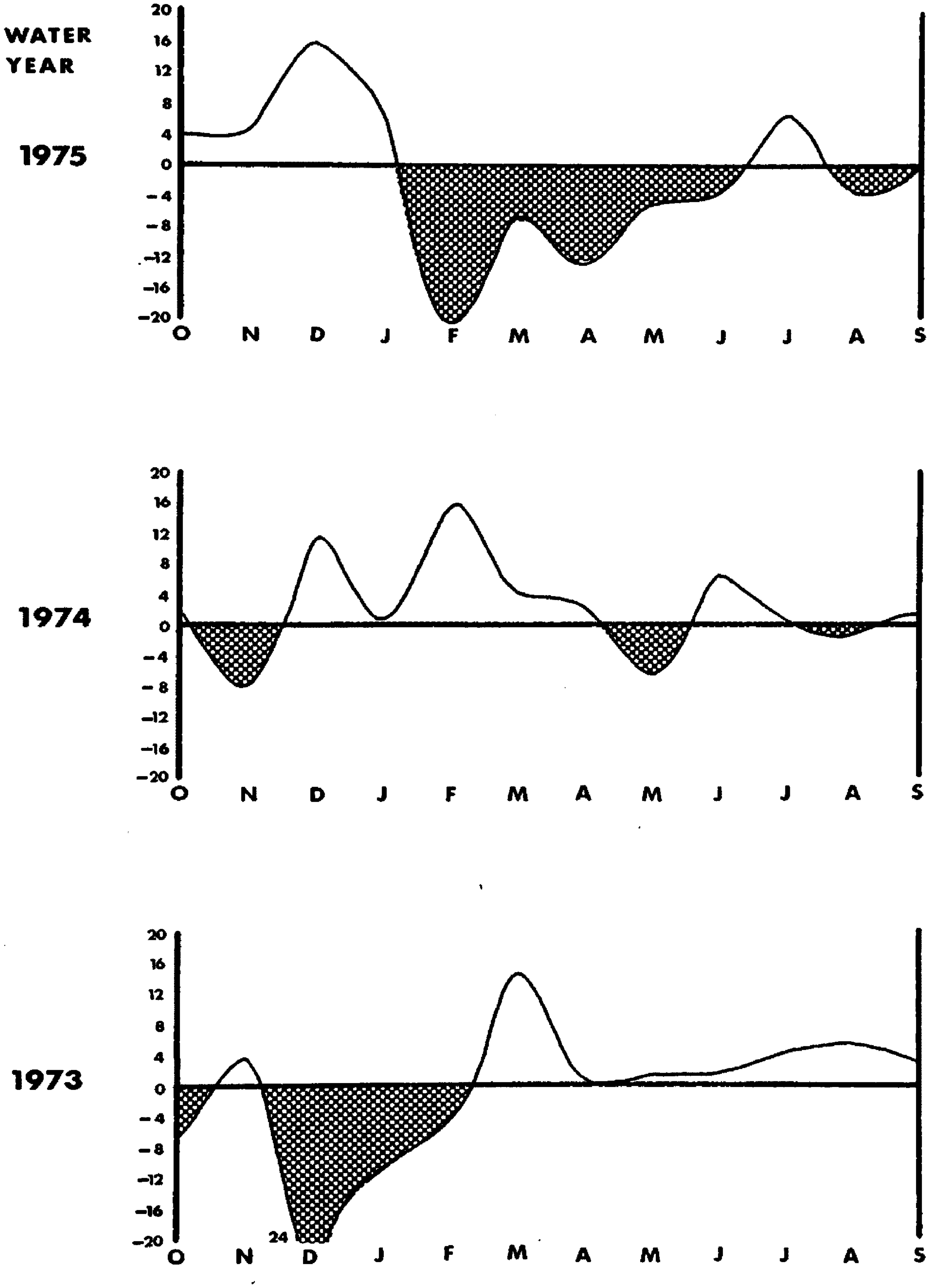
accumulation on all snowcourses in the Flathead River drainage was well above average, and high elevation snowcourses had a near-record water content (Anon. 1974f). On 1 May the National Weather Service predicted that discharge in the Columbia River basin would be the third highest since 1916 (Anon. 1974i). Winter precipitation in 1975, on the other hand, was near average and, based on snowcourse surveys alone, early predictions called for a normal runoff (Anon. 1975g).

Temperatures also varied widely among the 3 years (Fig. 13). Except for December, January, and February, mean monthly temperatures during the 1973 water year were above average. In 1974, temperatures were considerably above average throughout the winter and spring, and the cumulative runoff in the Middle Fork of the Flathead River between 1 October 1973 and 1 May 1974 was 142 percent of the 15-year average (Anon. 1974h). But, below average temperatures in May resulted in an increase in the water content of the mountain snowpack during the final 15 days of May (Anon. 1974g). Despite precipitation which was slightly below average from March through May, unusually low spring temperatures in 1975 (Table 17) substantially increased the water content of the snowpack through April (Farnes and Shafer 1975). The low temperatures retarded snowmelt, and through the end of April cumulative runoff in the Middle Fork of the Flathead River was only 40 to 50 percent of normal (Anon.

Fig. 13. Comparison of mean monthly temperatures, West Glacier, MT, for 1973, 1974, and 1975. Expressed as percentage deviation from normal. (From Anon. 1973b, 1974c, 1975d.)

MEAN MONTHLY TEMPERATURE

Percentage deviation from normal



1975i). Although total snowfall in 1975 was less than in 1974 and only slightly greater than in 1973, snow persisted much longer (Table 18). The majority of the winter's snow accumulation at middle and high elevations still remained in late May, and predictions indicated a delay in snowmelt of nearly a month (Anon. 1975h).

Table 17. Total number of heating degree days, West Glacier, MT. Expressed in °C, base temperature 36.11°C. (From Anon. 1973a, 1974b, 1975c.)

	Feb.	Mar.	Apr.	May	June	Total
1973	619	503	394	238	127	1,881
1974	534	565	371	307	92	1,869
1975	706	618	479	293	174	2,270

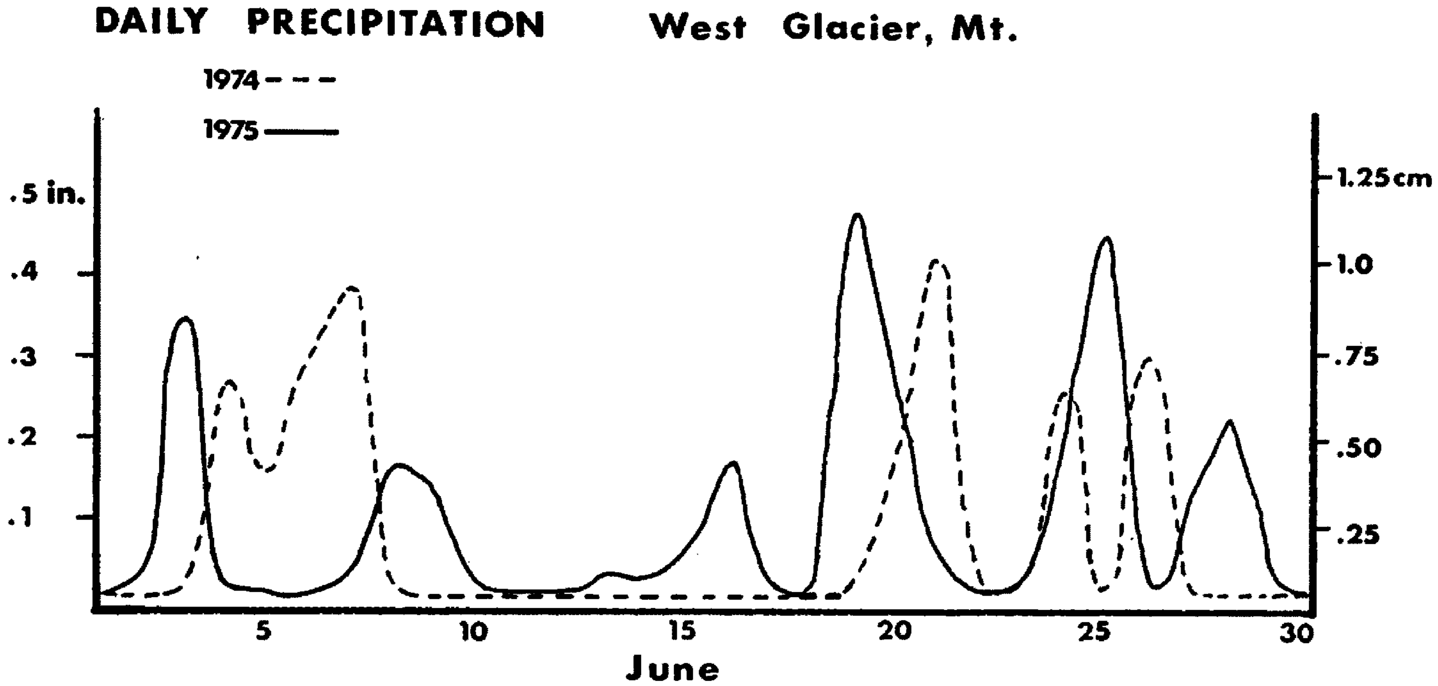
On 1 May 1975, the National Weather Service predicted a 50 percent probability of flooding in all streams of the Columbia River drainage, with a 90 percent chance in many small streams (Anon. 1975i). Forecasts also indicated a prolonged runoff and warned that any significant amounts of rain in June would cause a rapid rise in mountain streams (Anon. 1975h).

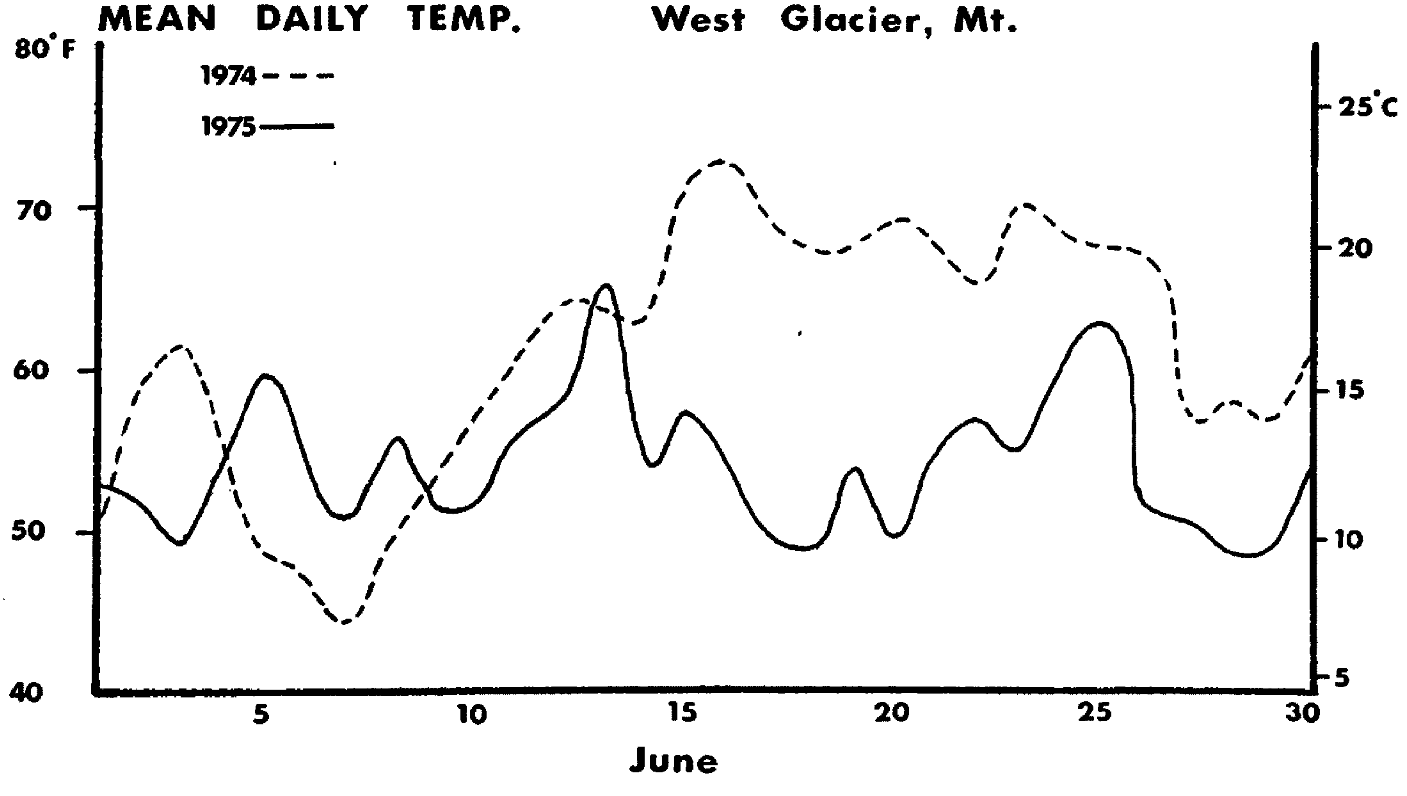
Daily precipitation and average daily temperatures during June directly influenced runoff by controlling the rate of snowmelt. Fig. 14 compares daily precipitation and mean daily temperatures in

Table 18. Total snowfall in cm, West Glacier, Montana. (From Anon. 1973a, 1974b, 1975c.)

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total precip. (cm)	No. days 2.54 cm or more on ground
1973	25.4	10.16	53.34	44.45	41.91	22.86	7.62	58.67	132
1974	0	129.54	83.82	88.9	86.36	27.94	2.54	83.77	156
1975	0	17.78	81.28	134.62	104.14	25.4	0	65.02	172

Fig. 14. Comparison of daily precipitation and mean daily temperature during June 1974 and 1975 at West Glacier, MT. (From Anon. 1974a, 1975b.)


DAILY PRECIPITATION West Glacier, Mt.
1974 - - -
1975 ——
.5 in.
.4
.3
.2
.1
1.25cm
1.0
.75
.50
.25
5
10
15
20
25
30
June


MEAN DAILY TEMP. West Glacier, Mt.
80°F
1974 - - -
1975 ——
70
60
50
40
25°C
20
15
10
5
5
10
15
20
25
30
June

West Glacier, Montana, during June of 1974 and 1975. In 1974 heavy precipitation occurred in early June followed by 2 weeks of unseasonably hot and dry weather. During this period daily maxima in West Glacier were over 30°C. The mean daily temperature during June was 2.11°C above the 15-year average. Several more heavy rains occurred in the last 10 days of June 1974. Temperatures gradually increased in June 1975 and, although total precipitation was not unusually high, several heavy rains occurred in the middle of the month; another 1.25 cm of precipitation occurred on 3 July (Anon. 1975c).

Runoff figures from the Middle Fork of the Flathead River provided a reasonably accurate index of runoff on McDonald Creek (Fig. 15). In 1973 peak runoff occurred on 18 May and water levels, though well below average, fluctuated until mid-June (Anon. 1973d). Stream levels remained below normal throughout the summer. In 1974 unseasonable temperatures resulted in a rapid increase in water levels until peak flow was reached on 18 June (Anon. 1974e). From 15 to 30 June water levels on lower McDonald Creek (Fig. 16) remained extremely high; streamflow declined little until July. During 1975 runoff increased through early June (Figs. 15, 16, 17), and following heavy rains, reached flood stage on 20 June. Peak discharge on the Middle Fork of the Flathead River in 1975 was nearly double that of the

Fig. 15. Streamflow measurement from gaging station, Middle Fork Flathead River near West Glacier, MT. (From Anon. 1973d, 1974e, 1976.)

DISCHARGE IN M³/SEC. Middle Fork Flathead River near W. Glacier, Mt.

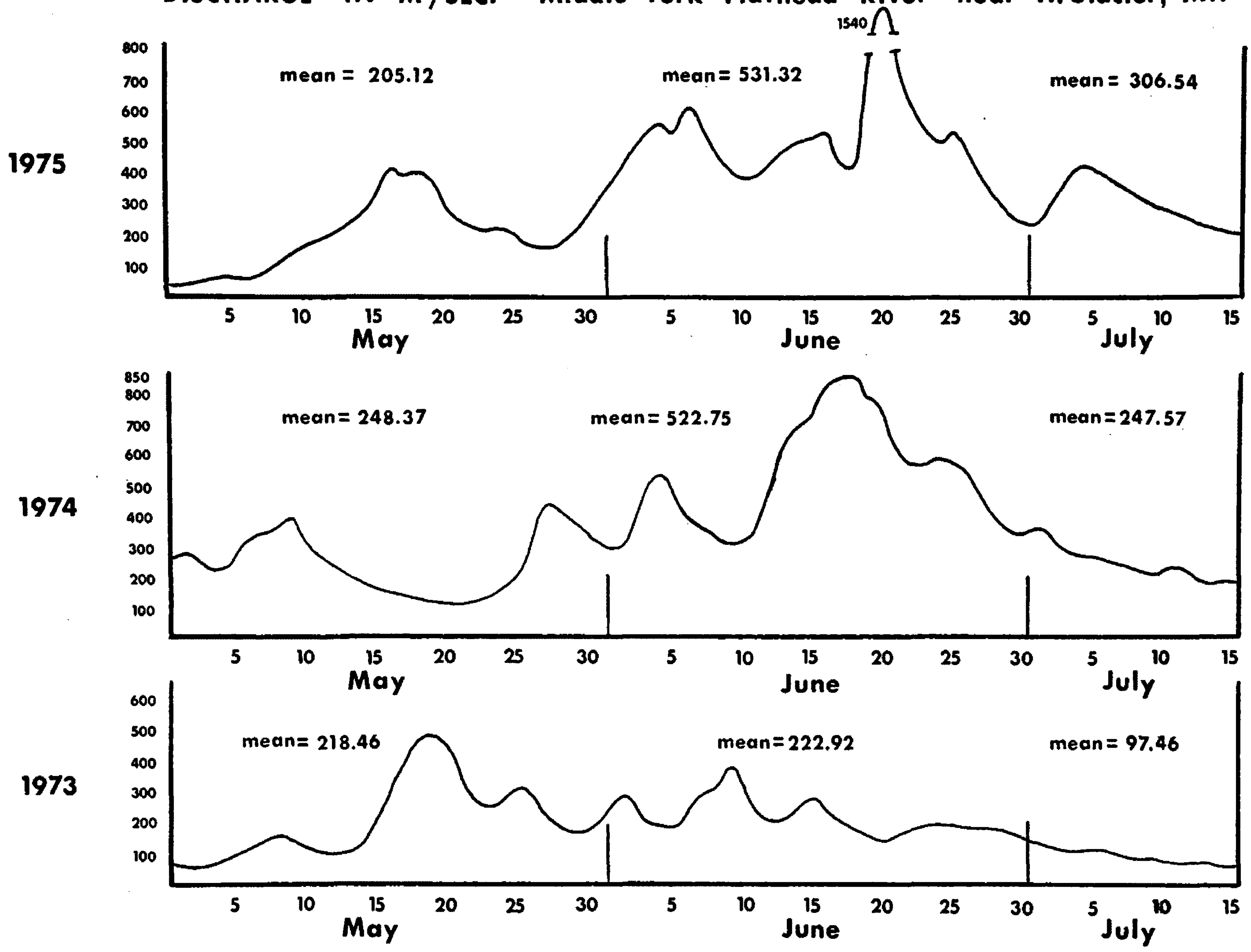


Fig. 16. Streamflow measurement from gage on Apgar Bridge, Lower McDonald Creek near West Glacier, MT. (From Anon. 1973c, 1974d, 1975e.)

GAGE HEIGHT IN CM - Lower McDonald Creek at Apgar Bridge

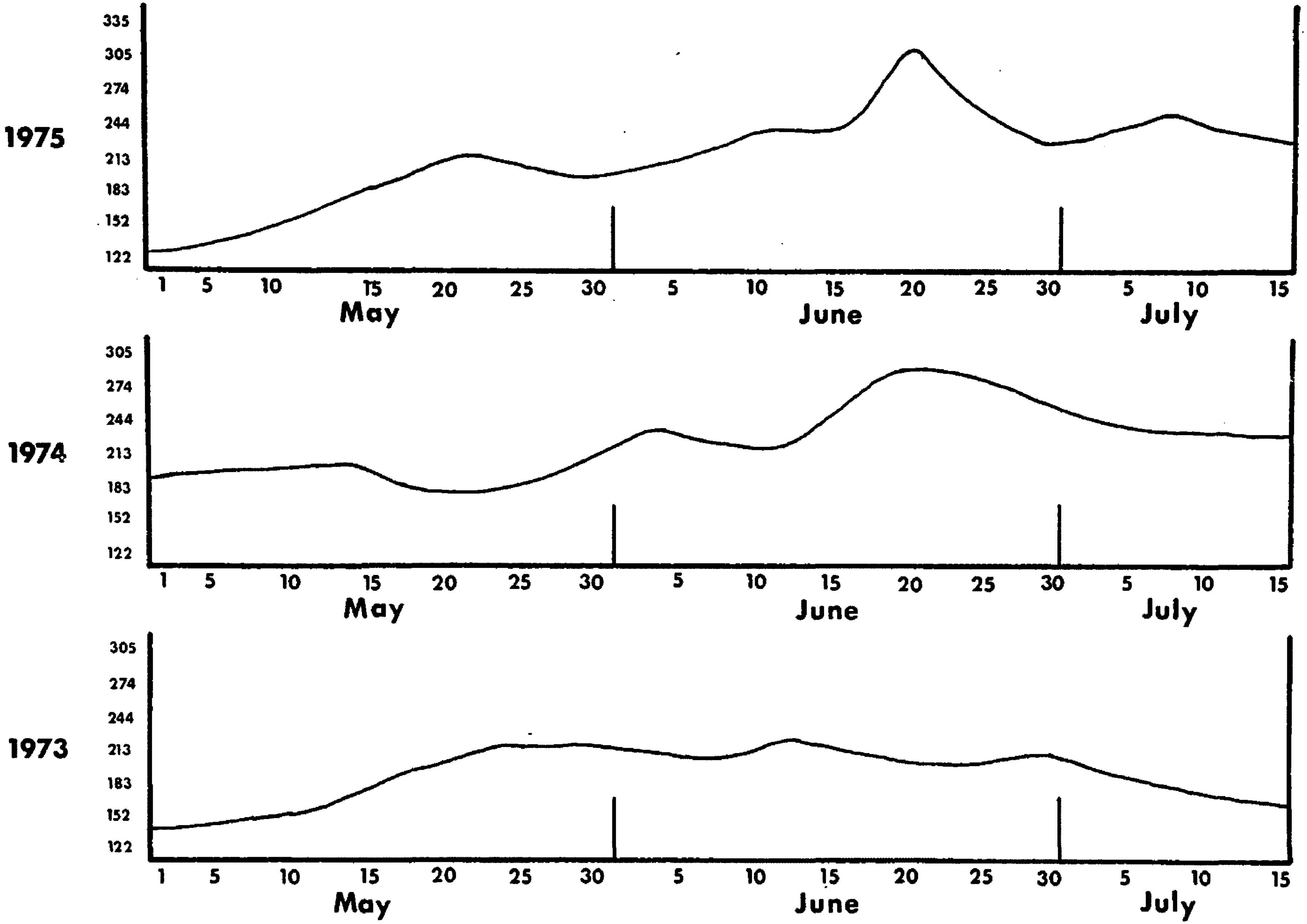
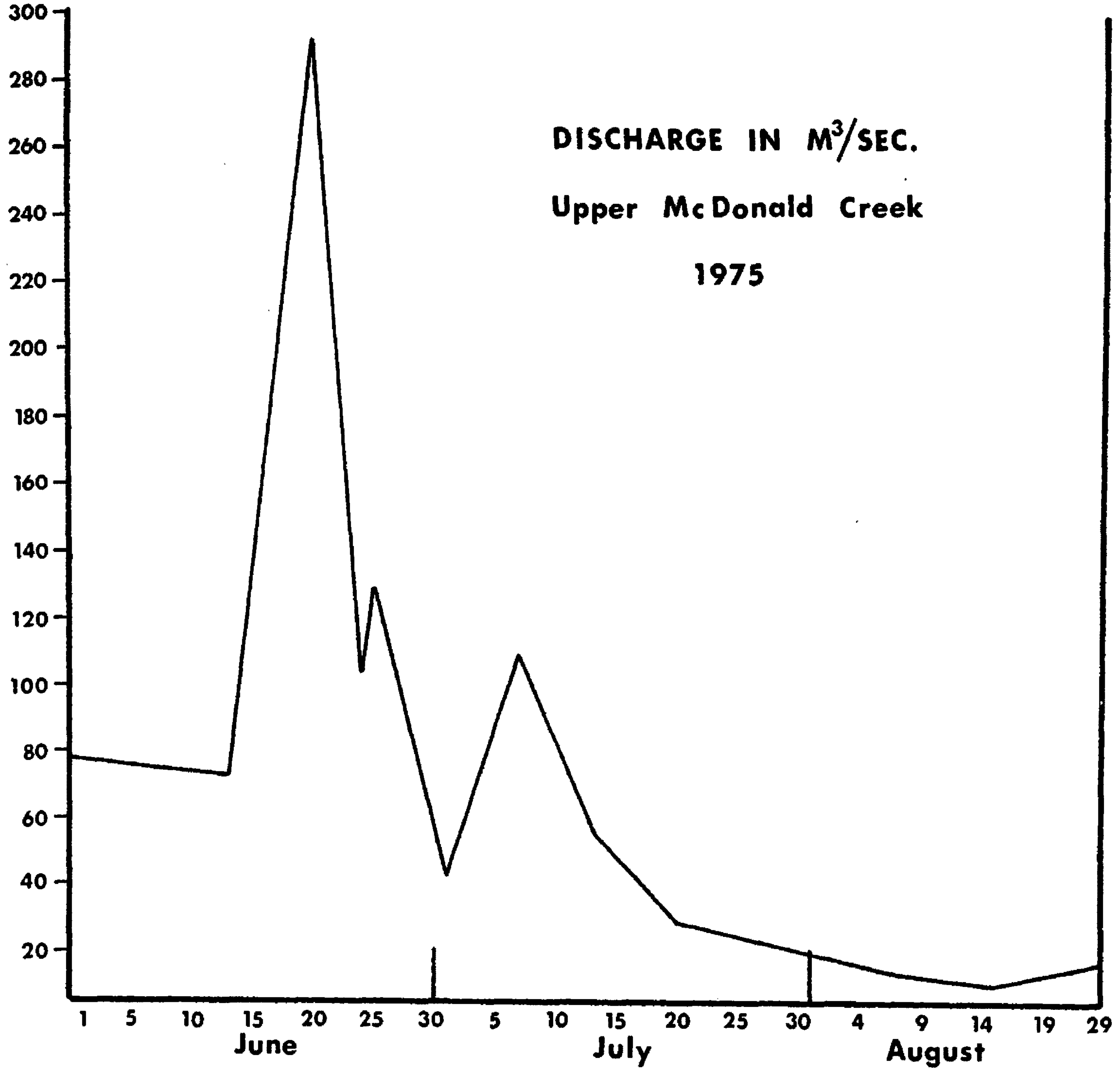


Fig. 17. Streamflow measurement from Upper McDonald Creek, 5 km above outlet into Lake McDonald.



DISCHARGE IN M³/SEC.
Upper McDonald Creek
1975

1974 flood (Anon. 1976). After the peak, stream levels began to subside quickly but more heavy rains caused discharge to remain high through mid-July.

CHAPTER V

DISCUSSION

Wintering and Premigration

During the winter months, Harlequin Ducks are much more sociable than during the breeding season. They occur in loose aggregations of 5 to 30 birds, but occasionally form dense flocks of 200 or more (Jewett et al. 1953). Information on wintering activities, chronology of pair formation, and spring migration in western North America is lacking. Bengtson (1966) reported that in Iceland some courtship behaviors began as early as December when he observed 12 pairs in a group of 200 ducks; paired birds avoided large courting parties and typically occurred alone or with other pairs. In April, Icelandic Harlequins abandoned wintering areas and began assembling near river outlets in fjords and bays (Gudmundsson 1971). Most pair formation is complete before spring migration commences (Bengtson 1972, Gudmundsson 1971, Palmer 1976, Salomonsen 1950). However, intense courtship activity continues even after Harlequins reach the breeding grounds. Erskine (1961), in his study of Buffleheads (_Bucephala_ _albeola_), disagreed with reports that pair formation in Buffleheads preceded migration. He felt that since copulations rarely occurred on the wintering grounds, and courtship continued during and after migration, most pair bonding also took place during or after spring migration. Data from my study indicated that all pair formation precedes arrival at the breeding grounds and probably occurs on wintering areas. I observed at least one case where the pair bond was renewed between the same male and female in 2 consecutive years; Bengtson recorded two similar instances. These data indicate that pairing probably takes place either on wintering grounds or very near the breeding grounds. The low probability of random meetings between two ducks in successive years during migration suggests that wintering areas may be traditional and specific to each breeding population.

Spring Migration

Spring migration of Harlequins, as described by Bengtson (1966) and Gudmundsson (1971) is unlike that of any other waterfowl species. Both felt that Harlequins, like salmon, traveled to their breeding areas by following the rivers, ascending the tributaries until reaching their respective breeding grounds. Migrating in this manner takes a considerable time as ducks are said to swim much of the way, making only relatively short flights (Bengtson 1966, Gudmundsson 1971). Palmer (1976) agreed that such a migration may be possible for populations which breed near the ocean, but speculated that birds breeding in inland mountain ranges in western North America must fly overland. No major migratory concentrations have been described either on lakes or rivers in western North America, and Harlequins seem to travel alone or in small groups. In Montana, those populations which breed west of the Continental Divide could reach their breeding grounds by following the tributaries of major river systems flowing into the Pacific. However, the few ducks which breed east of the Continental Divide in the Missouri River drainage must at least make short overland flights to reach creeks east of the mountains.

Gudmundsson (1971) stated that first-year Harlequins may accompany adults to the river outlets, but remain behind when breeding birds begin ascending the rivers; large flocks of yearlings are commonly seen at sea throughout the summer. Surplus adult males often accompany pairs to the breeding grounds and during my study a few males were always present on the creek nearly 2 weeks before any pairs arrived.

Migrational Homing

It is generally felt that migrational homing in waterfowl depends on the female's ability to locate her former breeding area (Hochbaum 1944, Lincoln 1934, Mendall 1958, Sowls 1955). Homing seems to be well developed in female Harlequins, and three females which returned to my study area in 3 consecutive years established seasonal home ranges in the same area each year. Bengtson (1972) also noted that females returned to the same stretch of creek each year.

Some homing tendency has been observed in male ducks (Sowls 1955), and Erskine (1961) felt that homing may be well developed in male Buffleheads. Four banded male Harlequins returned to my study area during 2 consecutive years. Three were paired on return and may have depended on their mates to lead them to the study area. One was unpaired during both years, indicating that he located the area independently.

Apparently male Harlequins which are unsuccessful in obtaining mates may home to the same area during successive years. The question remains whether bachelor males migrating for their first time to a breeding area return to their natal area, follow other paired ducks, or arrive by chance in a breeding area. The latter two seem less likely since early arrival of some males indicates that they need not depend on females, and chance wanderings would be extremely unprofitable as few inland mountain streams contain breeding populations. Bengtson (1972) found that males which had successfully obtained mates one year were never among the nonbreeding surplus the following year. Thus, it is likely that bachelor males include mostly younger birds or those which, because of behavioral anomalies, are unable to secure mates. Possibly included among the bachelor males are some which have just attained sexual maturity and are returning to their natal breeding grounds.

Early investigators doubted that female ducks breeding for the first time tended to home to their natal area. Lincoln (1934) felt that the homing instinct operated only after the female had nested, and the location of the first nest was primarily due to chance. Sowls (1955), however, found a substantial tendency for yearling females of several waterfowl species to breed for the first time at their natal breeding grounds. McCabe (1947) reported a similar tendency in Wood Ducks (*Aix sponsa*). The return in 1976 of two Harlequin females from a total of five juveniles of unknown sex which were banded in 1974 indicates a high degree of migratory homing in Harlequin females breeding for the first time.

Erskine (1961) found that Buffleheads display an ability to home to wintering as well as breeding areas. Circumstantial evidence indicates that Harlequins may winter in the same area each year, and it is possible that they may spend the winter in discrete groups consisting mainly of birds which comprise a breeding population.

Habitat Use

Bengtson (1966, 1972) and Gudmundsson (1971) stated that breeding Harlequin Ducks were strictly bound to running water habitats and occurred in lakes only near outlets where simuliid larvae abound. On McDonald Creek, the interspersion of standing and running water habitats was an essential feature. During spring arrival, the birds rarely entered backwaters, but throughout most of the courtship and nesting season, running and standing waters received use which was proportional to their occurrence on the area. My statistical analysis of habitat preference seems to imply that, during May, breeding Harlequins preferred areas accessible to humans. This seemingly anomalous implication seems erroneous and may be partially explained by two factors. First, during May numbers of humans are extremely low, and although Harlequins used habitats near human developments, virtually no people were present at that time. Second, the data may be biased since deep snow cover inhibited foot travel during early May, and I visited some of the more remote areas less frequently than easily accessible reaches.

Generally, preferred feeding and loafing areas were in fast waters. Canyons and gorges received a disproportionate amount of use during some periods, probably because the bedrock substrate offered numerous loafing sites and supported dense populations of small insect larvae. But shallow oxbows and other similar stretches of abandoned stream channel were also important habitat components. Several features, most of which were age-dependent, distinguished preferred ponds from those receiving little use. All calm areas served as alternate feeding sites for adults during high water; ponds also were frequented during the egg-laying period when females were probably searching for suitable nest sites and becoming familiar with potential brood-rearing areas. Use of secluded ponds enhanced duckling survival, but females with broods typically avoided ponds which were frequented by humans. Generally, old meanders were more stable than younger ponds and less affected by fluctuations in stream flow, except during extremely high water; those areas were selected for brood-rearing. Habitat washout occurred rarely in old ponds and emergence of adult insects was relatively dependable during the brood-rearing period. Siltation occurred more frequently in newly formed ponds and probably reduced both the diversity and abundance of insect fauna in those ponds. Older meanders which were fed primarily by spring seeps and small brooks were typically deeper and more persistent throughout the summer than newer ponds. Usable habitat in newer, shallower ponds deteriorated quickly after peak runoff when surface water and hyporheal flow subsided. Since older ponds usually carried little surface flow from McDonald Creek, water levels were quite constant, and suitable loafing sites typically did not become inundated during peak runoff.

Although benthic invertebrates were more numerous in stream habitats than in ponds, during spates many larvae in the stream were unavailable as they either sought refuge in the hyporheic zone or were washed downstream. During flooding, adult ducks moved into backwaters where food was still readily available. Emergence of adult insects in May and June combined with habitat washout to reduce both size and availability of food in the creek during early summer. Until the latter part of July, running waters contained few large food items. During late June, adults frequented stable bedrock areas; rooted plants in crevices harbored abundant larvae and Chironomidae were always numerous there. The small size of those larvae favored nonselective feeding and ducks typically sought irregularities in the substrate, scraping with their bills to dislodge food items. During that period the ducks' feces often had a greenish tint as they probably ingested some plant material while scraping food from rock surfaces.

When females with broods first ventured into the creek, they avoided rapids and canyons and frequented meander areas where current was slower. However, as diving and swimming skills developed, broods moved into rapid areas with bedrock substrates. The relative fertility of those reaches apparently enabled young ducklings to feed nonselectively, thereby obtaining adequate food even though they were less adept than adults at pursuing and capturing prey. The use of bedrock areas was especially pronounced in 1974 and 1975 when flooding and habitat washout in less stable cobble areas adversely affected insect populations there. When using stream habitats, females with young selected the same loafing sites which were used by breeding adults earlier in the season.

The avoidance of areas frequented by humans reflected the sensitivity of broods during their first weeks. Some pond habitats which otherwise seem to provide adequate brood-rearing habitat are rendered unsuitable by human presence. Even when juveniles approached fledging, broods still actively avoided contact with humans, and areas which were readily accessible to humans received little use.

Bedrock areas which were accessible to humans only by trail were used almost exclusively during the last weeks prior to fledging. However, since most of the areas with bedrock substrates were also only accessible by trail, I was unable to determine whether broods selected those areas in response to substrate and food availability or because they provided seclusion from humans. Kear (1972) felt that the security of Blue Ducks depended on the isolation of their habitat from man, and Bengtson (1972) reported that lower brood survival in some areas was probably attributable to human disturbance.

The Courtship and Nesting Season

Behaviors.

Harlequin Ducks, because of their unique preference for turbulent streams, have few competitors during the breeding season. However, the selective advantage of occupying a niche which is inhospitable to other waterfowl species requires a number of adaptations to enable efficient use of available resources. Specializations in feeding and locomotion are apparent.

Many mountain streams are comparatively infertile, and Bengtson (1966, 1972) felt that food availability was the most important factor limiting breeding populations of Harlequins. Clean, well-oxygenated waters are typically richer in benthic invertebrates than slower reaches (Hynes 1970), and Harlequins respond by selecting turbulent areas for feeding. Remarkable diving ability is requisite for efficient feeding in those areas. Dewar (1924) in Dow (1964) felt that diving efficiency could be measured by comparing the time a duck was submerged with the amount of time it spent resting at the surface between dives. Bengtson (1966) computed dive:pause ratios for several waterfowl species which fed on the River Laxá. Harlequins, with a dive:pause ratio of 4:1, were clearly superior to other species which occasionally occupied stream habitats; Barrow's Goldeneye, the waterfowl species which competes most closely with Harlequins on McDonald Creek, was much less efficient, with a dive:pause ratio of only 1.9:1.

The ability to use several different foraging methods further increases the Harlequins' potential for efficient exploitation of the available food resource. This flexibility enables Harlequins to respond not only to differences in stream habitats encountered, but also to seasonal fluctuations in insect abundance and changes in stream conditions.

Johnsgard (1966) regarded the White-capped Dipper (Cinclus leucocephalus) of South America as a food competitor of Torrent Ducks. On McDonald Creek, Harlequin Ducks and Dippers also frequented the same habitats; Dippers probably occur on most streams where Harlequins breed. Mitchell (1968) reported that Dippers occupying a western Montana stream fed primarily on the larvae of Trichoptera, Plecoptera, Ephemeroptera, and Diptera. On McDonald Creek Harlequins and Dippers probably compete for food to some extent, though selection of prey items of different sizes may reduce direct competition.

Some observers have speculated concerning the amount of energy expended by waterfowl diving in moving water. Typically those authors use the time submerged and the current speed at the surface to calculate the distance the duck would have to swim to maintain its position relative to the streambank. As Johnsgard (1966) stated, however, those computations do not accurately represent the effort expended during feeding. Friction between the substrate and the water cause current velocity to be almost inversely proportional to the log of the depth (Hynes 1970). Also, irregularities in the substrate further increase resistance to flow so that in most streams there is a boundary layer near the substrate where current velocity approaches zero. Diving Harlequins descend directly to the bottom before feeding or moving upstream, and although they are too large to occupy the boundary zone, much less energy is required than would be necessary to hold their position at the surface. Underwater propulsion is provided entirely by constant paddling of the feet, and Michael and Michael's (1922) and Bengtson's (1966) description of walking dipper-like on the bottom seems untenable.

Harlequins further reduce feeding effort by selecting feeding sites in stretches of creek which contain numerous emergent and partially submerged boulders. Current strength is reduced and insect abundance increased in pools and eddies on the lee side of such boulders; furthermore, the rocks provide preferred loafing sites. Midstream loafing sites seem to be selected because they offer unobscured vision of surrounding areas and preclude undetected approach by terrestrial predators.

Locomotory patterns employed by Harlequins also are closely attuned to the habitat they occupy. Downstream travel is extremely energy efficient since ducks depend almost entirely on the movement of the current to propel them. When traveling upstream, Harlequins reduce their effort by staying in slack areas near stream edges or using eddies and reverse currents to assist in moving upstream. The Torrent Duck has also evolved a dependence on stream currents for locomotion. Johnsgard (1966) and Moffett (1970) reported that, like Harlequin Ducks, Torrent Ducks rarely flew, but floated downstream and swam upstream, making use of eddies and pools and scooting over the surface where water was extremely turbulent.

Torrent Ducks also exhibit an escape reaction which is comparable to that of the Harlequin Duck (Johnsgard 1966). That evasive tactic is probably advantageous for several reasons. At the approach of a potential predator, ducks are able to flee quickly with a minimal expenditure of energy, and generally moving downstream a short distance is sufficient to remove the threat of predation. If the threat persists or a predator startles a Harlequin, the duck may either dive and escape under water or fly. At an early age young of both Torrent Ducks and Harlequin Ducks developed downstream movement as an escape reaction.

The behavior of Harlequins during winter provides evidence that this escape reaction and the reluctance to fly are related to use of running water; when at sea Harlequin Ducks flew readily (Bengtson 1966, Gudmundsson 1971). In that habitat, Harlequins cannot rely on currents to carry them safely out of reach of potential predators and must resort to flight to move quickly from one area to another. Harlequin Ducks tended to fly more immediately after arrival on the breeding grounds and before departure for wintering areas (Bengtson

1966, and information from my study). This behavior is probably advantageous when ducks first arrive because they can explore the breeding grounds and disperse quickly. Increased flight before and after migrations indicates that flight is probably used more during migratory movements than at the breeding grounds.

The pattern of flying near the water and following every irregularity in the stream's course may be an adaptation to the habitat since that pattern is typical of several birds occupying running water environments, including Dippers, Spotted Sandpipers (Actitis macularia), and Torrent Ducks (Moffett 1970).

At the breeding grounds, Harlequins are not gregarious and usually occur singly or in pairs. Johnsgard (1966) indicated that the solitary nature of Torrent Ducks may result from food limitations.

Erskine (1971) found that the behavior of Bufflehead pairs varied depending on the degree of concentration. Generally he observed conflicts only when the male was accompanying his mate, and on large lakes after the conflicts associated with initial spacing, there was little apparent aggression between breeding pairs. Bufflehead pairs, he felt, required some degree of isolation. When in a restricted area, this requirement resulted in aggressive behavior similar to true territorial defense.

Harlequin pairs on McDonald Creek were solitary throughout the breeding season; mutual intolerance resulted in fairly uniform spacing of breeding pairs along the study area. Mendall (1958) felt that the psychological requirement for isolation may significantly affect the breeding density of waterfowl. Harlequin pairs occupied a 1 to 2 km stretch of creek which they were reluctant to leave, though contiguous home ranges often overlapped considerably and more than one pair sometimes frequented preferred feeding sites simultaneously. Mutual avoidance generally provided the degree of isolation necessary, and only when in close contact did pairs interact aggressively. Bengtson (1966) originally described breeding pairs as being territorial. He later (1972) concluded that their site-tenacity had created a false impression of territoriality and that the male only maintained a mated-female defense. Though pairs on McDonald Creek were faithful to a section of creek, I observed no evidence of true territoriality. Late-arriving pairs were usually able to establish a home range and in 1976 the two late-arriving pairs containing known 2-year-old females superimposed their home ranges upon those of pairs which had been established for several weeks.

Though unpaired males tended to occur singly, they were the most sociable class. Loose associations between bachelor drakes continually formed and disintegrated as those ducks traveled along the study area.

In Iceland unusually dense populations of breeding Harlequins occur at the outlets of some lakes where food is extremely abundant.

Some members of those populations are highly sociable and form "clubs" containing 40 to 50 birds at favored feeding and loafing sites (Bengtson 1966). Club members, often single males and single females, loaf and feed in close proximity. I observed no aggregations of that type on McDonald Creek. The sparse distribution of Harlequins on McDonald Creek apparently resulted in a nonbreeding surplus which was lower than that reported in Iceland; among breeding pairs, solitary habits probably favor successful breeding. Only in late June when all males and most nonbreeding or failed-breeding females prepared to migrate did ducks on the study area tend to congregate. Then groups of five to six males and females often fed and traveled in close association. The "clubs" described by Bengtson (1966) probably are similar in nature to the small groups on McDonald Creek and the large size of clubs merely reflects the tremendous density and greater frequency of nonbreeding birds among Icelandic populations.

Harlequin displays have been discussed briefly by various biologists (Bengtson 1966, Johnsgard 1965, Myres 1959); all agree that Harlequins possess few ritualized behaviors.

The paucity of visual displays may be correlated with ancestral divergence from other forms (Bengtson 1966, Myres 1959), but it is likely that the nature of the breeding habitat is as important as systematic isolation. Elaborate posturing may be impossible in fast currents and it is noteworthy that the precopulatory sequence, which contains the greatest number of stereotyped visual displays, almost always occurs in ponds or other calm stretches. Head-nodding is the most prevalent display and it occurs in a variety of situations (Bengtson 1966, Myres 1959); it serves as a greeting, an expression of mild alarm, a low intensity threat, a pair-maintaining display, and a precopulatory display. Head-nodding develops at an early age and serves to reinforce social bonds among brood members.

Vocalization appears to be important and the Harlequin repertoire of calls may to some extent replace visual releasers (Bengtson 1966). Harlequin vocalizations are audible above the sound of the creek and members of the species seem to possess acute auditory senses. Harlequins are capable of detecting many sounds, including the approach of terrestrial mammals, even when the ducks are sitting on rocks in the midst of foaming rapids.

Inciting by female Harlequins was described by Bengtson (1966). I observed the same posturing described, but I did not feel that Inciting was as ritualized as Bengtson's description. I did not observe the head-turning he described, and the Inciting behavior seemed more like threat or intention movements of attack and indeed often led directly to attack. Females typically interspersed Inciting displays with short rushes toward the mate, during which both pair members displayed Chin-lifting and Head-nodding as pair maintaining behaviors.

Courtship activities continued after breeding birds arrived on McDonald Creek. Courtship behaviors between members of a pair probably functioned only to reinforce the pair bond, and I was able to observe pair-forming behaviors only when bachelor males were present and courting paired females. The wide-ranging travel of single males probably acted to increase the frequency of contact with potential mates. Usually attempts by surplus males to obtain mates by courting paired females were short and inconclusive. Fights occurred only when courting males were highly motivated. One marked male was unusually aggressive and resorted to fighting with one or both pair members nearly every time he interacted with a pair. Abnormal aggressive tendencies may have been the reason that particular male was unpaired in two consecutive breeding seasons. Erskine (1971) felt that in Buffleheads, mutual recognition by pair members reduced unprofitable courtship, but he concurred with Weller (1965) that courtship interactions with aggressive outside males may be important in testing pair bonds.

During aggressive interactions, ducks seemed aware of their positions relative to those of other ducks, even while diving. Bengtson (1966) never observed underwater attacks; several times, in backwaters, I observed paired males attacking intruding males from underwater. Paired males were often aggressive toward their mates during or after aggressive encounters with other ducks. Myres (1959) considered the high level of aggression between paired Harlequins a result of the absence of other visual displays.

Courtship flights were not observed and probably occur primarily at sea when pair formation is in early stages. Occasionally in late June when unescorted females became more numerous, aggressive courtship by several unpaired males caused a female to flee, and pursuit flights ensued.

Most traditional ideas concerning the systematics and phylogeny of the Anatidae are based primarily on morphological characteristics. However, several recent investigators (Delacour and Mayr 1945; Johnsgard 1960, 1962, 1964; Myres 1959) have used behavioral elements as taxonomic criteria among waterfowl. Some innate behavioral patterns, particularly those comprising the copulatory sequence, are highly conservative and therefore valid indicators of systematic affinities, especially at the generic and tribal levels (Delacour and Mayr 1945). The phylogenetic positions of several sea ducks are uncertain. Myres (1959) discussed behaviors of nine species of sea ducks in an attempt to clarify their systematic relationships. He had little success in placing the monotypic genus Histrionicus. Johnsgard (1960), in a study of classification and evolutionary relationships of sea ducks, observed behaviors in all genera except Histrionicus.

Few published records of copulatory behaviors of the Harlequin Duck exist. Bengtson (1966) provided a general description from "five more or less completed" and several other incomplete copulations. Two other published descriptions, each of single copulations (Michael and Michael 1922, Pearse 1945), and one unpublished account (R. Y. Edwards in Myres 1959) comprise the remaining literature.

I recorded a number of displays, previously unknown in Harlequins, which are similar to displays which have been used as ethological evidence of affinities among other Mergini. Many of the precopulatory and copulatory displays of Harlequins are comparable to those found in the Goldeneye complex. Though I lack sufficient data, both behavioral and morphological, the presence of displays common to Goldeneyes suggests the possibility that Harlequins are more closely related to the Goldeneye complex than previously believed.

The nesting period. Soon after pairs establish seasonal home ranges, the females begin searching for nest sites. Though I did not locate nests, on several occasions I observed females disappearing among shoreline vegetation while their mates remained in the water, alert and wary. Bengtson (1966) reported that males often accompanied their mates while the females searched the shoreline for over an hour. Since Harlequins begin breeding later than many other waterfowl species, the ability to establish a home range and locate a nest site quickly is important. Early pair formation probably insures that pairs are physiologically predisposed to begin breeding activities as soon as they arrive at the breeding grounds. Older females which know an area and have had more experience in locating suitable nest sites probably have an advantage. Those ducks which arrive later in May are quite likely less successful in breeding because preferred areas may already be occupied and those ducks have less time to select nest sites. Johnsgard (1973) stated that, in general, late-hatched waterfowl broods are less likely to survive than those hatching early. In 1976 the late arrival of two known-aged females which were breeding for the first time indicated that hormone levels in those ducks which have just become sexually mature may be retarded by several weeks. Sowls (1955) found that adult Pintail (*Anas acuta*) hens arrived on breeding marshes earlier than yearlings and thus had an advantage in competing for space.

The timing of nesting in 1974 and 1975 was closely correlated with the period of maximum runoff. Thus, females were on their nests when food was least available due to extreme turbidity, high water levels, and fast current. Soon after the onset of incubation, pair bonds disintegrated and males quickly began to depart from the study area. The departure of males also coincided with the period when food supplies were becoming more scarce and the energy required to obtain food was greatest. The timing of male departure probably tends to alleviate food shortages both for incubating females and for emerging broods (Bengtson 1972). However, since few males are present when high water subsides, females which lose nests to spring runoff rarely have an opportunity for a second nesting. Nest washout is probably an important factor affecting total production, particularly when spring melt is retarded.

Erskine (1971) reported that female Buffleheads tended to select nest sites which were outside the pair's territory. This may also be the case in Harlequin Ducks; during 1975 and 1976 at least one female raised her brood several kilometers upstream from the pair's home range, in an area which newly hatched ducklings could not have reached by swimming from the pair's home range. Possibly preferred nest sites are near ponds where water levels fluctuate less and newly hatched ducklings can quickly reach the relative safety of brood-rearing areas. Nesting away from the pair's home range would also eliminate the possibility that, in a year of food scarcity, the pair would deplete the food supply required by the broods for survival and growth.

The Brood-rearing Period

The chronology of breeding in most animals has evolved to insure the most efficient rearing of young (Lack 1954). Though several factors may be important, the hatching period is generally synchronized with a period of optimum food availability for newly hatched young. Bengtson and Ulfstrand (1971) showed that hatching in Icelandic Harlequins corresponded with an increase in the abundance of those insect larvae necessary for the growth and survival of young. Crouch (personal communication) felt that in the State of Washington, the availability of bottom organisms influenced the timing of breeding activities, and he indicated that hatching may be timed to correspond with increased day length, facilitating the securing of food by juveniles. Similarly, the timing of hatching on McDonald Creek coincided with a period of increased food availability. By the time juveniles became mature enough to use running water habitats, insect larvae were increasing both in size and abundance. Other subsidiary factors also seemed to influence the timing of breeding on McDonald Creek. Because nests are generally located close to water (Bengtson [1972] found only 7 of 98 nests more than 5 m from water) and renesting is infrequent, nest washout during spring freshets constitutes a potential limiting factor. Kear (1972) also found nest washout to be a natural hazard encountered by Blue Ducks. A selective advantage is conferred upon those females which delay nesting until runoff is well underway before selecting nest sites. Nest sites were usually selected during the latter half of May when spring melt had already produced fairly high water levels; in average years, although peak runoff does not occur until June, water levels do not increase markedly after the third week in May.

My previous discussion suggested the possible advantage of incubating during high water since during that period, food is scarce and difficult to obtain. Generally, by the time broods emerge, water levels are rapidly receding. Although the creek may remain high for several more weeks, overflow into the ponds virtually ceases by the first week in July.

During years of average runoff, pond habitats provided conditions favoring the survival of young. Ponds selected by females with broods provided adequate food supplies, seclusion from human intrusion, and relatively safe loafing sites away from the shoreline. Even though benthic productivity is less in ponds than streams, food is more available to young ducklings since they can obtain it without diving; current is slack and imagoes float on the surface. Numerous snags and exposed roots which protrude from the undercut banks also provide excellent foraging sites. Bengtson (1972) found that stomach samples from juvenile Harlequins contained disproportionate amounts of adult insects.

The amount of time new broods spent in backwaters was flexible and depended on the condition of the creek. In 1973 when runoff was abnormally low, even very young broods spent nearly

40 percent of their time using running water habitats. In 1974 and especially 1975, retarded runoff created hazardous water conditions and broods avoided the creek. During 1975 water levels were so extreme that, well into July creek overflow inundated even the most isolated ponds. Even in optimal brood-rearing habitats, newly hatched young encountered strong currents, loss of loafing sites, and reduction of food due to siltation and habitat washout.

Typically, after 3 to 4 weeks, broods abandoned ponds to spend increasing amounts of time in running water. The shift to the creek occurred as soon as ducklings developed enough proficiency to feed and travel efficiently in current. Use of stream habitats, especially bedrock areas may be necessitated by the need for richer food sources to meet the demands of growth and development. Safety from terrestrial predators is probably also enhanced in running water (Johnsgard 1966).

As broods begin frequenting the creek, movement is more extensive and home ranges are quickly expanded. But, despite increased mobility of broods, physical barriers continue to restrict movements. Immature ducklings easily maneuver downstream through turbulent areas, but are unable to move back upstream through reaches with large rapids and waterfalls. Therefore, except when an area is being abandoned entirely, females do not lead young into extremely turbulent stretches until they approach fledging.

Home range expansion alleviates congestion, reduces interbrood competition, and avoids over-exploitation of the ponds' limited food resources. Dispersal over a larger proportion of the study area probably also reduces the likelihood of attracting predators.

Since broods are unable to move upstream through the gorges, they continually expand the home range in a downstream direction. Eventually each brood abandons the brood-rearing area and moves downstream toward the mouth of the creek. Though it may take place over several weeks, downstream expansion of home range seems to constitute the beginning of fall migration. In most broods the timing of downstream movement was closely correlated with the developmental stage of the juveniles. Bengtson (1966) reported that some broods begin migratory movements soon after hatching, presumably taking several weeks to reach the ocean. It would seem that broods which abandon brood-rearing habitats early suffer higher mortality since creek life is more hazardous for young ducklings than life in secluded backwaters and the juveniles do not have an opportunity to become familiar with feeding areas, loafing sites, and escape routes.

In 1974 some broods on McDonald Creek either migrated early or suffered total mortality. Possibly the unusual concentration on some pond complexes created conditions unfavorable for survival of young. In crowded areas I observed unusually frequent interbrood strife as broods competed for restricted feeding and loafing sites.

The concentration may also have attracted predators; in one crowded pond a female with a brood of seven was apparently killed by an aerial predator.

In some sea ducks (Erskine 1971), females abandon their young prior to fledging and gather in molting flocks near the breeding grounds. Harlequin Ducks do not abandon young broods and female Harlequins were never observed molting while on the breeding grounds. Gudmundsson (1971) reported that female Harlequins do not begin to molt until they have led their broods to sea. The hostility of the brood-rearing environment maximizes the importance of maternal care for survival of young. During early weeks, juveniles depended entirely on the female to locate feeding and loafing sites, to select safe routes when traveling on the creek, to provide shelter at night and during inclement weather, and to guard the young and lead them away from potential predators. The female's importance in insuring survival of young was illustrated by the fate of the juveniles in the orphaned brood. Within hours after the loss of the female, group cohesion disintegrated; the ducks spent less time feeding and resting and more time traveling. Though they frequented the same areas as when accompanied by the female, the number of orphans remaining dropped steadily. Within 1 week all but one duckling had presumably perished. The duckling which remained after 1 week survived to fledging and returned as a paired female in 1976.

Females readily defended their broods against other waterfowl which approached; I observed female Harlequins with broods attacking female Goldeneyes and female Mallards as well as other female Harlequin Ducks. Brooding females led the young away from potential predators and if startled at close range, thrashed and flapped over the water while escorting the brood to a safer area. Predation of a duckling by a terrestrial predator, presumably a mink (Mustela vison), was observed on one occasion. The brood was feeding in a shallow inlet off the side of the main pond and several juveniles were out of sight. Suddenly with loud vocalization, the female rushed and flapped away from the shoreline, hovering above her young and herding them ahead of her. One duckling was absent from the group, and as soon as the female led the remainder to a safe position near the opposite bank, she returned to the site of the attack. Several times she approached the shore watching warily and vocalizing. Finally after 20 minutes, she returned to her brood and led them quickly from the pond. Investigation of the site revealed mink tracks at the water's edge, but no sign of a struggle or of the duckling. When threatened, very young broods conceal themselves by remaining motionless under overhanging banks, but very early they develop the same escape reactions as adults.

While young Harlequin Ducks are usually quite secure from predators as they feed and travel against banks which are vertical or undercut, the continual exposure of the female while guarding her brood increases her susceptibility to predation, particularly by aerial predators.

Most observers (Bengtson 1966, Gudmundsson 1971, Kistschinskii 1968, Palmer 1976) have indicated that brooding female Harlequins are highly sociable and that there is a strong tendency for two or more broods to merge. They report that nonbreeding females or those which have failed to breed successfully may also participate in the rearing of young, and several females commonly escort the creches. There was no tendency for broods to form creches on my study area. Group integrity was maintained by active avoidance and interbrood aggression. Females accompanying broods were not only intolerant of other female Harlequins, but also threatened juveniles which did not belong to them. With rare exceptions, solitary females avoided broods and, though several lone females were approached by the seven orphans, there was no evidence of maternal behavior. The rejection of the orphans by females escorting juveniles of approximately the same age indicated that females recognize and care for only their own young. Appearance, vocalization, and other behaviors may provide the basis for individual identification. The feeling that females are able to identify their own young was further supported on the few occasions when broods did merge temporarily. Within minutes in each case, the females moved away, leading only their own broods.

Only two instances of actual brood-mixing and exchange of young occurred. On 2 consecutive days in 1974 I observed a brood with one extra juvenile which was 5 to 7 days younger than the remainder. Another brood was missing one duckling. The young duckling had difficulty keeping up with the rest, especially in running water; unfortunately, both broods disappeared from the study area, so I was unable to document the survival of the younger juvenile. Brood mixing was extremely rare and occurred only in 1974 when several broods crowded into a restricted brood-rearing area. Erskine (1971) felt that in Buffleheads, high density populations exchanged young more frequently, but where brood density was low, no brood mixing occurred.

The avoidance of brood mixing and formation of creches appears adaptive where food is a limiting factor and the parental investment is high. The species has evolved an optimum brood size which enables maximum survival of each young by providing juveniles with food and loafing sites and reducing excessive intrabrood competition; the group size is also small enough to be unobtrusive and not attract predators. Acceptance of additional young by a female may jeopardize her ability to rear her own offspring successfully. Most maternal behaviors which I observed emphasized brood isolation and group fidelity, both of which minimize the probability of parental investment in the offspring of others.

Bengtson (1966) and Derscheid (1941) reported an extremely rapid rate of development of juvenile Harlequins. Faber (1822, cited by Bengtson 1966) stated that fledging requires approximately 40 days. Gudmundsson (1971) disputed those data, feeling that fledging occurred between 60 and 70 days. Except for a few tufts of down on the rump, a captive Harlequin described by Delacour (1959) was fully feathered at 8 weeks and 3 days. Pengelly and Kear (1970) reported that Blue Ducks were fully feathered at 8 weeks, but did not fly until 10 or 11 weeks. Kear (1972) felt that slow growth and the prolonged parent-offspring relationship evolved in relationship to a limited food supply. Since Bengtson (1972) reported that the food supply in July was incapable of supporting as many ducks as in June or August, it seems that a restricted food supply probably limits early development of young Harlequins. Lack (1968) stated that, although it is advantageous for young to develop quickly, growth may be restricted by the amount of food available. The rate of development which I observed corresponded more closely to rates reported in Buffleheads (Erskine 1971) and other diving ducks (Gollop and Marshall 1954). Juveniles became fully feathered at approximately 7 weeks but did not fly until 8 weeks; faster development seems improbable.

Ecological Adaptations and Factors Influencing Production

Harlequin Ducks have a very scattered breeding distribution and populations are nowhere really abundant. Only a limited number of mountain streams in western North America meet the species' requirements. The size and density of breeding populations seem to be closely linked with food abundance and availability of suitable habitat, both of which may be modified by climatic and other environmental factors. Bengtson (1972) and Bengtson and Ulfstrand (1971) provided evidence that populations of Harlequins breeding in Iceland were food-limited. Population density varied with the productivity of the stream, and concentrated populations occurred only near food-rich lake outlets. During years of food scarcity, Bengtson found a high incidence of nonbreeding females.

Several other general characters indicate that food-availability is probably the ultimate factor determining the breeding strategy of Harlequins. Neither the male nor the female molt at the breeding grounds; both delay the molt until they have returned to coastal waters where food is comparatively abundant. Early departure of males probably is a direct response to the food shortage in late June (Bengtson 1972), however, absence of males when broods emerge also reduces intraspecific competition for food. The clutch size is small while eggs are fairly large (Lack [1968] reported that each egg comprises 9.6 percent of the female's body weight). Various authors

(Johnsgard 1973; Lack 1967, 1968) have discussed the evolution of clutch size in waterfowl. Each species tends to evolve an optimum clutch size which, on the average, results in the maximum number of young surviving. Mean clutch size reflects the difficulty of breeding successfully (Lack 1968). In nidifugous birds, two major factors restrict clutch size: the food supply available to females while forming and laying eggs, and the ability of young to obtain sufficient food for successful growth and development (Lack 1968). The latter appears to be a primary factor influencing clutch size in Harlequins.

Clutch size and egg size are generally inversely proportional; ducks which produce large eggs lay smaller clutches. In spite of the reduced number of young produced, large eggs may be advantageous because young from large eggs are more likely to survive their early days than ducklings from smaller eggs. Newly hatched young from relatively large eggs have greater fat reserves which enable them to cope with adverse environmental conditions. Ducklings with large body reserves are more resistant to cold weather than those with small reserves (Koskimies and Lahti 1964). Even when severe weather or hazardous water conditions restrict feeding, thermoregulation can be maintained for several hours (Koskimies and Lahti 1964). Kear (in Lack 1968) felt that the large egg size found in the tribe Mergini related to the fact that newly hatched ducklings dive for food and that diving is more strenuous and hazardous than surface feeding. Although newly hatched Harlequins do not dive much during the first week, the time they spend in running water undoubtedly requires a substantial energy expenditure and large fat reserves probably enhance survival. Other diving ducks restricted to swift waters also lay small clutches with large eggs (Kear 1972, Lack 1968). Moffett (1970) felt that the large size of eggs in Torrent Ducks was partially explained by the ducklings' unusually large feet, an adaptation for survival in their vigorous environment. In spite of the advantage of large eggs, small clutches are adaptive only if predator pressure is low and each juvenile produced has a high probability of surviving (Kear 1972, Lack 1968).

The length of the incubation period in ducks varies with the size of the egg, and a long incubation period enables greater development prior to hatching. Harlequins have an incubation period which is longer than that of most comparably sized waterfowl. Lack (1968) showed that the incubation period also correlates broadly with the rate of development after hatching. Though fast growth minimizes susceptibility to predation and other environmental stresses, food supply limits the rate of growth.

Small clutch size and the resultant low reproduction rate are adaptive only in animals which are relatively long-lived and occupy fairly stable habitats (Miller and Botkin 1974). To succeed, those organisms must be able, in the long run, to produce more offspring than they could if they diverted more energy to the reproductive effort and less into their own survival (Williams 1966). The reproductive strategy of Harlequins corresponds quite closely to Wilson's (1975) description of breeding strategies in K-selected species. The reproductive rate is low, both juveniles and adults have a high probability of survival, the onset of breeding is deferred, and the species is highly specialized and has narrow habitat requirements. Southwood et al. (1974) also felt that K-strategists were favored where breeding sites were relatively free from predators. Species in which survival of juveniles is unpredictable and which suffer occasional catastrophic breeding seasons, also tend to be K-selected (Wilbur et al. 1974). Delayed sexual maturity is advantageous only in long-lived species where the nonbreeding period represents a small proportion of the reproductive life span. Even in long-lived species, deferred breeding must reduce mortality enough to offset the disadvantage of failing to reproduce during that period. Several factors may favor delayed maturity in birds.

Young birds are less efficient at finding food and avoiding predators, so both the female and her offspring are less likely to survive (Lack 1968). Also, first-breeding females may be less able to compete with adults for nest sites and preferred brood-rearing areas. Individuals breeding for the first time typically breed later than older birds (Lack 1968, Wilson 1975). Lack (1968) hypothesized that among birds, late breeding was caused by the inability of young females to find sufficient food to produce eggs; his thesis seems inapplicable in the case of most waterfowl. In Harlequins, females which are breeding for the first time seem to arrive 3 to 4 weeks late, and probably the entire breeding cycle is retarded. The frequency of breeding success in 2-year-old female Harlequins is unknown. Wilson (1975) discussed the possible advantage of spending a preparatory breeding season where birds engage in pair formation and other breeding activities, but actual breeding does not occur. Familiarity with feeding and nesting areas may improve the chance of breeding successfully in the following season. Nonbreeding is only advantageous, though, if there is little chance of breeding successfully during the year concerned. Possibly there is some flexibility in the breeding effort of 2-year-old Harlequin females. Their late arrival may even increase the chance of success in years when high runoff destroys the nests of older birds which began nesting earlier; nest washout would be less likely among late-arriving females since they could locate nests with respect to peak water levels. However, only unusual circumstances would favor late arrivals and most years they probably are at a disadvantage. The nonbreeding surplus reported by Bengtson (1972) and Bengtson and Ulfstrand (1971) probably contained many inexperienced adults. The frequency of nonbreeding on McDonald Creek is probably somewhat lower than the 15 to 30 percent observed in Iceland; possibly the high density of Icelandic populations creates greater competition for limited resources and requires that proportionately fewer birds breed. Breeding levels probably are adjusted to the amount of food available during midsummer when food is in shortest supply.

Estimates of the total number of Harlequins hatching on Upper McDonald Creek, though quite reliable, probably contained a conservative bias since high water in early July made some brood-rearing areas inaccessible. Highest mortality occurred during the first 2 weeks and some young probably succumbed before I was able to count them. Accurate estimates of the total number hatching, a reflection of the minimum brood size (Bengtson 1966), require daily brood censuses in late June and early July. The high mortality suffered during the first week reflects the hostility of the environment and emphasizes the premium on factors which enhance early survival under adverse conditions.

On McDonald Creek, few factors other than the need to establish a home range seem to limit the number of adults which breed once they have reached the breeding grounds; feeding, loafing, and nesting sites are relatively abundant and do not appear to limit breeding density. During some years, though, food availability may be limiting, and it is likely that on smaller mountain streams food availability always limits the number which can breed successfully.

Adverse environmental conditions in 1974 caused events which indicated that, at least during years when runoff is high and late, the lack of sufficient brood-rearing habitat to provide each brood with some seclusion as well as food and loafing sites may place constraints on production.

Foremost among the factors which are commonly felt to regulate bird populations are food supply, habitat availability, predation, and climatic or environmental factors.

Bengtson (1972) and Bengtson and Ulfstrand (1971) thoroughly discussed the role of food in limiting Harlequin production in Iceland. Although I lacked quantitative data on the standing crop of benthic invertebrates, I did obtain circumstantial evidence regarding the relationship between food availability and production. Bengtson (1972) found that the frequency of nonbreeding females increased as food supplies decreased. It seems unlikely that Harlequins on McDonald Creek during May and June could deplete their food supply, except possibly in backwaters during extended periods of high water when no food was available in the creek. Effects of food scarcity seemed most likely to operate primarily on broods and then only indirectly. During 1974 and especially 1975, extremely high water forced broods to concentrate in ponds for food and protection from the current. Both years broods remained on the ponds even after the runoff began to subside, as substrate washout probably caused a shortage of food in the creek. The stream received little use until the young developed enough proficiency to use the rapids and gorges with bedrock substrate. Those areas were quite stable and habitat washout and depletion of invertebrates during flooding was less likely.

I obtained no direct evidence of the effects of predation on Harlequins. Predation, though infrequent, may be a major mortality factor on the breeding grounds. Probably few adult Harlequins succumb to predation. Circumstantial evidence of predation of a female escorting a brood as well as at least one juvenile from another brood suggested that predation is most important during the brood-rearing season. Predation of a female may cause an entire brood to perish. Mink were the most abundant predators on the study area; though weasels (*Mustela* sp.) and martens (*Martes americana*) were occasionally observed near water, the mink is probably the only significant mammalian predator on McDonald Creek since mink frequent the same areas used by Harlequin broods for feeding and loafing. Bengtson (1966) reported that mink, an introduced mammal, and bad weather were the two major causes of prefledging mortality in Iceland. Some avian predators also frequent habitats used by Harlequins. Ravens (*Corvus corax*), Goshawks (*Accipiter gentilis*), Cooper's Hawk (*Accipiter cooperii*), and Great Horned Owls (*Bubo virginianus*) all lived on the study area. Ravens tended to feed mainly on carrion and were largely ignored by Harlequin Ducks. I did not observe attempts by hawks to prey on Harlequins, but it is likely that they occasionally take young or females which are guarding their young.

Vagaries of climate caused the greatest observed losses and appeared to be the most significant element limiting production. The most important environmental factors were the timing, intensity, and duration of spring runoff. Runoff is ultimately dependent on precipitation and temperature during winter, but spring climate may modify effects considerably. Direct effects of climate on production were minimal. Some young probably succumbed to chilling during cold, rainy periods. Erskine (1971) felt that young Buffleheads resorbed yolk material rapidly during cold, wet weather, and mortality of juveniles was highest during years when hatching coincided with adverse weather.

Indirect climatic effects, mainly in the form of fluctuating water levels, greatly influenced production. Runoff may affect the initial production of young as well as the survival of juveniles after hatching. Differential rates of initial production during the 3 years illustrate the effects of runoff on incubating females and emphasize the importance of the timing of nest site selection. There is a much greater tendency for nest washout during years when runoff is retarded. In 1974, though flooding occurred suddenly in June, early runoff was more than average and most of the snowpack had already melted. Nest losses due to flooding were not too severe and several broods hatched. In 1975, however, little spring runoff occurred and June rains caused sudden melting of the remaining snow. The result was a short period of near-record water levels. At peak flow, total discharge was nearly double that of the 1974 flood. Few nests escaped destruction and apparently only three broods hatched.

Mortality of juveniles after being led to water was also greatly influenced by the chronology of spring runoff. High, late runoff caused both density-dependent and density-independent mortality. Density-independent effects included losses of ducklings in heavy current, inability to feed in the turbulent water, and other mortality attributable to the effects of high water levels. In 1975 even the ponds were inundated and feeding and loafing sites were unavailable unless broods moved up into extremely small spring inlets which were 2 to 3 inches deep. Those areas were easily accessible to predators. I observed an unsuccessful attempt by one female to move her brood up the creek toward another pond. The young were unable to maneuver in the strong current, and within 13 days that female had lost all seven of her young. Density-dependent mortality occurred as broods crowded into small backwaters. Intraspecific competition and aggression caused early dispersal and abandonment of brood-rearing areas. Mortality probably increased as newly hatched ducklings were exposed to the full strength of the flooding creek.

The breeding chronology is closely attuned to spring runoff, and any natural or man-caused alteration of the flow regime has potentially devastating effects on Harlequin breeding success. If, as some scientists predict, we are entering a long-term trend toward colder climates, the Harlequin population on McDonald Creek will be affected adversely; cold, late springs retard runoff and may virtually eliminate Harlequin production. Forestry practices which increase surface runoff and expose streams to sunlight alter the stream environment through warming, erosion, and siltation. Kear and Burton (1971) reported that the introduction of trout into streams in New Zealand adversely affected the Blue Duck by increasing competition for limited food supplies. McDonald Creek has very few trout, but any increase in trout population would intensify competition for food and may be detrimental to Harlequin Ducks.

Draining of flood plain ponds to facilitate human development is a common practice on many streams. Those activities may eliminate habitat which Harlequins require for successful reproduction. Though ponds have not been drained in Glacier, at least two areas of prime brood rearing habitat are never used because road construction has isolated them from the creek. Even though they connect with the creek, Harlequins will not swim under the road to reach them. Any attempt to restrict the natural meandering of the stream eliminates the formation of new habitats which are essential to successful breeding.

Erskine (1971) stated that since Buffleheads do not breed until 2 years old, loss of production in 1 year may have little effect on populations. Deferred maturity in Harlequins would also dampen population fluctuations. However, several consecutive years of little production may completely eliminate a local population. Since breeding populations of Harlequins display fidelity to a specific area and females tend to home to their natal area, repopulation of an area would occur very slowly. Repopulation would probably occur by random wandering of birds which breed in nearby drainages; elimination of the population in an entire geographic region would drastically reduce the possibility of repopulation. The possibility that breeding populations also home to discrete wintering areas suggests that any factor which might destroy a wintering population or winter habitat may also eliminate an entire breeding population.

CHAPTER VI

MANAGEMENT RECOMMENDATIONS

Populations of Harlequin Ducks, particularly those which breed on mountain streams in the interior of North America, enjoy an extremely fragile existence. The environment is hostile, food supplies limit carrying capacity, and breeding success is very low. In response to their low reproductive rate, Harlequins have evolved a breeding strategy which depends on high survival among adults as well as the relatively few young which are produced. When several successive catastrophic breeding seasons occur, total mortality may exceed production and recruitment. Southwood et al. (1974) suggested that since K-selected species are so closely adapted to their niche, those species have a high potential for extinction. During the late 1800's Harlequins became extinct in Colorado (Parkes and Nelson 1976) and relatively few breeding populations remain in Wyoming and Montana. Those breeding populations which persist are extremely vulnerable to manipulation of habitat by man, and recent extinctions of local populations have been recorded (P. L. Wright personal communication). Without careful management it is likely that many more streams presently capable of supporting limited breeding populations will no longer meet the species' precise requirements.

For successful breeding, Harlequins require pristine habitat and relative seclusion from human interference. Inaccessible streams in remote mountain wildernesses probably best meet the species' breeding requirements, but those areas continue to dwindle as human population grows. Any effort to manage for successful Harlequin reproduction must focus not only on preserving those ecosystems which remain in relatively pristine conditions, but also on restoring disturbed stream ecosystems to a natural state, while insuring that human development will be compatible with the maintenance of healthy streams. Implementation of proposals which favor balanced stream ecosystems is consistent with administrative policies adopted in 1970 by the National Park Service for managing natural areas. Among the major goals was to insure that "the biotic associations within each park be maintained, or where necessary recreated, as nearly as possible in the condition that prevailed when the area was first visited by the white men" (Anon. 1970).

Following are some management suggestions, several of which apply specifically to McDonald Creek, and others which may be general enough to apply to other streams within the species' breeding range which have some potential to support populations of Harlequins.

Preservation of Pristine Habitats

Where stream ecosystems are intact, all development by humans should be prohibited and human intrusions structured to minimize the impact on aquatic habitats.

Restriction of Natural Changes in Stream Course

The natural occurrence of floods and concomitant changes in stream course should be anticipated and human development of floodplains eliminated. Except where flooding endangers human life or existing property, no attempt should be made to restrict the natural meandering of streams. Fallen trees and other debris which clog channels and alter stream course should not be removed.

Identification of Critical Aquatic Habitats

An inventory should be conducted to identify streams containing habitat features essential to successful breeding of Harlequins. Once identified, critical habitats should be protected and human access to sensitive areas strictly controlled. Construction of new bridges, roads, or trails which provide increased accessibility to crucial areas should be avoided. Any new roads or trails which are deemed necessary should be carefully placed so that they do not disrupt or isolate large segments of aquatic habitats. During any construction or maintenance projects, extreme caution should be exercised to prevent erosion, siltation, or destruction of vegetation near streams.

Restriction of Human Use

Every effort must be made to disperse human impact by altering patterns of human use. Concentrations of human use should be avoided except in presently developed areas where impact on Harlequins is minimal (i.e., Avalanche Picnic Ground and some of the scenic overlooks along Glacier Route 1). Sanitary facilities may have to be increased to avoid contamination of aquatic habitats with human sewage.

Preservation of Natural Biotic Associations

Because they compete directly for limited food supplies, abundant populations of trout and Harlequins probably rarely occur on the same streams. Management of streams for fishing should be accorded a lower priority than management to maintain natural biotic associations. Fishing regulations should reflect each stream's ability to withstand pressure from anglers, not only on fish populations but also on entire aquatic communities. If sport fishing is to be continued within the park, high quality fishing streams should be identified and fishing encouraged there. Streams with poor fishing should also be identified and managed to enhance other values. On some streams, preservation of the natural fauna may preclude fishing.

Education

Attempts should be made to educate park employees as well as tourists concerning the delicate balance of stream ecosystems. Interpretive efforts should be designed to increase awareness of non-game species and emphasize the importance of all elements of park ecosystems.

CHAPTER VII

SUMMARY

Behavior and ecology of a population of Harlequin Ducks breeding in the McDonald drainage of Glacier National Park, Montana, were investigated between 1973 and 1976.

Most males in the population spent less than 60 days on the breeding grounds while the females remained for approximately 110 to 120 days. While on the breeding grounds, ducks restricted nearly all activities to the running waters of the creek, though during the nesting and brood-rearing periods, they made considerable use of abandoned oxbows and ponds which adjoined the creek.

To facilitate the collection of data regarding population numbers, movements, migrational homing, reproductive success, and survival of young, 27 ducks were captured and marked using colored plastic leg bands in addition to aluminum U. S. Fish and Wildlife Service bands. Of 12 adults banded during 1974 and 1975, eight (67 percent) returned during at least one subsequent breeding season. Although no males were banded in 1974, four (67 percent) of the six banded during 1975 were present on the study area again in 1976. Of six adult females banded during 1974 and 1975, four

(67 percent) returned at least once. Only three adult females were banded during 1974; all three returned to the study area during the 1975 and 1976 breeding seasons. Five juveniles, sex undetermined, were banded in 1974. Two of those birds returned to the study area in 1976 as paired females.

Harlequins arrived on the study area in late April or early May. All of the females arriving on the breeding grounds had paired prior to their arrival. Each year, there was a surplus of males on the breeding grounds with males comprising approximately 64 percent of the breeding population. Courtship and copulation, although underway before the ducks reached McDonald Creek, continued into early June. Backcounting from the approximate hatching dates of 15 broods which were produced on McDonald Creek, provided an estimate of the timing of egg-laying and incubation. Egg-laying occurred between 18 May and 8 June. Incubation lasted throughout June, and coincided with the peak of spring runoff in 1974 and 1975. Pair dissolution began soon after the onset of incubation and most males departed the breeding grounds during the latter half of June.

Censuses indicated that peak numbers occurred near the middle of May. The greatest number of pairs counted was 11 in 1974 and 14 in 1975. Based on those data, minimum breeding density during the 2 years was one pair per 1.5 km of stream habitat in 1974 and one pair per 1.1 km in 1975. Pairs established linear home ranges along the stream, confining most activities to 1 to 2 km of creek habitat. Home ranges of pairs overlapped considerably and although paired ducks generally reacted aggressively to the presence of other pairs, there was no evidence of territoriality. Surplus males ranged extensively along the study area and frequently interacted with pairs.

Harlequins fed almost entirely in running water and typically selected loafing sites in midstream. A significant shift to the use of backwaters corresponded to the period of nesting and the first week of brood-rearing.

The majority of broods hatched during the first week of July. During the first 2 weeks, broods spent 83 percent of their time in secluded backwaters, feeding only occasionally in the creek. The percentage of time spent in running water increased as juveniles developed proficiency in swimming and diving. The last 3 weeks were spent almost entirely in running waters. During the entire brood-rearing period, there was a significant preference for areas which were inaccessible to humans. Family units remained intact during the entire prefledging period and brood mixing was virtually nonexistent. Females with broods typically left the brood-rearing area and began moving downstream during the sixth or seventh week. Most broods disappeared from the study area a few days before juveniles were fully fledged; the beginning of migration consisted of downstream movement. The preflight period of those young which remained on the study area until fledged was approximately 55 days.

Production and survival of young were highest during 1973. Eighty-three percent of observed young survived until migration. In 1974, 40 percent survived until migration, but in 1975, only 18 percent reached the nearly fledged stage. At least 17 young were successfully reared on the study area in 1973 while only 12 survived until migration in 1974 and only two in 1975.

Breeding success was directly related to the timing, duration, and intensity of spring runoff. Environmental factors, including winter and spring precipitation, and spring temperatures played an important role in controlling runoff. High water levels and late runoff adversely affected production through increased nest washout and high mortality of newly hatched juveniles.

Like many other K-strategists, the species' reproductive rate is low and it is extremely vulnerable to alteration of habitat. Management suggestions included identification of critical habitat, recreation and preservation of pristine conditions in aquatic ecosystems, and comprehensive planning to minimize the impact of humans on sensitive areas.

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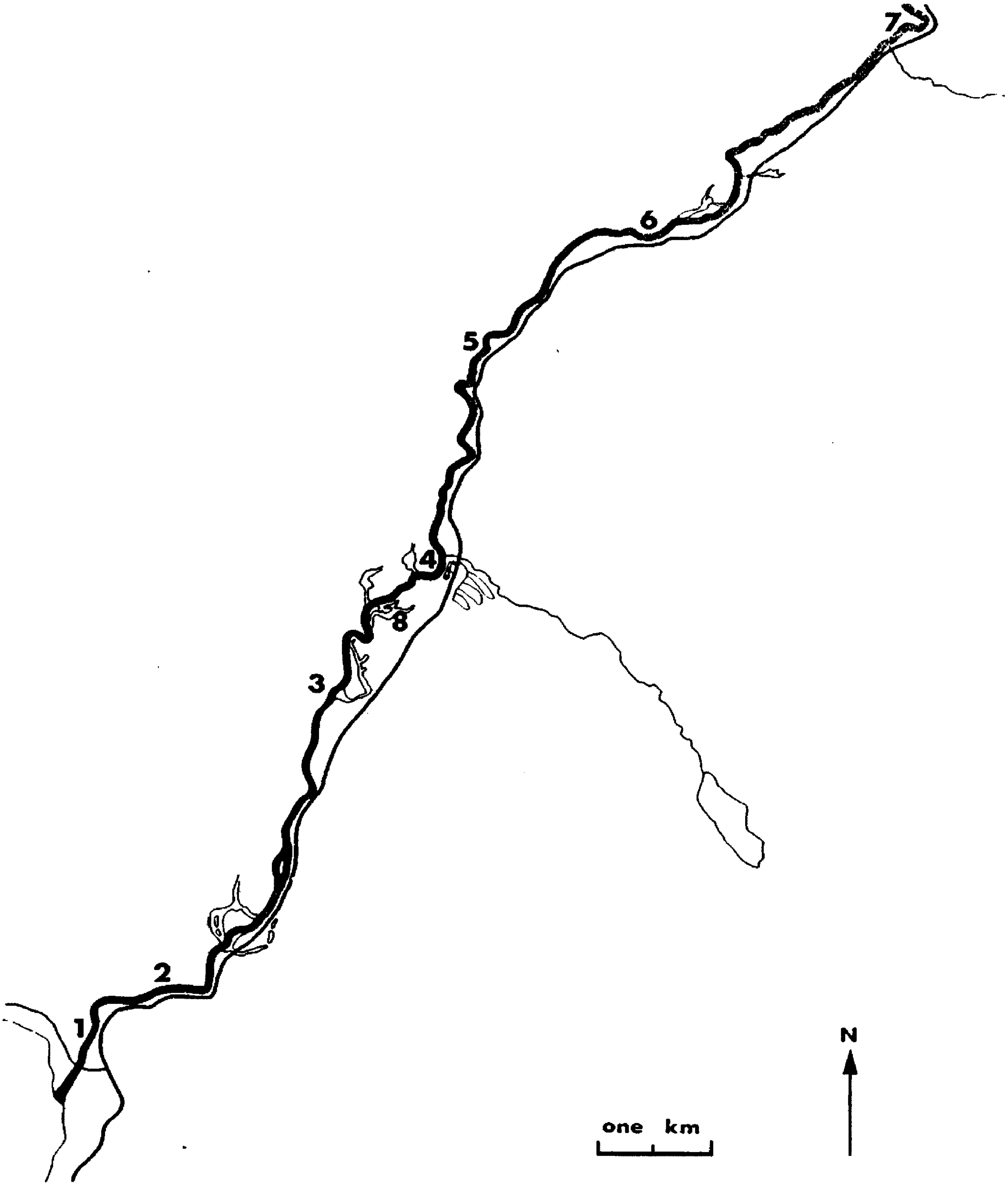
APPENDIX I

LOCATIONS AND HABITAT DESCRIPTIONS OF SITES OF COLLECTION OF BENTHIC INVERTEBRATES

Collection Site	Habitat Description
1	Rapids with bedrock substrate
2	Rapids with bedrock substrate
3	Riffles with cobble substrate
4	Riffles with cobble substrate
5	Riffles with cobble substrate
6	Riffles with cobble substrate
7	Riffles with cobble substrate
8	Abandoned meander with silt substrate


7
6
5
4
8
3
2
1
one km
N

APPENDIX II

INSECTS COLLECTED FROM MC DONALD CREEK

Genus or Family

- Ephemeroptera
  - Baetidae
    - *Baetis* sp.
  - Ephemerellidae
    - *Ephemerella* sp. ? of *walkeri* group
    - *E. doddsi*
    - *E. prosperina*
    - *E.* sp. ? of *invaria* group
    - *E.* sp. ? of *hecuba* group
  - Heptageniidae
    - *Cinygmula* sp.
    - *Rhithrogena* sp.
  - Siphlonuridae
    - *Ameletus* sp.
  - Leptophlebiidae
    - *Leptophlebia* sp.

- Plecoptera
  - Nemouridae
    - *Nemoura* sp.
    - *Leuctra* sp.
    - *Brachyptera* sp.

- Perlodidae
  - *Isoperla* sp.
  - *Isogenus* sp.
  - *Arcynopteryx* (*Megarcys*) sp.
- Chloroperlidae
  - *Alloperla* sp.
  - *Paraperla* sp.
- Perlidae
  - *Acroneuria theodora*
  - *A. pacifica*

Hemiptera
- Corixidae (unidentified genus)
- Gerridae (unidentified genus)

Megaloptera
- Sialidae (unidentified genus)

Trichoptera
- Rhyacophilidae
  - *Rhyacophila* sp.
- Psychomyiidae
  - *Polycentropus* sp.
- Hydropsychidae
  - *Hydropsyche* sp.
  - *Parapsyche* sp.
- Hydroptilidae (unidentified genus)
- Limnephilidae (unidentified genus)
- Leptoceridae (unidentified genus)
- Brachycentridae
  - *Brachycentrus* sp.

Coleoptera

- Dytiscidae (unidentified genus)
- Elmidae (unidentified genus)

Diptera

- Tipulidae
  - *Hexatoma* sp.
  - (other unidentified genus)
- Simuliidae (unidentified genus)
- Chironomidae (unidentified genus)
- Rhagionidae
  - *Atherix* sp.
- Tabanidae (unidentified genus)

APPENDIX III

MEASUREMENTS OF ADULT HARLEQUINS BANDED ON MCDONALD CREEK
(measurements after Baldwin et al. 1931)

	Males			Females		
	N	$\bar{x}$	Range	N	$\bar{x}$	Range
Weight (g)	12	684.2	660-710	10	626.5	545-660
Total length (mm)	12	427.8	410-449	7	396.9	387-405
Exposed culmen (mm)	12	28.8	27.5-29.9	7	26.3	24.9-28.0
Closed wing (mm)	12	195.7	180-201	7	187.0	181-198
Tail (mm)	12	99.1	92-106	7	87.0	84-93
Tarsus (mm)	12	38.1	35-42	7	38.1	36-40
Middle toe (mm)	12	53.6	51-57	7	53.3	49-55

APPENDIX IV

SUMMARY OF HARLEQUIN COPULATORY BEHAVIORS

	Male						Female					
	Successful copulation		Unsuccessful copulation		Total observed		Successful copulation		Unsuccessful copulation		Total observed	
	no.	(%)	no.	(%)	no.	(%)	no.	(%)	no.	(%)	no.	(%)
Precopulatory displays	14		5		19		14		5		19	
Head-nod	14	(100)	5	(100)	19	(100)	5	(36)	1	(20)	6	(32)
Follow	14	(100)	4	(80)	18	(95)	xx		xx		xx	
Zig-zag	14	(100)	2	(40)	16	(84)	xx		xx		xx	
Nibble	14	(100)	5	(100)	19	(100)	xx		xx		xx	
Upwards stretch with wing-flap	2	(14)	0	(0)	2	(11)	xx		xx		xx	
Upwards stretch	10	(71)	2	(40)	12	(63)	xx		xx		xx	
Vocalize	1	(7)	0	(0)	1	(5)	xx		xx		xx	
Bill-dip	7	(50)	1	(20)	8	(42)	xx		xx		xx	
Chase	1	(7)	0	(0)	1	(5)	1	(7)	0	(0)	1	(5)
Assume prone posture	xx		xx		xx		14	(100)	2	(40)	16	(84)
Copulatory behaviors	14						14					
Female prone							14	(100)				
Male grabs nape	13	(93)										
Male wing-tail flick	6	(43)										
Rotations by male during dismount	13	(93)										
Postcopulatory displays	12						12					
Chase	10	(83)					xx					
Sentinel	2	(17)					xx					
Preen	2	(17)					3	(25)				
Bathe	1	(8)					1	(8)				
Dive	11	(92)					11	(92)				
Leading	xx						2	(17)				

Reason for incomplete sequence (precopulatory, copulatory or postcopulatory sequence broken off)

Sequence disrupted by stream current	3	(43)
Sequence disrupted by intruding male	2	(29)
Female unreceptive (fled)	2	(29)

APPENDIX V

BREEDING DENSITIES OF HARLEQUINS, BLUE DUCKS, AND TORRENT DUCKS

Species	Estimate of density (breeding pairs)	Location	Reference
Harlequin Duck	2 pairs/km	River Laxá at Svínavatn, Iceland	Bengtson and Ulfstrand 1971
	1 pair/km	River Svartá, Iceland	Bengtson and Ulfstrand 1971
	1 pair/km	River Suderá, Iceland	Bengtson and Ulfstrand 1971
	6.8 pairs/km	River Laxá at Lake Mývatn, Iceland	Bengtson and Ulfstrand 1971
	.16-.31 pairs/km	Streams in Washington State	D. E. Crouch, pers. comm.
	.67-.91 pairs/km	McDonald Creek, Montana	This study
Torrent Duck	1 pair/km	Andean streams	Johnsgard 1966
Blue Duck	1.25 pairs/km	Streams of New Zealand	Kear 1972

APPENDIX VI

HARLEQUIN DUCKS BANDED 1974-1976

Band no.	Age and sex	Breeding season			Status
		1974	1975	1976	
03	Adult ♀	Resident	Resident	Resident	Paired to no. 14 in 1975, 1976
04	Adult ♀	Resident	Resident	Resident	Paired to unbanded male in 1975, 1976
06	Adult ♀	Resident	Resident	Resident	Paired to unbanded male in 1975, 1976
05	Juvenile	Resident	x	Resident	Orphaned juvenile in 1974, paired in 1976
07	Juvenile	Resident	x	x	Progeny of no. 06
08	Juvenile	Resident	x	x	Progeny of no. 06
09	Juvenile	Resident	x	Resident	Progeny of no. 06, paired in 1976
10	Juvenile	Resident	x	x	Progeny of no. 06
13	Adult ♂	- - - - - - - -	Resident	Resident	Unpaired in 1975, paired in 1976
14	Adult ♂	- - - - - - - -	Resident	Resident	Paired to no. 03 in 1975, 1976
15	Adult ♀	- - - - - - - -	Resident	Resident	Paired to unbanded male in 1975, 1976
16	Adult ♂	- - - - - - - -	Resident	Resident	Unpaired in 1975, 1976
17	Adult ♀	- - - - - - - -	Migrant	x	Paired to no. 18, not relocated after banding
18	Adult ♂	- - - - - - - -	Migrant	x	Paired to no. 17, not relocated after banding
19	Adult ♂	- - - - - - - -	Resident	x	Unpaired in 1975
20	Adult ♀	- - - - - - - -	Resident	x	Paired in 1975 (unproductive), not seen in 1976
21	Adult ♂	- - - - - - - -	Resident	Resident	Paired, occupied same home range in 1975, 1976
22	Juvenile	- - - - - - - -	Resident	x	Progeny of no. 03
23	Juvenile	- - - - - - - -	Resident	x	Progeny of no. 03
24	Adult ♂	- - - - - - - -	- - - - - - - -	Migrant	Unpaired in 1976, not relocated after banding
25	Adult ♂	- - - - - - - -	- - - - - - - -	Resident	Unpaired in 1976
26	Adult ♂	- - - - - - - -	- - - - - - - -	Resident	Unpaired in 1976
27	Adult ♂	- - - - - - - -	- - - - - - - -	Resident	Unpaired in 1976
28	Adult ♂	- - - - - - - -	- - - - - - - -	Migrant	Paired to no. 29, not relocated after banding
29	Adult ♀	- - - - - - - -	- - - - - - - -	Migrant	Paired to no. 28, not relocated after banding
30	Adult ♀	- - - - - - - -	- - - - - - - -	Resident	Paired to no. 31
31	Adult ♂	- - - - - - - -	- - - - - - - -	Resident	Paired to no. 30

APPENDIX VII

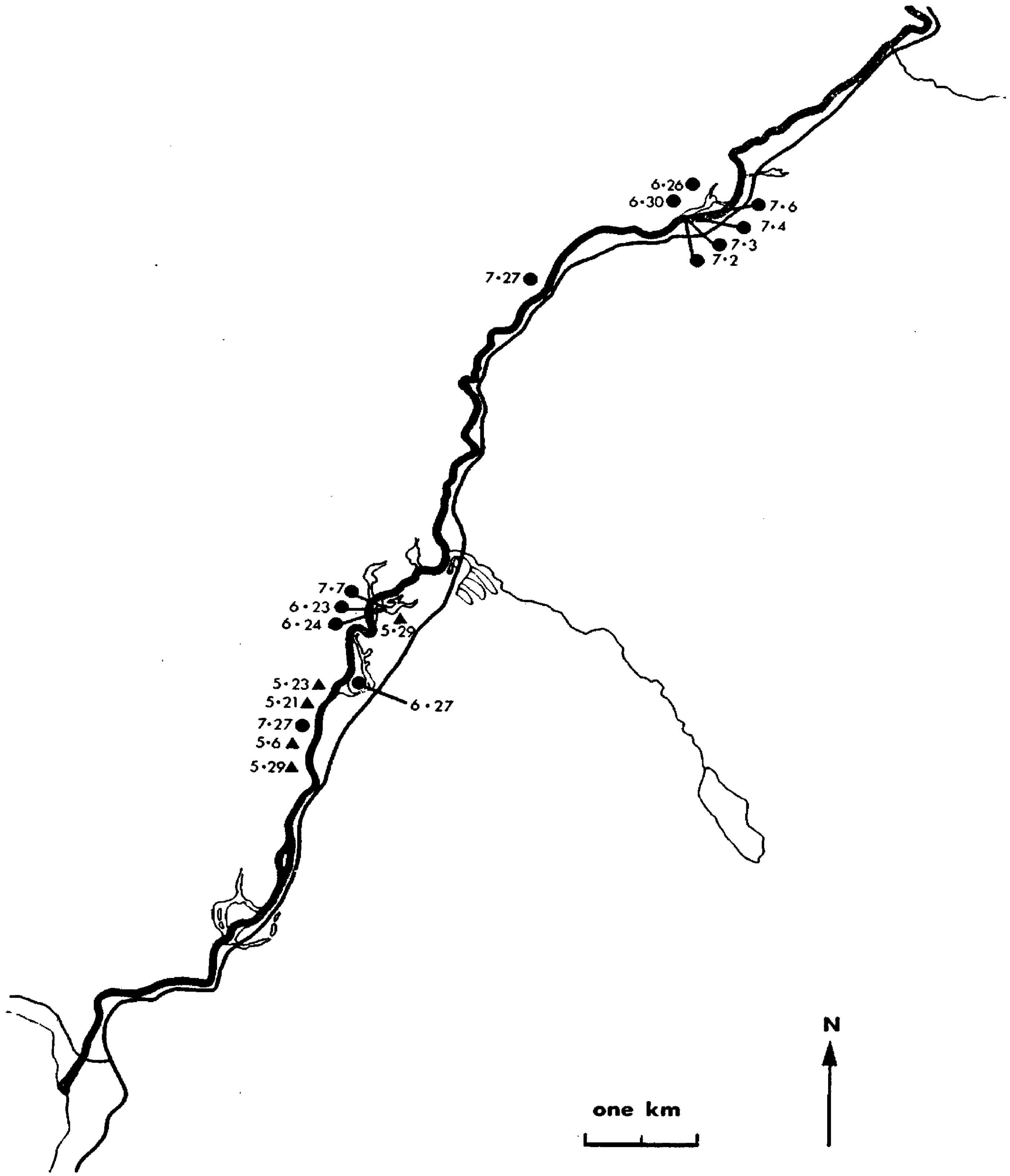
MAPS DEPICTING MOVEMENTS OF INDIVIDUAL HARLEQUINS

APPENDIX VIIa

Locations of Unproductive Female (No. 15) During 1975
(Paired with Unmarked Male)

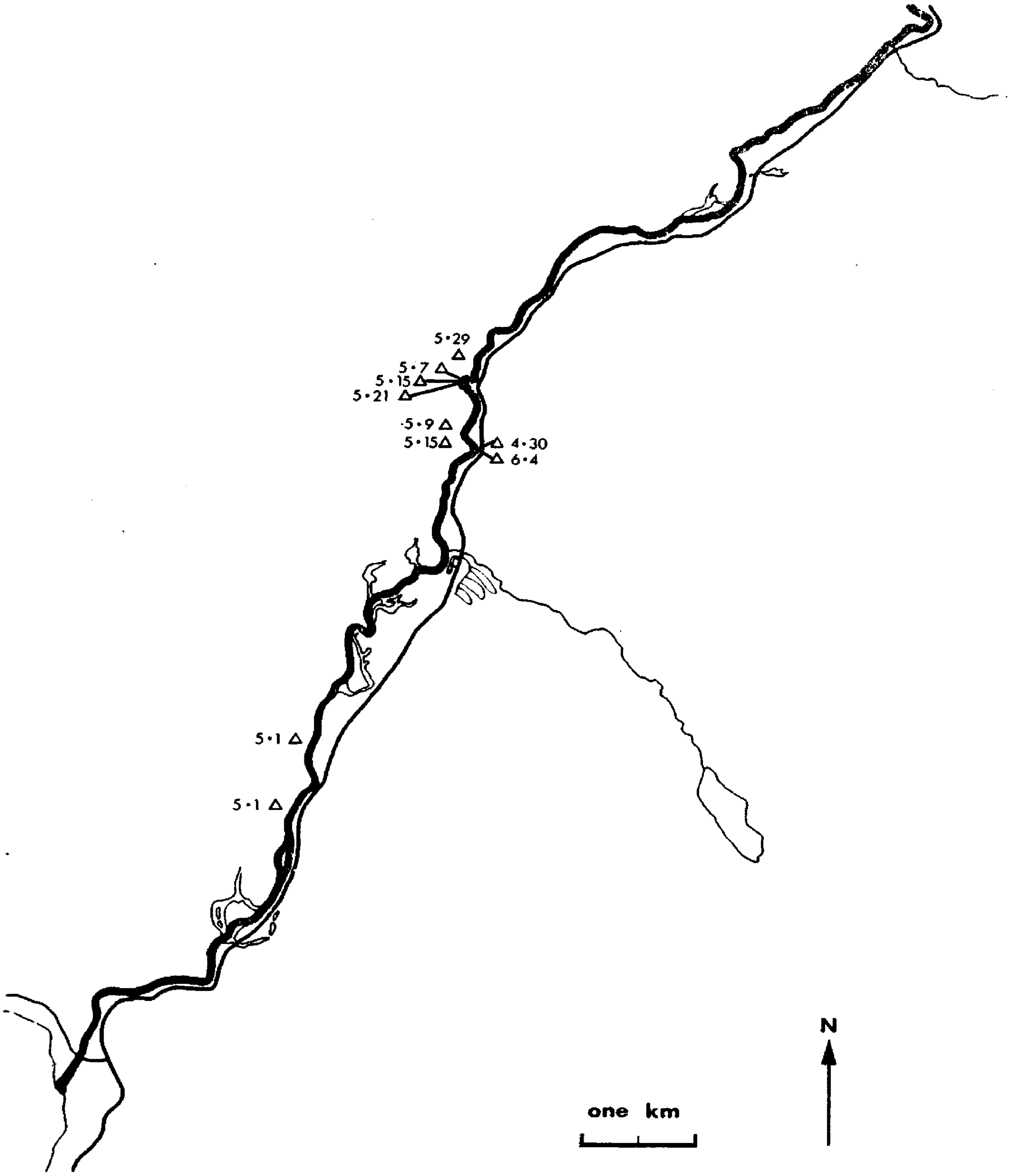
▲ Attended by mate

● Unattended


6·26
6·30
7·6
7·4
7·3
7·2
7·27
7·7
6·23
6·24
5·29
5·23
5·21
6·27
7·27
5·6
5·29
N
one km

APPENDIX VIIb

Locations of Female (No. 15) During 1976
(Paired with Unmarked Male)


5·29
5·7
5·15
5·21
5·9
5·15
4·30
6·4
5·1
5·1
one km
N

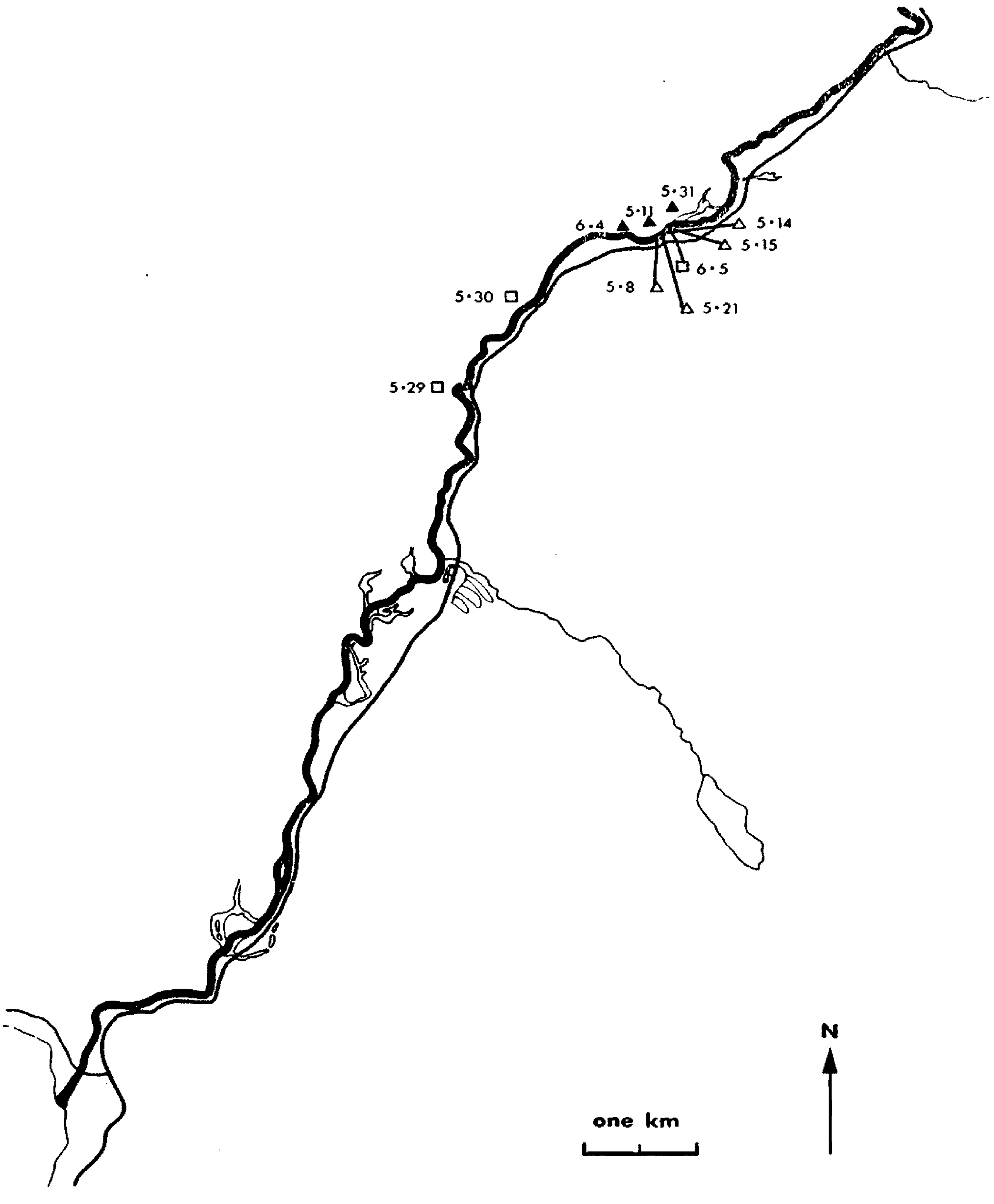
APPENDIX VII c

Locations of Male (No. 21) During 1975 and 1976
(Paired with Unmarked Female Both Years)

▲ Accompanying mate 1975

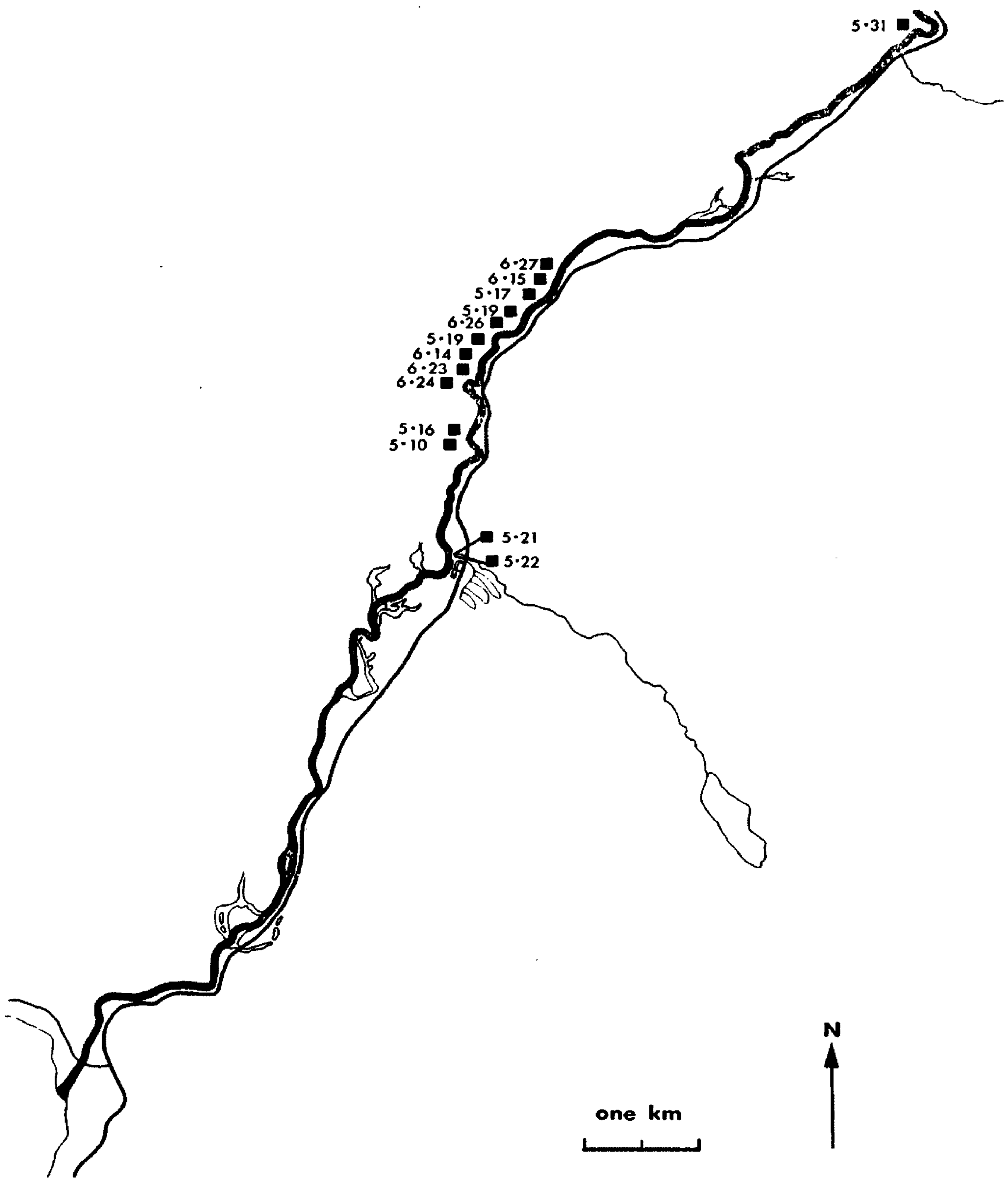
△ Accompanying mate 1976

☐ Observed without mate 1976


5·31
5·11
6·4
5·14
5·15
6·5
5·8
5·21
5·30
5·29
one km
N

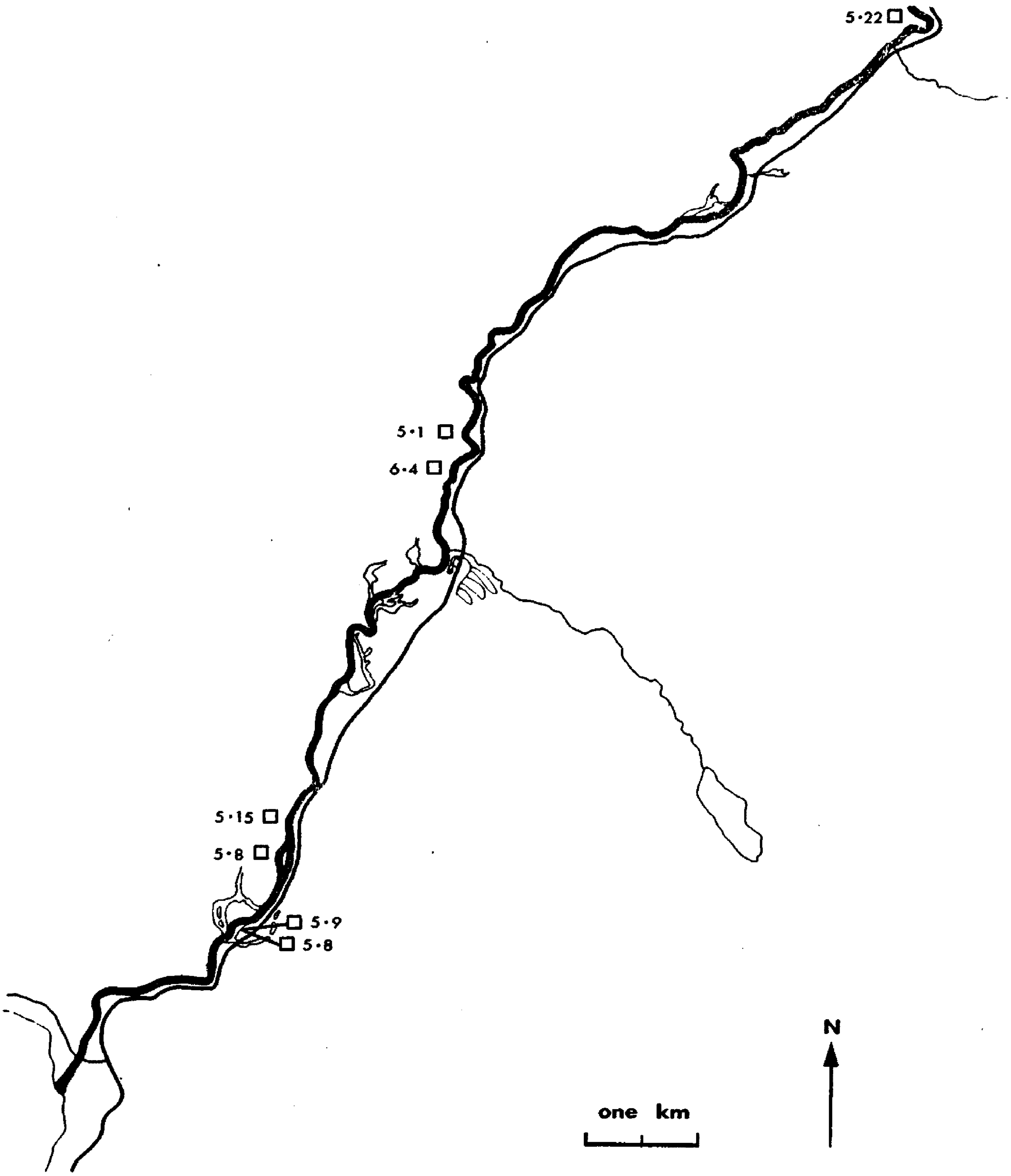
APPENDIX VIId

Locations of Male (No. 19) During 1975
(Surplus Male)


5·31
6·27
6·15
5·17
5·19
6·26
5·19
6·14
6·23
6·24
5·16
5·10
5·21
5·22
one km
N

APPENDIX VIIe

Locations of Male (No. 25) During 1976
(Surplus Male)

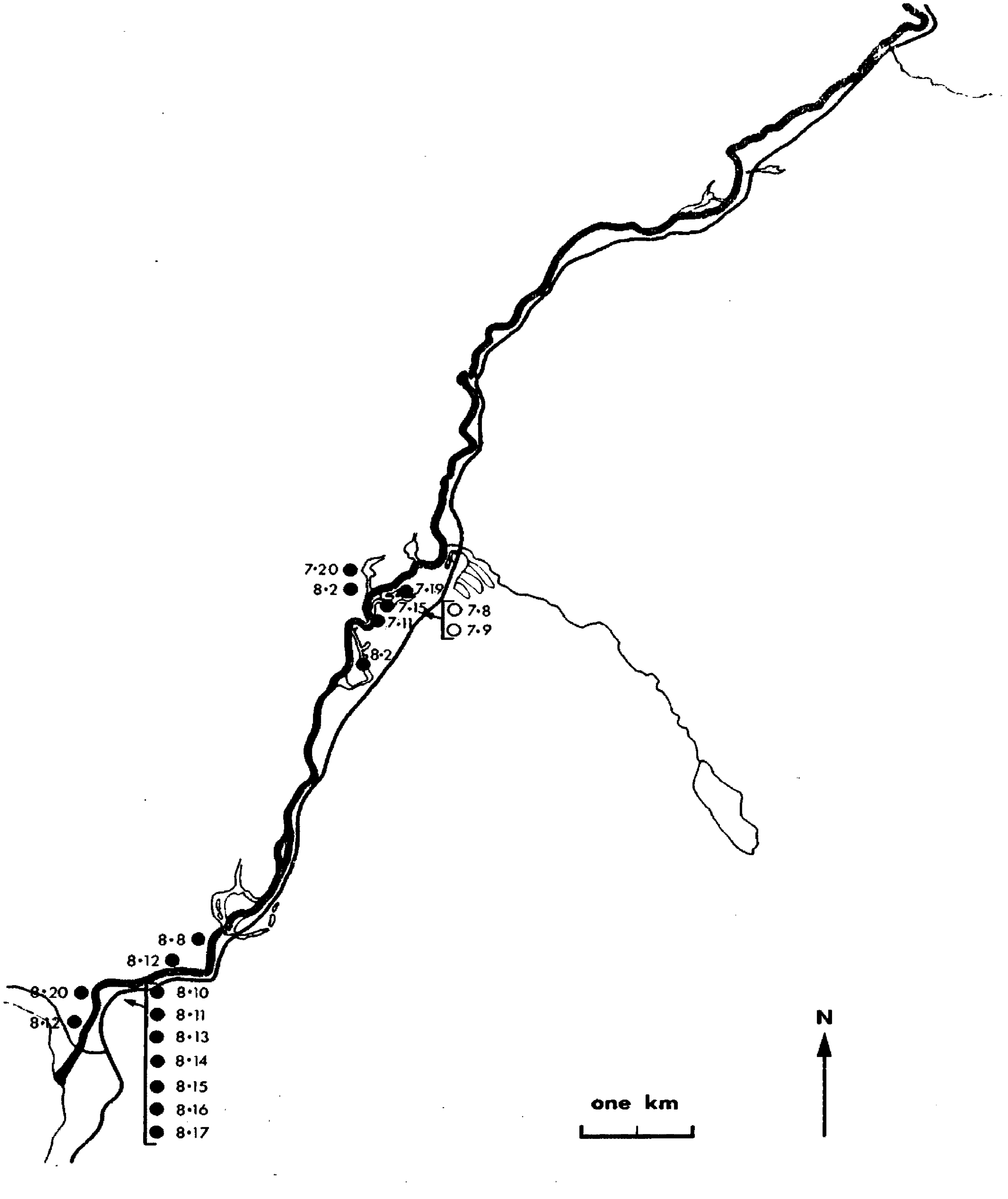

5·22
5·1
6·4
5·15
5·8
5·9
5·8
one km
N

APPENDIX VIIf

Locations of Female (No. 3) and Brood During 1975 and 1976

● 1975 locations

○ 1976 locations


7·20
8·2
7·19
7·15
7·11
7·8
7·9
8·2
8·8
8·12
8·20
8·12
8·10
8·11
8·13
8·14
8·15
8·16
8·17
one km
N