Winter Segregation and Timing of Pair Formation in Red-breasted Merganser *Mergus serrator*

JOHNNY KAHLERT[1], MALCOLM COUPE[2] and FRED COOKE[2]

[1] National Environmental Research Institute, Dept. of Coastal Zone Ecology, Grenåvej 12, DK-8410 Rønde, Denmark

[2] Simon Fraser University, Dept. Biological Sciences, 8888 University Drive, Burnaby, B.C., V5A 1S6 Canada

During the late winter and spring of 1997, sex-ratios and pairing chronology of Red-breasted Mergansers were studied in the Fraser River Estuary, south west Canada. Until late March at one site, English Bay, there was a strong male-bias, whereas a female bias was evident at the nearby Boundary Bay. This pattern was interpreted as sexual winter segregation. At the male-biased site, antagonistic and kleptoparasitic behaviour initiated by males towards females could not account for the winter segregation. In late March and April, the sex ratios at the two study sites converged to similar values. This trait coincided with an increase in the number of courtship displays and percentage of paired birds. Although the majority of mergansers exhibited this pairing chronology, pairs were observed as early as mid-February, suggesting a gradient in the timing of pair formation. Pairs tended to segregate from flocks. If pairs are able to segregate throughout the winter, early pairing may be beneficial as food resources could be monopolised and interference with conspecifics avoided. However, the frequency of interactions with conspecifics tends to be unpredictable, since local population size fluctuated considerably.

Keywords: Red-breasted Merganser, Sex-ratio, Winter Segregation, Pair Formation, Courtship, Antagonistic Behaviour

Introduction

In populations of unpaired Anatidae, males tend to be dominant (Paulus 1983, Hepp & Hair 1984, Alexander 1987) which enables them to exclude females and immatures from the higher quality habitats (Choudhury & Black 1991). The conventional outlook regarding timing of pair formation in the waterfowl of the northern hemisphere has developed from the idea that pairing benefits the female by increasing her dominance rank, which provides enhanced foraging opportunities (Afton & Sayler 1982, Paulus 1983, Hepp & Hair 1984). By contrast,

pairing may lead to energetic costs to males, which must perform a strenuous courtship behaviour (Afton & Sayler 1982) and subsequently guard their females in the presence of unpaired males, restricting the mobility of the paired male and interrupting feeding activities (Spurr & Milne 1976, Paulus 1983, Wishart 1983).

Assuming that females benefit from pairing and suffer a cost by the use of male-biased habitats while unpaired, either in increased winter mortality or decreased reproductive output, pair formation should occur shortly after unpaired birds arrive at their wintering

grounds, in autumn and early winter (pair formation strategy one). However, if it is in the interest of individual males to participate in the exclusion of females from higher quality habitats, while it is costly to males to form pair bonds, the sexes should become spatially segregated during the winter, and pair formation should occur in late winter or early spring (pair formation strategy two). The assumptions behind the prediction of pair formation strategies suggest a conflict, if either sex try to maximise their reproductive interests (Trivers 1972). By early pairing under the above assumptions males are expected to compromise their interests.

In many diving ducks, pair formation occurs shortly before migration to the breeding grounds (Rohwer & Anderson 1988), which is in contrast to many species of dabbling ducks whose pair formation occurs in autumn or early winter. Among the late-pairing diving ducks, there are several examples of habitats, which are dominated by females during the winter, for example for Goldeneye *Bucephala clangula* and Goosander *Mergus merganser* (Nilsson 1970, Anderson & Timken 1972, Duncan & Marquiss 1993) or at least diverging from the usual pattern of strong male bias in the winter quarters, for example for Canvasback *Aythya valisineria*, Pochard *Aythya ferina*, Bufflehead *Buchaphala albeola*, Lesser Scaup *Aythya affinis*, Ring-necked Duck *Aythya collaris* and Ruddy Duck *Oxyura jamaicensis* (Nichols & Haramis 1980, Bergan & Smith 1989, Carbone & Owen 1995). Habitats with a bias towards females, as well as habitats with strong male bias which cannot be accounted for by the male biased sex ratio of the population, are indications of sex class segregation.

If sex class segregation during the winter is a result of males excluding females from good foraging habitats (Nichols & Haramis 1980), we would predict that females in male-biased habitats would be subject to antagonistic and kleptoparasitic behaviour rather than courtship displays. We would further predict that adult males would initiate more antagonistic and kleptoparasitic interactions towards females than females would towards males. We would

also expect males to be more successful in these interactions, either by chasing females away or by stealing prey items from them.

In this study, sex ratios during the non-breeding season and timing of pair formation were studied in an unmarked population of wintering Red-breasted Merganser *Mergus serrator*. The aim was to determine whether one of the proposed pair formation strategies is an accurate description of its behaviour. In order to test whether adult male dominance is the cause of sex class segregation, we recorded incidences of antagonistic behaviour and kleptoparasitism.

Methods

Counts and sex ratio estimation

The study was conducted at two sites in the Fraser River Estuary of British Columbia, Canada. English Bay and Boundary Bay are approximately 30 km apart (**Figure 1**). Boundary Bay comprises relatively shallow water (< 4 m), whereas the deeper parts of English Bay extend down to 20 m, areas which were frequently visited by the mergansers.

In 1997, English Bay was visited 28 times during mornings from sunrise and three hours ahead in the period 17 February to 24 April. Boundary Bay was visited nine times in the late morning between 22 February and 23 April. Observations were conducted as a series of point counts from strategic positions along the coastline (points, bridges *etc.*). The water surface was scanned slowly in order to give full observational coverage to the entire point count area. All Red-breasted Mergansers were counted, and if possible aged and sexed using a 20-60 x telescope. Double counts were minimised by noting the movements of mergansers.

The Red-breasted Merganser acquires breeding plumage in November-December (eg Palmer 1962), yet adult females and immature birds ('brown heads') may be difficult to distinguish at a distance and in poor light. One identification mark which appears to be reliable for adult females is a blackish spot around the
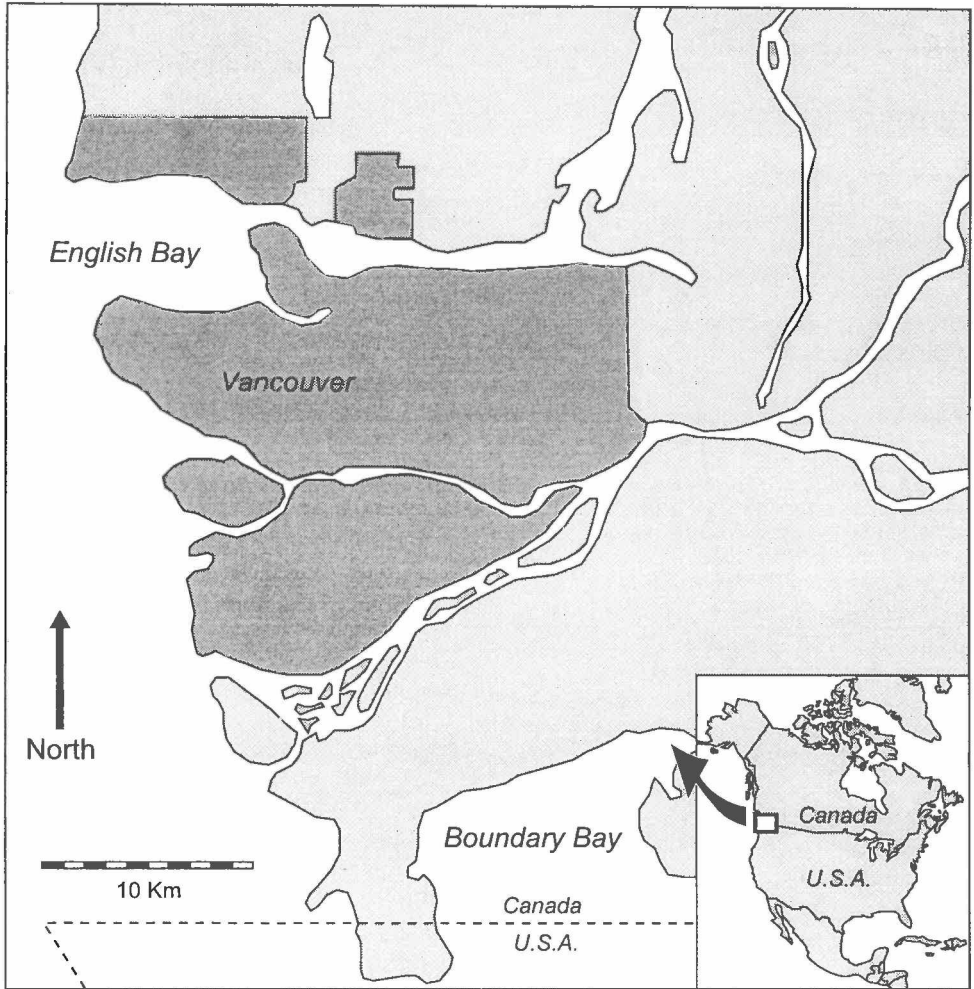
Figure 1. Map showing the position of the two study areas near Vancouver, British Columbia.

eye which sometimes extends along the forehead. Examination of museum specimens collected 1 January to 30 April in British Columbia, Greenland and Denmark showed that this trait was likely to be diagnostic. Only one out of 24 examined adult females had no black spot and this was a Danish bird from before 14 February, ie before the study period.

A proportion of 'brown-headed' birds could not be sexed and aged due to poor observation conditions. In order to estimate the number of females present, a model was used which incorporated the number of females and immatures observed, and the number of undetermined adult females or immatures (hereafter referred to as IF's). Assuming that the probability of identifying an IF as an immature or an adult female is a linear function of their respective frequencies in the count population, we predicted:

$$F_{tot} = F_{obs} + IF_{unk} \left(\frac{F_{obs}}{F_{obs} + I_{obs}} \right) \quad (1)$$

Where F_{tot}= total number of adult females, F_{obs}= number of observed adult females, I_{obs}= number of observed immatures and IF_{unk}= number of birds which could not be aged or sexed.

The sex ratios were calculated thus:

$$\frac{F_{tot}}{M_{tot}} \quad (2)$$

Where M_{tot} represents the total number of adult males.

Pairing chronology

A flock was defined as a unit of mergansers, that stayed close together (< 50 bird lengths) for a period of at least two and a half minutes during a five-minute focal sampling period. Within a flock, a pair was defined as an adult male and female which exihibited synchronised behaviour during the entire focal sampling period (five minutes). Observations of copulation events, and adult males consistently guarding females against males were also interpreted as being indicative of a pair bond. Mate-guarding was exhibited either as swim-guarding, in which the male consistently placed himself between the female and another male, or as aggressive behaviour such as charging and bill threats.

The pairing chronologies were prepared by plotting the proportion of females in pair bonds for each date of observation. It was considered that the difficulty of distinguishing adult females from immatures had the potential to lead to an underestimation of the number of pairs. For example, flocks of IF's with no adult males cannot be paired, but a flock consisting of an adult male and an IF may have been a pair. Therefore, the number of pairs in each point count had to be modelled. All observed combinations of IF's and adult males were included in the model, but groups of one male and one IF were the only compositions to contribute to an increase in the suggested total number of pairs. Therefore, the model could be written:

$$P_{tot}=P_{obs}+MIF_{seg}\left(\frac{P_{seg}}{P_{seg}+MIseg}\right) \quad (3)$$

Where P_{tot}= total number of pairs, P_{obs}= observed number of pairs, MIF_{seg}= number of flocks with one adult male and one IF, P_{seg}= number of flocks consisting of a pair, and $MIseg$= number of flocks consisting of an adult male and an immature.

Interactions between unpaired males and unpaired females

In order to determine the effect of the presence of each sex on the behaviour of unpaired individuals before and during the pairing process, the response of unpaired individuals was assessed for individual mergansers sitting in the same flock as conspecifics of the opposite sex. Three response types, namely antagonistic behaviour, courtship and no response, were noted during focal observations for periods of five minutes. At English Bay the response types of 105 unpaired males and 15 females were sampled.

Antagonistic behaviour was defined as swimming raids with bill charging towards conspecifics. Kleptoparasitism was noted when an individual brought prey to the water surface and other mergansers tried to steal the prey. In all incidents of antagonistism and kleptoparasitism, the initiator of the behaviour, the recipient and the outcome (win/defeat) was noted. A win was defined as an initiator, which stimulated the recipient to escape, or as an initiator, which succeeded in stealing a prey from the recipient. A defeat was assigned to events where the initiator escaped or did not succeed in stealing prey.

Courtship behaviour included head jerks and nods, air-pointing bill and head withdrawal, water kicking and display-skating (Johnsgard 1965). Courtship behaviour tended to occur in large flocks. Thus, the sex and age class composition of these flocks was noted in order to test whether the presence of a particular sex or age class stimulated unpaired males to exhibit courtship displays. The response

variable (presence or absence of courtship) was tested in a logit model with different categories of mergansers as independent variables.

Results

Seasonal count trends and sex ratio

Total numbers of Red-breasted Mergansers fluctuated throughout the study period in both study areas (**Figure 2**). There were other occupied merganser habitats within short distances of English Bay and Boundary Bay, hence a great potential for local movement. Furthermore, the latter part of the study period coincided with spring migration from more southerly habitats to the breeding grounds in the arctic and subarctic (Campbell *et al.* 1990). Thus, migrants may also have contributed to the observed fluctuation in numbers.

Despite these fluctuations in numbers and possible turnover of flocks, the sex ratio showed a rather consistent pattern in both study areas. In February and early March, English Bay was dominated by males, whereas Boundary Bay held a majority of females (**Figure 3**). From late March onwards, the sex ratios converged to similar values (0.6:1.0). At English Bay, this change was facilitated by an increase in the number of females whereas the number of males remained relatively constant throughout the study period (see **Figure 2**). At Boundary Bay, the number of adult males

increased while the number of females was relatively constant (**Figure 2**).

Pairing chronology

At English Bay, pairs were present in small numbers during February (**Figure 4**). The pairs were likely formed between flight feather moult (in early autumn) and late winter. However, the rate of pair formation increased from late March onwards. A comparison of the pairing chronology with the seasonal trends in sex ratio (**Figure 3**) showed that the highest rate of increase in the percentage of pairs occured simultaneously with the convergence of the sex ratios at English Bay and Boundary Bay.

At English Bay the percentage of paired individuals was significantly lower for males than for females (comparison of intercepts between cubic regression lines on arcsine-transformed data: $t_{7,1147}=7.14$, $P<0.0001$, **Figure 4**). This may indicate that some males were unable to pair due to a general male bias in the population (see **Figure 3**). At Boundary Bay, such a difference was not detected (comparison of intercepts $t_{7,122}=1.16$, $P<0.25$; all slopes were equal: P-values between 0.05 and 0.07).

Pairs segregated from larger flocks; 61% ($n=114$) of all pairs were seen in groups of one male and one female. For comparison, 'flocks' with solitary males constituted 30% ($n=303$) of all flocks with unpaired males ($x^2=35.20$, DF=1, $P<0.0001$), and solitary females constituted 33% ($n=70$) of all flocks with unpaired females ($x^2=14.14$, DF=1, $P<0.0002$).

Table 1. Maximum likelihood ANOVA of presence or absence of courtship behaviour for unpaired males in the presence of other unpaired males (male **UPD**), unpaired females (female **UPD**) or pairs.

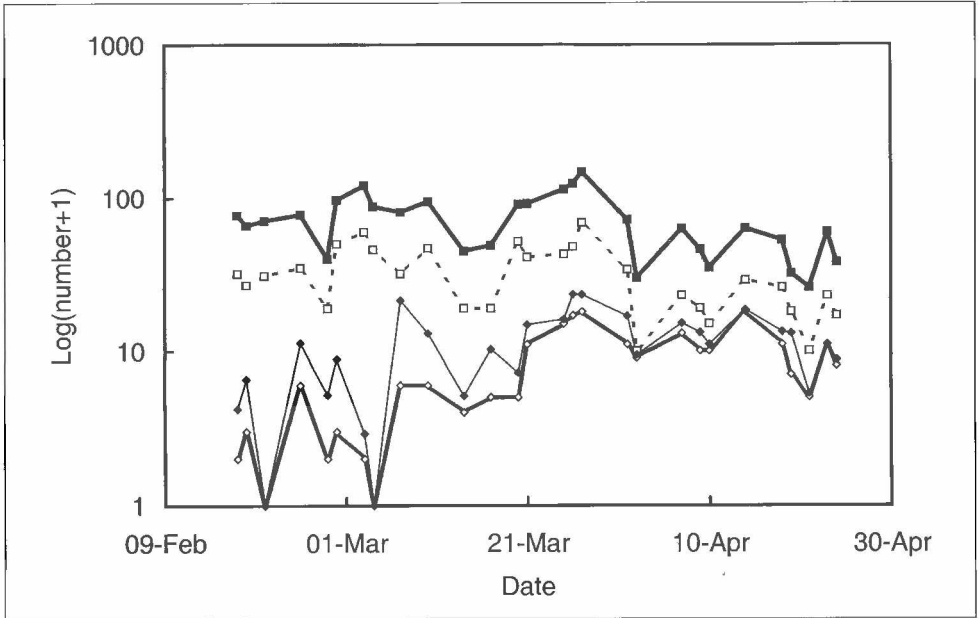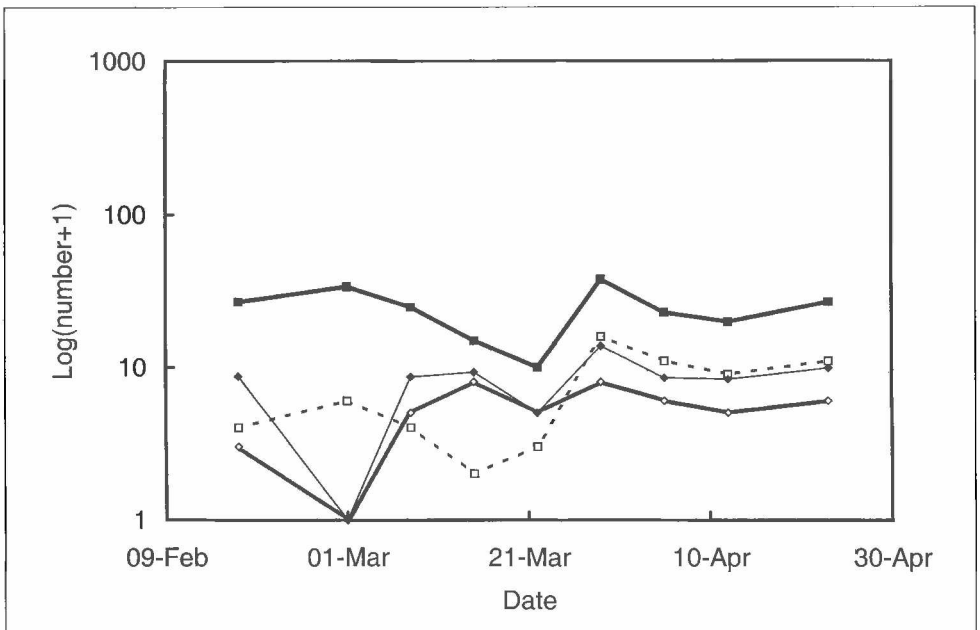| Presence of	x^2	P
Male UPD	0.02	0.88
Female UPD	12.05	0.0005
Pair	0.11	0.74
Likelihood ratio	1.07	0.90

Figure 2. Total number of Red-breasted Mergansers in English Bay (upper) and Boundary Bay (lower) from February to April 1997 broken down by males and females. Estimated number of females were based on equation (1). For clarity numbers were presented on a log scale.
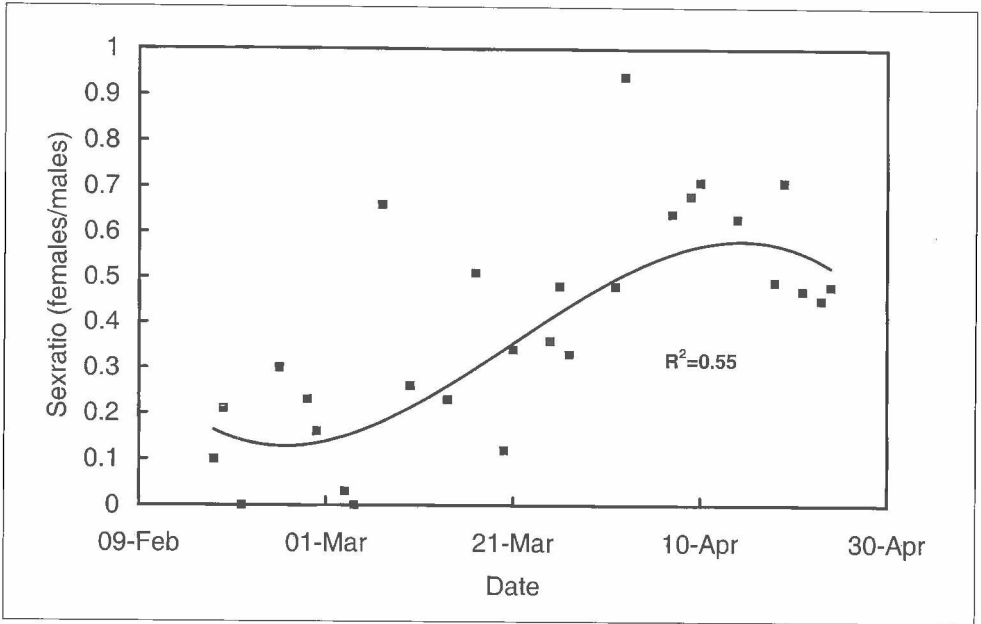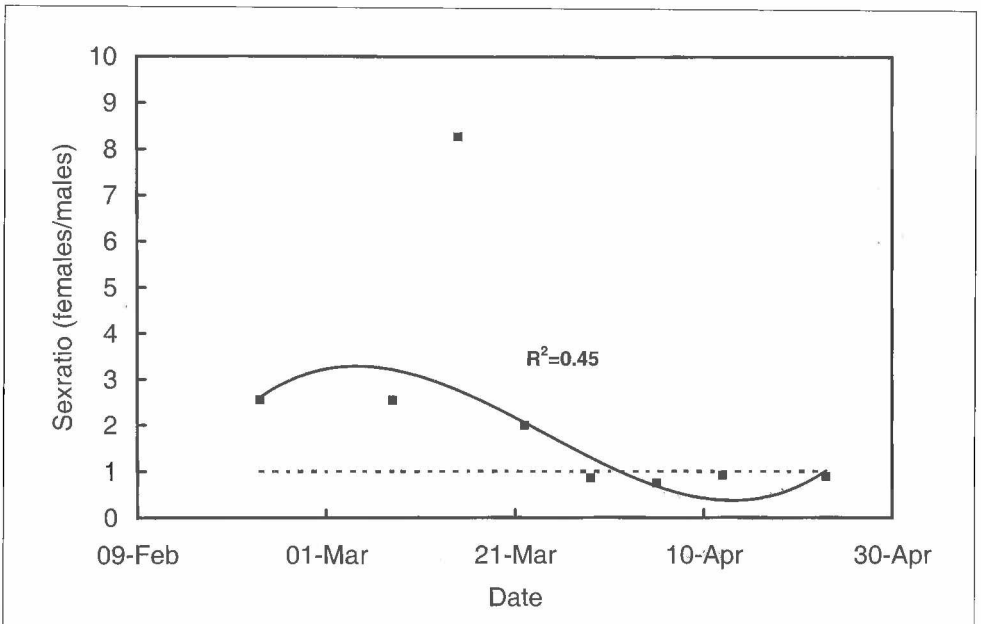
Figure 3. Sex ratio in Red-breasted Mergansers in English Bay (upper) and Boundary Bay (lower), February to April 1997. Cubic regression lines weighted by the denominator.
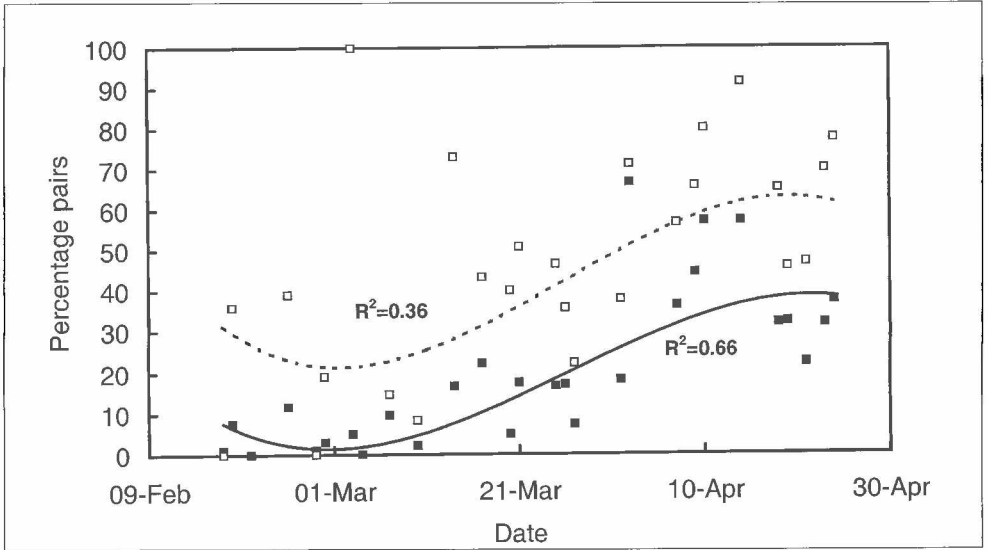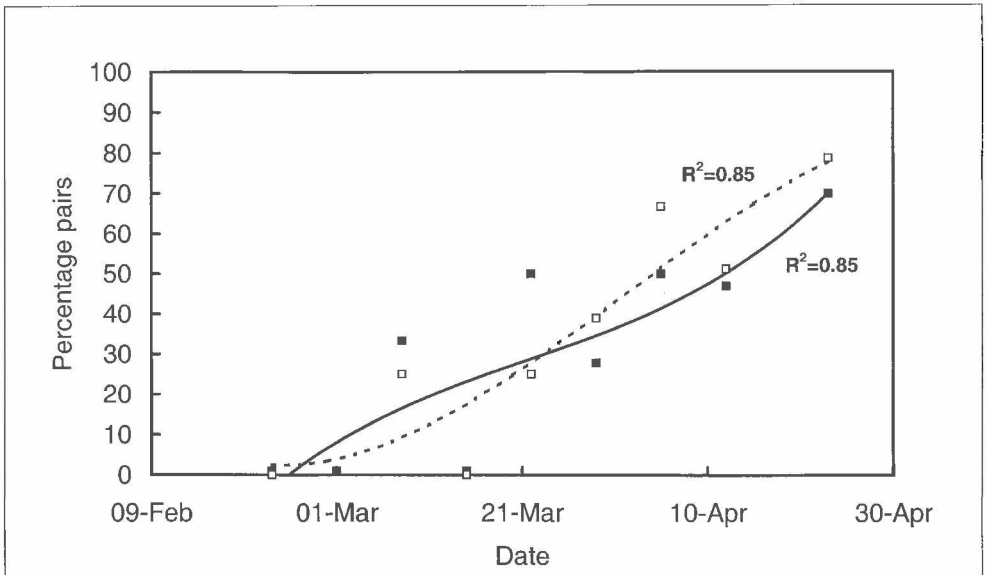
Figure 4. Percentage of merganser paired males to total number of males, and percentage paired females to total number of females in English Bay (upper) and Boundary Bay (lower), February to April 1997. Cubic regression lines for males (solid) and females (dashed) weighted by the denominator.

Antagonistic, kleptoparasitic and courtship behaviour

Unpaired males initiated antagonistic behaviour against unpaired females twice during the focal behaviour sampling. This translates to 0.89 events/hour, n=27 focal samples (**Figure 5**). One attack was considered unsuccessful as the female responded by attacking the male. In another incident, an unpaired female initiated antagonistic behaviour towards an unpaired male and was considered to have won the contest (**Figure 5**).

Kleptoparasitism initiated by unpaired males towards unpaired females was not observed. However, two incidents (0.47 events/hour, n=51 focal samples) were noted in which unpaired males kleptoparasitised IF's (immature/female). In one of these cases, the male succeeded by stealing the prey item. Unpaired females never initiated kleptoparasitic behaviour.

Courtship behaviour among unpaired males occurred significantly more in the presence of unpaired females (5.78 events/hour, n=27 focal samples) compared to the presence of other conspecifics (v. 1.54 events/hour, n=78 focal
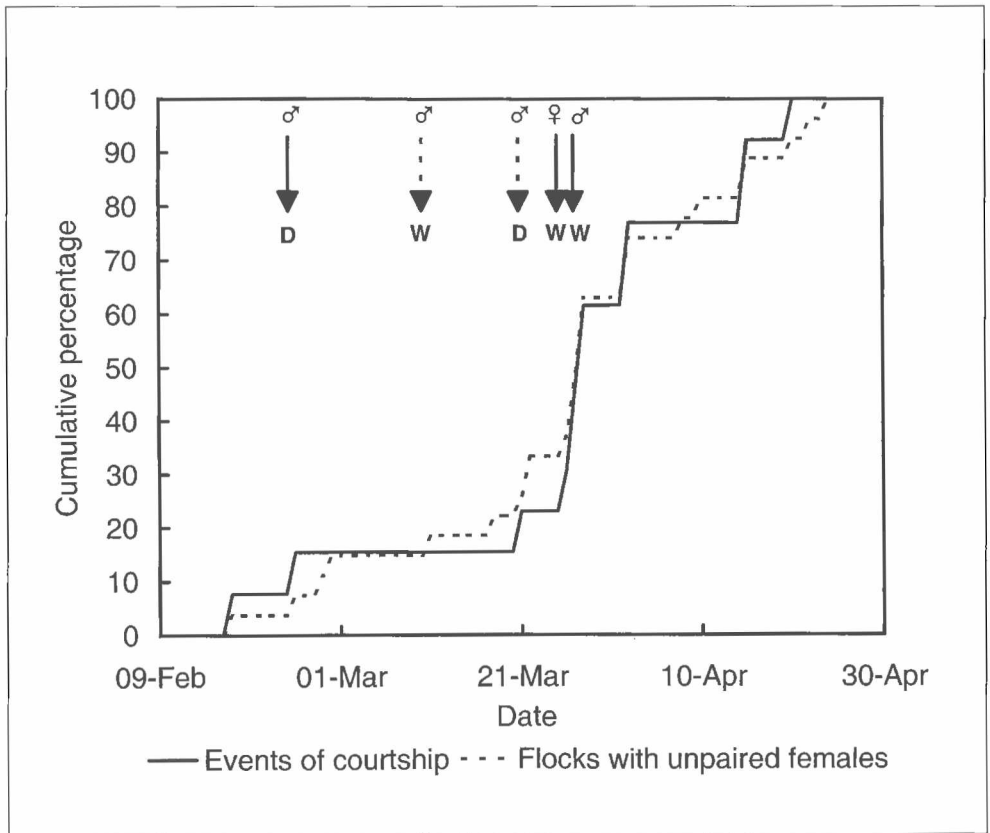

Figure 5. Cumulative percentage number of courtship events exhibited by unpaired males compared to the cumulative percentage number of flocks with unpaired females, February to April 1997. Arrows denote events of antagonistic (solid) and kleptoparasitic (dashed) behaviour iniated by unpaired males (♂) and unpaired females (♀). The outcome is denoted by 'W' or 'D' to define win or defeat outcomes.

samples; **Table 1**), and we suggest that unpaired females acted as a stimulus to initiate this behaviour. The presence of courtship behaviour at the male-biased habitat at English Bay during February suggests that unpaired males were ready to pair when unpaired females appeared. In fact, the presence of courtship behaviour showed no seasonal trend other than was expected from the presence of females (x^2=0.37, DF=2, P=0.83, Kolmogorov-Smirnov Test; **Figure 5**).

Discussion

This study confirmed that the Red-breasted Merganser is a late pairing species (Cramp & Simmons 1977, Johnsgard 1978). The main period for pair formation was initiated by the end of March. Before pair formation, sexual segregation was observed, and therefore the behaviour for the majority of Red-breasted Mergansers complied with pair formation strategy two. The convergence of sex ratios at the two habitats occurred simultaneously with the commencement of pair formation. This is compatible with both sexes seeking mates at the same time. However, a study involving marked birds will be necessary to show the extent and direction of mate-seeking movement by each sex.

The suggestion that sex class segregation should be a result of antagonistic or kleptoparasitic behaviour from unpaired males imposed on females was not supported. Assuming that courtship behaviour is the prelude to pairing, the unpaired males showed willingness to pair when encountered by an unpaired female rather than being aggressive, even in February (see also Johnsgard 1978).

A recent study by Platteuw & van Eerden (1997) suggested that sex class segregation may result from a sexual dimorphism among mergansers, which enables the males to perform deeper dives and exploit more profitable food resources. Although based on restricted data this may apply to the present study, as males constituted the majority in the deeper English Bay, whereas in the shallower Boundary Bay showed a female bias before the main period of pairing.

Other alternative explanations of sex class segregation related to climatic conditions (Carbone & Owen 1995) or male advantages of being closer to the breeding grounds (Anderson & Timken 1972) are unlikely to be applicable in the present scenario, as the male and female-biased habitats were only 30 km apart.

As already emphasised the majority of mergansers complied with a strategy of sex class segregation during the winter and late pairing. However, variation in the timing of pair formation was observed, suggesting that timing of pair formation should rather be considered as a gradient. A few paired birds were already apparent in mid-February, one month before the main pair formation period. This, together with observations of unpaired females showing up at the male-biased habitat at English Bay, and unpaired males appearing at the female-biased Boundary Bay, suggests that some individuals do not comply with the conventional pair formation strategy for Red-breasted Merganser.

There are potential advantages of early pairing. Weller (1967) suggested that early pairing prolongs the period of mate testing, and Paulus (1983) suggested that early pairing in Gadwall allows the male to defend high quality food resources on the female's behalf. The first of these hypotheses remains rather speculative in this context, whereas resource defence may be an option in early paired mergansers. Thus, 61% of the pairs were segregated from other flocks of mergansers. This could be interpreted as territoriality, as was also suggested for Barrow's Goldeneyes (Savard 1988), and the potential that food resources could be monopolised.

However, pair segregation and aggressive behaviour may also be interpreted as avoidance of interference with conspecifics. For pairs in a male-biased habitat, with high density of unpaired males, the best solution may be to segregate from conspecifics at the flock level. If pair segregation is possible, then early pairing may be less costly to the male, because the frequency of interactions with unpaired males will be reduced. However, the frequency of interactions may be quite unpredictable, as local population size fluctuated. For example, in late

February the numbers trebled in four days. This unpredictability may explain why pair formation among mergansers in the Fraser River Estuary is highly synchronised to a period close to the breeding period and why early pairing is such a rare event.

References

Afton, A.D. & Sayler, R.D. 1982. Social courtship and pairbonding of Common Goldeneyes *Bucephala clangula*, wintering in Minnesota. *Can. Field Nat.* 96:295-300.

Alexander, W.C. 1987. Aggressive behavior of wintering diving ducks *Aythyini*. *Wilson Bull.* 99:26-29.

Anderson, M.W. & Timken, R.L. 1972. Sex and age ratios and weights of Common Merganser. *J. Wildl. Mgmt* 36:1127-1133.

Bergan, J.F. & Smith, L.M. 1989. Differential habitat use by diving ducks wintering in south Carolina. *J. Wildl. Mgmt.* 53:1117-1126.

Campbell, R.W., Dawe, N.K., McTaggart-Cowan, I., Cooper, J.M., Kaiser, G. & McNall, M.C.E. 1990. *The Birds of British Columbia* Vol. 1. Royal British Columbia Museum.

Carbone, C. & Owen, M. 1995. Differential migration of the sexes of Pochard *Aythya ferina*: results from a European survey. *Wildfowl* 46:99-108.

Choudhury, S. & Black, J.M. 1991. Testing the behavioural dominance and dispersal hypothesis in Pochard. *Ornis Scand.* 22:155-159.

Cramp, S. & Simmons, K.E.L. 1977. *Handbook of the Birds of Europe, the Middle East and North Africa; the Birds of the Western Paleartic. Vol. 1.* Oxford Univ. Press, Oxford.

Duncan, K. & Marquiss, M. 1993. The sex/age ratio, diving behaviour and habitat use of Goldeneye *Bucephala clangula* wintering in northeast Scotland. *Wildfowl* 44:111-120.

Hepp, G.R. & Hair, J.D. 1984. Dominance in wintering waterfowl *Anatini*: effects on distribution of sexes. *Condor* 86:251-257.

Johnsgard, P.A. 1965. *Handbook of waterfowl behaviour.* New York.

Johnsgard, P.A. 1978. *Ducks, Geese and Swans of the World. Univ. of Nebraska Press.* Lincoln and London.

Nichols, J.D. & Haramis, G.M. 1980. Sex specific differences in winter distribution of Canvasbacks. *Condor* 82:406-416.

Nilsson, L. 1970. Local and seasonal variation in sex-ratios of diving ducks in South Sweden during the non-breeding season. *Ornis Scand.* 1:115-128.

Palmer, R.S. 1962. *Handbook of North American Birds.* New Haven.

Paulus, S.L. 1983. Dominance relations, ressource use, and pairing chronology of Gadwalls in winter. *Auk* 100:947-952.

Platteuw, M. & van Eerden, M.R. 1997. Sex-dependent differences in exploitation of fish stocks in Red-breasted Mergansers Mergus serrator utilising a two-prey system in winter. In: van Eerden, M.R. *Patchwork: patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands.* Published Ph.D.-thesis. Rijkswaterstaat, Lelystad, The Netherlands. Pp. 403-420.

Rohwer, F.C. & Anderson, M.G. 1988. Female-biased philopatry, monogamy and the timing of pair formation in migratory waterfowl. *Current Ornithol.* 5:187-221.

Savard, J.-P. 1988. Winter, spring and summer territoriality in Barrow's Goldeneye: characteristics and benefits. *Ornis Scand.* 19:119-128.

Spurr, E. & Milne, H. 1976. Adaptive significance of autumn pair formation in the Common Eider *Somateria mollissima. Ornis Scand.* 7:85-89.

Trivers, R.L. 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.). *Sexual selection and the descent of man, 1871-1971.* Chigaco, pp. 136-179.

Weller, M.W. 1967. Courtship of the Redhead *Aythya americana. Auk* 84:544-559.

Wishart, R.A. 1983. Pairing chronology and mate selection in the American Wigeon *Anas americana. Can. J. Zool.* 61:1733-1743.