HARLEQUINS *HISTRIONICUS HISTRIONICUS* IN A ROCKY MOUNTAIN WATERSHED I: BACKGROUND AND GENERAL BREEDING ECOLOGY

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The Maligne Valley, a watershed draining into the Athabasca River in the Rocky Mountains, in Jasper National Park, Canada, is a breeding area for Harlequin Ducks (Histrionicus histrionicus). Based on peak counts, some 30 - 40 adults enter the valley each spring, arriving in early May along the Athabasca River. Numbers build steadily in the valley until the period of peak flow, and individuals are highly faithful to particular sections of the main watercourse. Feeding is intensive prior to nest initiation. Harlequins use lakes, outlets, rivers, and tributaries in the valley in a variety of ways. Along the Lower Maligne River, a few Harlequin pairs defend territories, but the majority of birds feed in aggregations at major lake outlets and inlets, likely highly productive places. On Maligne Lake birds feed in scattered pairs, generally situated at stream inlets. Females begin nesting in mid-June following peak flow, and males depart the valley shortly thereafter. Nests are placed along both the main course of the Maligne River and along several tributaries, but the upper and lower sections of the Maligne River accounted for 11 of the 14 broods located. Many females move their broods to two large lakes for rearing.

Key Words: Harlequin Duck, *Histrionicus histrionicus*, Rocky Mountains, river outlets

Only a decade ago, Harlequin Ducks *Histrionicus histrionicus* were considered poorly known (Breault & Savard 1991), but knowledge of their distribution, habitat requirements, and reproductive biology have recently expanded (Robertson & Goudie 1999). Their breeding ecology was first investigated in Iceland (Bengtson 1966; Bengtson 1972; Bengtson & Ulfstrand 1971). In western North America, many studies of breeding biology have been undertaken (Kuchel 1977; Dzinbal 1982; Dzinbal & Jarvis 1982; Wallen 1987; Markum 1990; Cassirer & Groves 1991; Schirato & Sharpe 1992; Wallen 1992; Diamond & Finnegan 1993; Crowley 1993; Zwiefelhofer 1994; Smith 2000) but due to the low density of breeding Harlequins most have been able to observe only a few pairs. These studies indicate that Harlequins breed throughout the Western Cordillera, and are present on mountain lakes and rivers from May to September. As in Iceland, males actively defend their mates, while females focus on feeding (Inglis *et al.* 1991). Benthic macroinvertebrates, especially larval plecopterans, trichopterans and simuliids, as well as other insects account for most of the diet on breeding ranges, though fish eggs are taken opportunistically. Details are known of plumages and moult (Robertson *et al.* 1997; Smith *et al.* 1998), pair formation (Gowans *et al.* 1997; Robertson *et al.* 1998), site fidelity (Robertson *et al.* 1999), breeding productivity (Crowley 1993), brood rearing (Smith 2000) and recruitment (Smith *et al.* submitted).

Recent concern about sea duck population trends (Goudie *et al.* 1994) has prompted further study of the factors influencing sea duck populations. In Iceland at least, Harlequin productivity and habitat selection seem linked to macroinvertebrate density (Bengtson & Ulfstrand 1971). In this paper a study of the breeding ecology of Harlequins in a Rocky Mountain valley is described. The purpose is to establish their general phenology and ecology in this watershed, as part of a larger study of how human activities and climate change may be affecting Harlequin ecology.

Methods

Study Area

The study was conducted from May to September, 1993 to 1997, in the Maligne Valley (**Figure 1**), the watershed of a second order stream that originates in the Rocky Mountains and descends over a distance of 70km to its confluence with the Athabasca River, near the town of Jasper, Alberta, Canada. The entire watershed is contained within Jasper National Park.

The main watercourse through the Maligne Valley has six distinct sections. The Upper Maligne River originates at an altitude of about 2400m and flows into Maligne Lake (altitude 1676m). Water leaves the lake almost silt-free at the Maligne Lake Outlet (MLO) and descends through the Mid-Maligne River, entering Medicine Lake (altitude 1436m) through a braided gravel delta. Below Medicine Lake, the Lower Maligne River runs into the Athabasca River at an elevation of 1100m. The Maligne watershed also contains 11 tributaries judged potentially suitable for Harlequin breeding (see **Figure 1**).

Medicine Lake drains through a karst formation. In spring the flow of the Mid-Maligne River into the lake rises and exceeds the underground drainage rate; as a consequence Medicine Lake fills in the

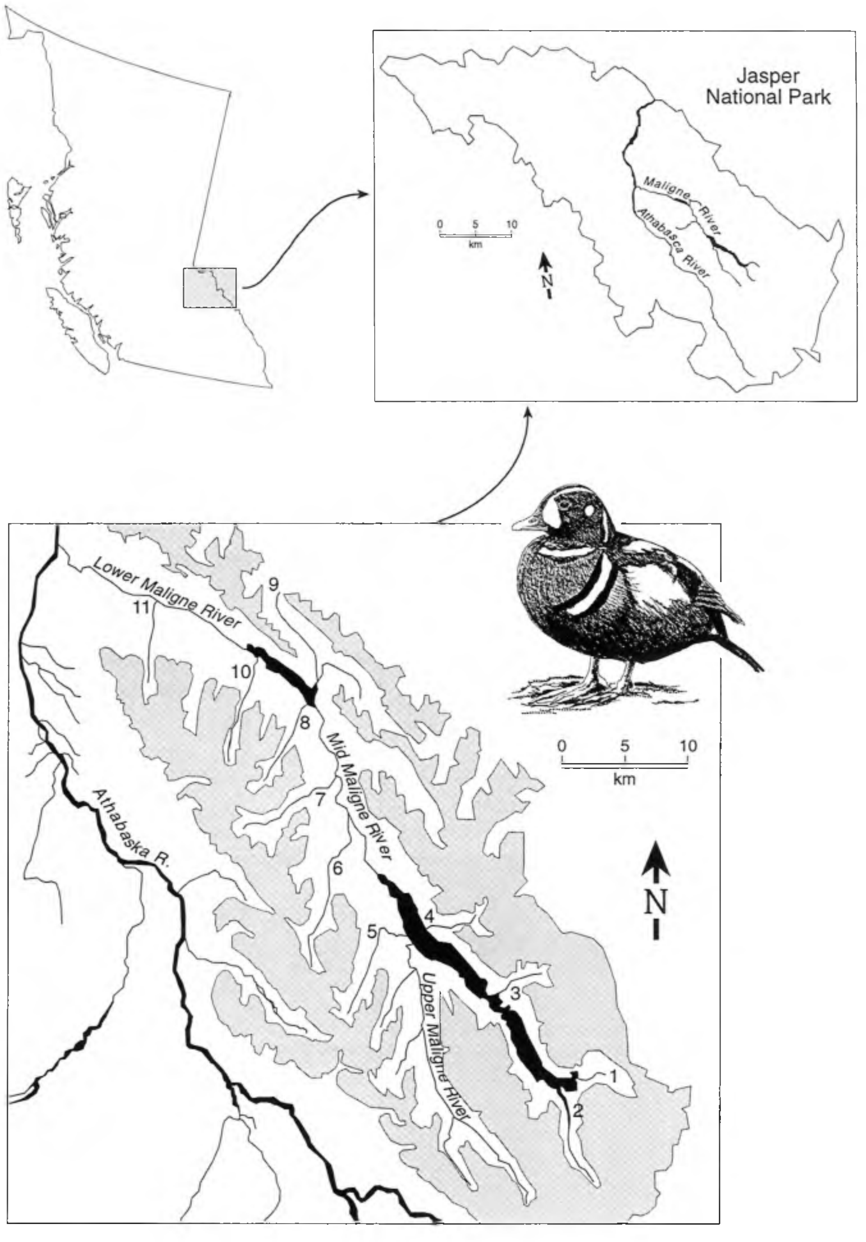

Figure 1. The Maligne Valley watershed in Jasper National Park, Alberta, Canada. Shading shows alpine areas, and the numbers identify tributaries given in **Table 2.**

course of the summer, but drains in winter when stream flow is reduced. The lake does not drain directly into the course of the Lower Maligne River except in occasional years of high freshet, when it may overflow. Instead, the Lower Maligne River is supplied with water by tributaries and from a partial resurgence of the underground stream downstream of Medicine Lake. From here, the Lower Maligne River descends gradually, until it enters a narrow and steep canyon, below which it joins the Athabasca River. These barriers prevent colonization, and the Lower Maligne River has few or no fish.

Environmental variables

Weather data were recorded daily at the Warden Station at Maligne Lake. Several staff gauges and an automated stream flow recorder were used to monitor stream flow at locations along the Mid- and Lower Maligne Rivers. Stream flow diminishes greatly in winter, though the Mid-Maligne River maintains a small, regular flow. Flow rises abruptly in late May or June, and the ice leaves Maligne Lake over a period of several days. We termed this the 'spring event' and define it as the first day on which the water level on the staff gauge at the MLO rose above 0.5m (see **Figure 2**).

Surveys

To monitor Harlequin abundance on the Mid- and Lower Maligne Rivers, a weekly survey was conducted from the Maligne Lake Road, which traverses the valley bottom from its confluence with the Athabasca to the MLO. Harlequins were counted from each of 37 viewing sites, which together give a nearly complete view of the Lower Maligne River, Medicine Lake, the Mid-Maligne River, and the MLO. Banded individuals were identified

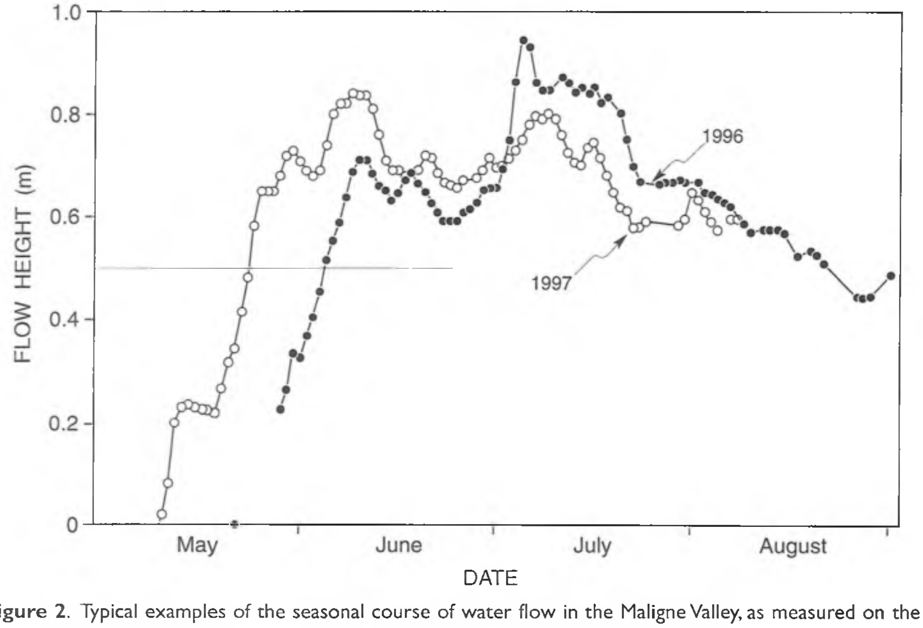

Figure 2. Typical examples of the seasonal course of water flow in the Maligne Valley, as measured on the staff guage at the Maligne Lake Outlet. The date of the 'spring event' is defined as the first day on whch the water level rises above 0.5m.

whenever possible. Surveys began in the first week of May, and after ice-out Maligne Lake was surveyed on the same days, using a small boat to patrol the lake perimeter at five to 10km/h, 10 to 50m from shore. These surveys were concluded in late August. In addition to the weekly survey, the number of Harlequins at the Maligne Lake Outlet was counted every day. From these data a peak count for each year was derived, and the cumulative usage (measured in duck-weeks) of each section of the main watercourse was tabulated. Unfortunately, the difficult access to the Upper Maligne River meant that it could be surveyed only occasionally later in the summer.

Tributary surveys

From mid-June to early September of each year, hiking surveys were conducted along the Maligne River tributaries shown on **Figure 1** in search of Harlequin broods. When possible the age of sighted broods was classified, based on body shape and plumage development (Gollop & Marshall 1954). Assuming 28 days incubation, a mean clutch size of 5.7 and a typical laying interval of two days (Bengtson 1972), hatch date (catch date minus estimated age), the start of incubation (hatch date minus 28 days incubation) and the start of laying (start of incubation minus 12 days laying) were estimated from the estimated age.

Harlequin capture and banding

Harlequins were captured in mist nets and banded at locations throughout the Maligne Valley. Weight (pesola scale, ±5g), wing and tarsus length, age (estimated from plumage) and sex (determined by plumage in adults and cloacal examination of young) were determined. Females were examined for signs of breeding, including the development of a brood patch, pelvic opening, or the presence of an egg in the oviduct. The presence of a mate was also noted.

Food Sampling

In 1993-1995, the diversity and abundance of benthic macroinvertebrates was sampled at the MLO by collecting 'kick' samples at two week intervals. This method was used because the substrates at the MLO were too large to allow effective sampling with area samplers such as the Hess or Serber samplers, and Harlequins typically did not feed in shallow areas or finer substrates. To collect a sample, one waded into the current and kicked the substrate, within an approximate one square metre area, for two minutes while holding a dip net (45cm diameter), approximately 40cm downstream, to collect the invertebrates as they washed off the substrate.

Samples were preserved in 85% ethanol and sorted by hand under a dissecting microscope, keying out invertebrates to family following Clifford (1980). Some specimens could only be keyed only to subclass or order (Annelida, Pelecypoda, Hirundinea, and salmonid eggs). Each specimen (excluding salmonid eggs) was assigned to a foraging guild based on the primary foraging mode of the species within that taxa, after Cummins (1973), and into one of seven size classes, based on five millimetre increments. Samples from each size and taxonomic class were weighed, and the total dry weight of each sample computed.

Table 1. Usage of the main Maligne watercourse by Harlequins 1993-1997, measured as 'cumulative duck-weeks'.

Year	Peak Count	Lower Maligne	Medicine Lake	Mid-Maligne	MLO	Maligne Lake	Total
1993	28	7	78	0	60	9	154
1994	27	24	118	0	58	44	244
1995	38	3	121	10	28	58	220
1996	34	2	54	4	11	65	136
1997	24	3	23	2	20	26	74
Average Annual %		4.3	45.0	2.0	22.2	26.6	100

Results

General description

Harlequin arrival in Jasper National Park was noted each year in late April along the Athabasca River, where they on occasion congregated in small side channels to feed on the eggs of spawning long-nosed suckers *Catastomus catastomus*. Harlequins were first sighted in the Maligne Valley on average 9 May, and increased in abundance steadily until mid-June, peaking just after the spring event (**Figure 3**).

Harlequins used all parts of the main Maligne watercourse, but in varying amounts, in different ways, and usage varied from year-to-year (**Table 1**). In terms of total usage, the Lower Maligne River was used comparatively little. Harlequins pairs appeared to defend territories along the Lower Maligne River, and females nested there (see below). Medicine Lake accounted for the greatest proportion of Harlequin usage. Here the birds fed intensively in a loose flock along the delta of the Mid-Maligne River at the upstream end of the lake in May and June, and in August broods appeared on the lake. The Mid-Maligne River was little used, except at the outlet of Maligne Lake (MLO) into the river, where the birds clustered and fed intensively in May and June prior to nesting. On Maligne Lake the birds fed as scattered pairs. The MLO and Medicine Lake together account for 70% of all of the usage by Harlequins of the main Maligne watercourse.

The main watercourse of the Maligne is used most intensively in May and the first half of June. Half (50%) of the total seasonal usage is attained on average by 8 June. Harlequin numbers are greatest from mid- to late June, during the period that nests are initiated and clutches laid (see below). The numbers of birds seen falls shortly after, as incubating females become secretive, while males depart for coastal moulting areas. The rise in numbers at the end of August occurs as broods begin to appear on Medicine and Maligne Lakes.

Resighting pattern

A total of 86 adult Harlequins were captured and ringed on the Athabasca River and in the Maligne Valley, 39 males and 47 females. (The excess of females is

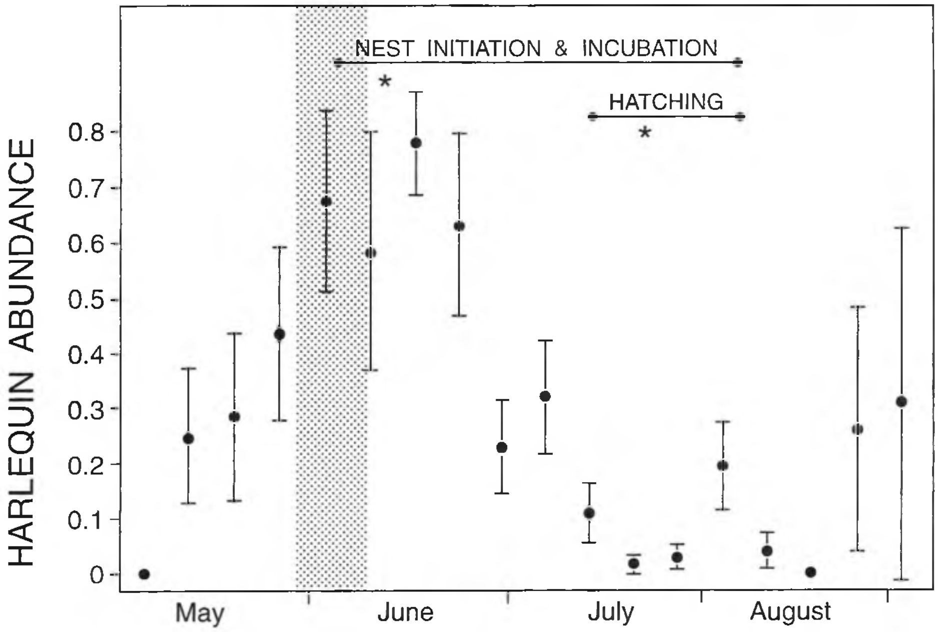

Figure 3. Harlequin phenology in the Maligne Valley. Abundance is represented here as the mean (± s.d.) proportion of the annual peak counts given in **Table 1**. The shaded area indicates the mean (±s.d.) date of the spring event. The periods of nesting and the timing of hatch are shown above, with an asterisk indicating peak occurrence.

expected, because males are present for a shorter period.) Of these, 22 (25.6%) were resighted, many on multiple occasions. All but five resightings were made on the same or on the adjacent sections of the Maligne system. Of these five, two involved males that moved from the Athabasca River to the Maligne Valley, one female moved between the MacLeod River (about 50 km distant) and the Maligne, and one female moved between the MacLeod and Athabasca Rivers. Thus, some of the ducks in the Maligne Valley may also use other watersheds. The only resighting within the Maligne Valley involving a separation greater than adjacent watercourse sections was of a male who moved from the Lower to the Mid-Maligne River.

Of 69 Harlequins individually identified in the Maligne Valley, 17 were resighted there in a subsequent year. Of 19 birds banded on the Athabasca River, three were seen again: one in the following year on the Athabasca, and two in the Maligne Valley. The resighting rate in the Maligne Valley (17/69, or 24.6%) is more than double that on the Athabasca (2/19, or 10.5%), supporting the idea that only some of the Harlequins migrating along the Athabasca enter the Maligne Valley.

Feeding

Harlequins in the Maligne Valley fed intensively during May and June, prior to nest initiation (Hunt 1998). Ducks fed mostly by diving, but also skimmed eclosing insects on the surface of the lakes,

Table 2. Brood surveys of tributaries and the main river stem. N is the number of surveys made, and b is the number of broods detected. River segments and tributaries are identified in **Figure 1.**

	1993		1994		1995		1996		1997		Totals	
Tributary	N	b	N	b	N	b	N	b	N	b	Surveys	Broods
Upper Maligne R.	6	1	5	3	3	3	1	0	1	0	16	7
1 - Warren Cr.	1	0	1	1	1	0	1	0	1	0	5	1
2 - Coronet Cr.	1	0	0	/	1	0	2	0	0	/	4	0
3 - Sandpipe Cr.	1	0	0	/	1	0	0	/	0	/	2	0
4 - Leah Cr.	0	/	0	/	2	0	0	/	1	-	3	0
5 - Trapper Cr.	0	/	0	/	0	/	1	0	1	0	2	0
6 - Evelyn Cr.	2	0	4	0	3	1	2	0	1	0	12	1
7 - Stovepipe Cr	0	/	1	0	0	/	0	/	0	/	1	0
Middle Maligne R.	0	/	0	/	0	/	1	0	0	/	1	0
8 - Excelsior Cr.	0	/	3	0	0	/	1	1	0	/	4	1.
9 - Beaver Cr./Jacques Lake	4	0	1	0	1	0	1	0	2	0	9	0
10 - Watchtower Cr.	4	0	1	0	5	0	2	0	0	/	12	0
11 - Signal Mtn Cr./Tekerra L..	0	/	2	0	0	/	0	/	0	/	2	0
Lower Maligne R.	2	0	15	3	4	0	4	1	2	0	27	4

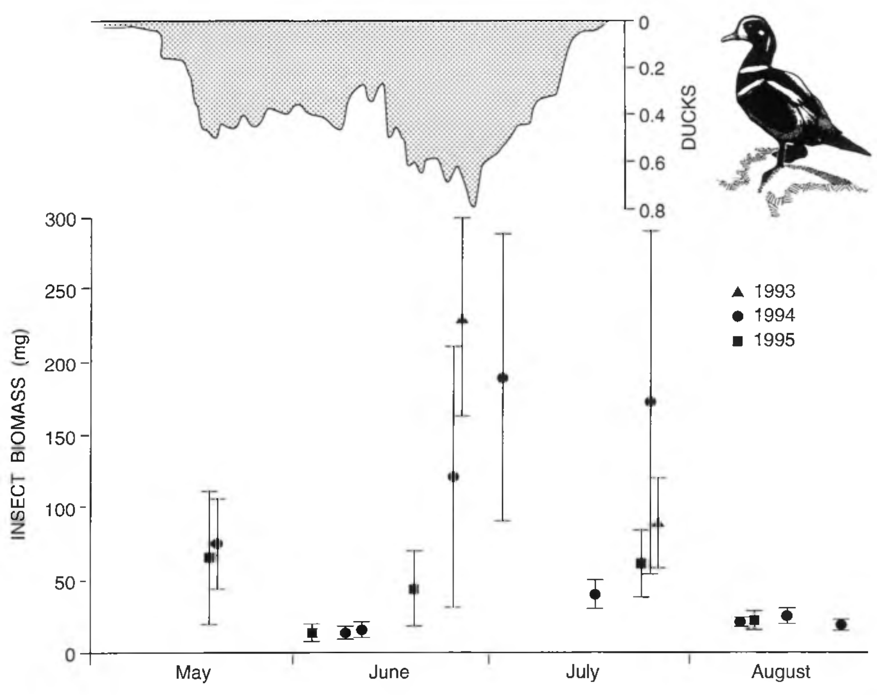

Figure 4. The abundance of benthic insects in kick samples (n=58) at the MLO in relation to the presence of Harlequins (along top axis, as mean daily proportion of annual maximum).

and walked along the edges of watercourses, pecking at small items in the water. Most of our feeding observations were made at the MLO, where they fed in the rapids of the first 500m of the Mid-Maligne River. Birds often fed in pairs, making a series of dives as they descended the rapids. At the bottom they emerged briefly to rest and preen before flying or walking to the top of the rapids to repeat the sequence. A more extensive rest and preening session followed several such circuits. Harlequins also fed in the pool above the rapids by raiding the redds of Rainbow Trout *Salmo onchorhyncus* spawning there.

Prey items were sampled at the MLO and in the Mid-Maligne River. The major prey items for Harlequins here are likely large stoneflies *Plecoptera*, whose true abundance in the MLO is undoubtedly under-represented by our sampling methods. Large stonefly larvae concentrate under large cobbles and boulders where Harlequins forage actively (pers. obs.), but that were very difficult for us to access and sample in a manner representative of Harlequin foraging. The prey of Harlequins diving in the lakes remains unknown.

Insect abundance in the kick samples at the MLO is highly variable (**Figure 4**). Nevertheless, the data indicate a curious pattern: insect biomass in the samples is lowest during the period of active feeding in late May and early June. The data show

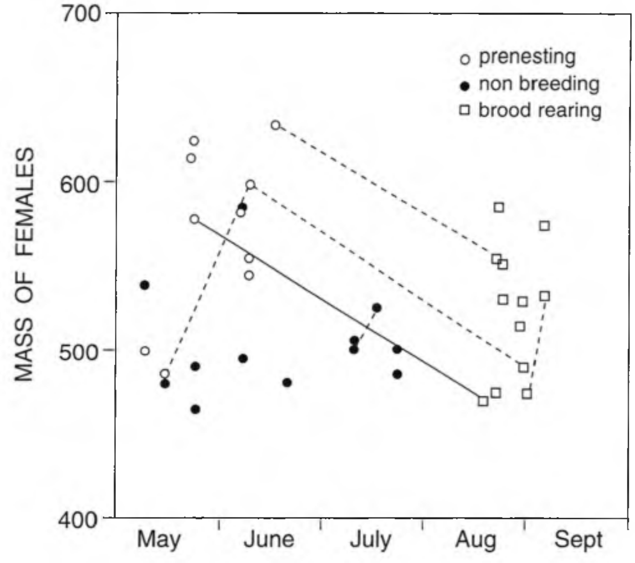

Figure 5. Body mass of female Harlequins in relation to breeding status and date. Dots are nonbreeding females. Open circles are prenesting females with breeding indicators (paired, brood patch, open pelvis, egg in abdomen). The open squares represent brood rearing females. Lines connect individuals measured twice (solid line - in same year; dotted line - in different years).

higher abundances just prior to and just after this time, and the same pattern is indicated in different years. Data collected since using other methods confirm the pattern (Ydenberg unpubl.), and this phenomenon will be investigated in more detail in a subsequent paper.

Body Condition of Females

Adult males were significantly heavier than adult females (female mean = 536.6g, n=38; males 580.1g, n=34; t-test, $P<0.001$). **Figure 5** shows that females showing signs of breeding have high body weight early in the season, and lower weight later. Changes in the mass of five hens caught and weighed more than once show the same pattern.

Nesting

Based on attendance patterns at the MLO and the overall seasonal pattern (**Figure 3**), females began to nest about mid-June. Mean hatch dates estimated from brood captures are 15 July 1993 (n=4, s.d.=5.7), 25 July 1994 (n=10, s.d.=9.2), and 4 August 1995 (n=5, s.d.=12.8; overall mean is July 25). Based on an estimate of 40d (12d laying + 28d incubation) from the start of laying to hatch, laying began about mid-June. Hatching occurred on average 45d (s.d. 3.6d) after peak tributary flows, so nests seem to be initiated just a few days after peak flow is reached. This relationship also held within years. There was a positive relationship between estimated hatch date and the residuals of the duckling mass on age regression (Hunt 1998). Later hatched young were heavier, relative to their age (n=41, r=0.54, *P*=0.001). This relationship was robust and also holds when considering broods as a whole (n=12, r=0.75, *P*=0.024).

Tributary surveys

In addition to the weekly road surveys, which covered the Lower and Mid-Maligne Rivers, we conducted a total of 100 hiking surveys of the three river sections (44 surveys) and eleven tributaries (56 surveys) over the period 1993-1997 (**Table 2**). The number of broods located varied from year to year. This likely reflects true annual variation. Evidence of breeding was found on all three river sections. Most broods were located on the upper (n=7) and lower (n=4) Maligne Rivers. The Mid-Maligne was little used, and no broods were observed there, though older broods may have travelled along the Mid-Maligne as they moved from nesting tributaries to Medicine Lake.

The effort and distribution of hiking surveys over the tributaries was not regular. Tributaries on which females, nests, or broods were seen or reported were searched most intensively, but most could be surveyed only a few times. Four of the tributaries are known to have produced broods (Warren, Evelyn, and Excelsior Creeks in this study; and on Watchtower Creek in 1992 prior to the start of this study), but no tributary is known to have produced more than one brood over the five years of the study. The upper Maligne produced broods in three of five years, and the lower Maligne in two of five years. Together they produced broods in four of the five study years. No more than one brood is known to have been produced on the tributaries as a whole in any year of the study, while the upper and lower Malignes together produced an average of 2.2 broods per year. In all, 14 broods were located, of which the upper and lower Maligne Rivers together accounted for 11, while all the tributaries together contributed three broods.

Discussion

Harlequins use most of the main Maligne watercourse, and some of its tributaries for feeding, breeding and brood-rearing. Harlequins enter the valley in early May from the Athabasca River, and numbers peak as nesting is initiated in mid-June, just after peak flow. Individual Harlequins seem highly site-specific within the Maligne Valley, but do not appear to form a closed population, as evidenced by movements to and from the nearby MacLeod River watershed.

Harlequin pairs on the Lower Maligne River defended territories, but on Medicine Lake they fed in a loose flock, as scattered pairs on Maligne Lake, and in an aggregation of up to 12 pairs in some years over a short (500m) stretch of rapids at the Maligne Lake Outlet. This complex social pattern may be related to the abundance and defendability of food resources (e.g. Richardson & Mackay 1991).

Feeding took place mostly on the lakes, but all known Harlequin nesting took place along rivers and streams, and broods appeared on Medicine and Maligne Lakes in late August. The upper and lower Maligne Rivers accounted for the majority of broods (79%) observed during the study, and we were able to locate only three broods in 56 hiking surveys of eleven tributaries.

Based on these observations, it seems the social organisation of Harlequins in the Maligne Valley consists of territorial pairs along the lower Maligne River, of single birds and pairs that feed in flocks at the MLO and Medicine Lake, and of scattered pairs on Maligne Lake. The lower and upper Maligne Rivers are the best nesting locations, but the reasons for this are unknown as yet. Tributaries, in contrast, seem to offer less desirable nesting options.

Like most sea ducks, Harlequin forage little or not at all during incubation. The intensity of feeding during the six weeks prior to laying suggests that at least part of the necessary reserve is built up on the breeding grounds. Females with no signs of breeding show no mass increase (**Figure 5**).

Bengtson & Ulfstrand (1971) reported a relationship between breeding productivity and macroinvertebrate density for Harlequins in Iceland (see also Gardarsson & Einarsson 1994). They observed the population level production of offspring was correlated with the abundance of chironomid larvae in the River Laxa, where females fed prior to nesting. However, the social system and diverse feeding habits observed in this study complicate the relationship between food availability and reproduction. Our observations suggest that at least some of the reserves for breeding are gathered during the five or six weeks of intense feeding prior to breeding, but many females feed at sites distant from their eventual breeding site, and a variety of feeding sites are utilized. While there is substantial annual variation in nestling productivity we are not yet able to relate this to the availability of food resources in the Maligne Valley, and other factors may be involved. Better knowledge of Harlequin food resources and how it relates to the variable social dispersion observed is required before any conclusions can be drawn.

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