Brood amalgamation in Surf Scoters *Melanitta perspicillata* and other Mergini

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Brood amalgamation is frequent within the Tribe Mergini. We quantified amalgamation in the Surf Scoter (Melanitta perspicillata) by a combination of observations on marked and unmarked broods at Lake Malbaie, Québec. Brood amalgamation was frequent, especially when brood density was high. Broods, amalgamated or not, were always tended by a single female. Lone females sometimes associated with broods for short periods of time, but occasionally threatened and attacked young. Most often, lone females were chased off by the attending female. Females with young did not try to attract other young and were quite aggressive towards strange young. No behaviour suggesting any voluntary abandonment of young by females was observed. Brood amalgamation in this population apparently occurred accidentally, presumably favoured by crowding, a variable level of aggressiveness between females and apparently weak female-young bonds. A review of the literature on brood amalgamation in the tribe Mergini supports these findings.

Keywords: Crèching, Brood Amalgamation, Surf Scoter

Brood amalgamation (sometimes called crèching or brood mixing) occurs when the young of some broods become mixed with the offspring of others during the rearing period. It is common within the Tribe Mergini and has been well documented in the Common Eider (*Somateria mollissima*; Munro & Bédard 1977a), Barrow's Goldeneye (*Bucephala islandica*; Savard 1987, Eadie & Lyon 1998) and Bufflehead (*Bucephala albeola*; Savard 1987), Shelduck (*Tadorna tadorna*; Williams 1974, Patterson 1982) and White-winged Scoters (*Melanitta fusca*; Kehoe 1986). Several hypothesis have been proposed to explain the phenomenon (Eadie et *al.* 1988, Beauchamp 1997). Two main lines of thought have developed to explain brood amalgamation. Firstly, the accidental mixing hypothesis suggests that the behaviour is accidental, due in part to crowded conditions, and is facilitated by various disturbances. It results from the accidental mixing of broods before the development of strong mother-young bonds (Munro & Bédard 1977a, 1977b, Williams 1974, Patterson et *al.* 1982). The second line of thought incorporates several hypotheses which more or less assume that some females abandon their young to the care of other females and that such behaviour is adaptive by enhancing the survival of the donating female and/or that of the abandoned young and/or the survival of the young of the receiving female (Eadie et *al.* 1988, Afton & Paulus 1992, Bustness & Erikstad 1991, Poysa 1995, Hori 1964a, 1964b, 1969, Gorman & Milne 1972). Proximate and ultimate causes of brood amalgamation are still highly argued (Bustness & Erikstad 1995, Poysa 1995, Eadie & Lyon 1998).

Brood amalgamation has been reported in Surf Scoters (*Melanitta perspicillata*; Savard & Lamothe 1991) but detailed studies were lacking. The discovery of a lake with over 30 pairs just 95 km north-north-east of Québec city provided an opportunity to study brood

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amalgamation in the species (Reed *et al.* 1994).

The objectives of our study were: 1) to compare the frequency of brood amalgamation in Surf Scoters at Lake Malbaie and in the centre of their breeding range; 2) to document the dynamic of brood amalgamation at Lake Malbaie; 3) to briefly review published literature on brood amalgamation.

Study area

Most observations were conducted at Lake Malbaie (47°34'N, 71°00'W) in the Laurentide Wildlife Reserve, 95 km north-north-east of Québec City. It is the most southerly known breeding location (Savard *et al.* 1998). Two wooded islands are found on this 664 ha lake. The lake is shallow, with about 70% of its water area less than 2 m deep. It is located within a mountainous enclave located 820 m above sea level characterised by high boreal plant communities typically found farther north (Richard, 1975). Lake Malbaie supports a healthy endemic brook trout (Salvelinus fontinalis) population and is frequented by an average 3,500 anglers each year. A maximum of 59 and 68 pairs of Surf Scoters were seen on the lake in 1995 and 1996 (Morrier *et al.* 1997). Intensive observations were conducted at lake Malbaie in 1994-1996.

Additional observations were conducted in 1995 in a 9400 km^2 study area in north-central Québec (54°N, 72°N). This area is within the typical high boreal forest breeding range of the species and is characterised by the presence of numerous lakes of various dimensions (Bergeron *et al.* 1996, Decarie *et al.* 1995)

Methods

Surf Scoters were captured with mist nets on Lake Malbaie or trapped on the nest (Lesage *et al.* 1997). Adult females were fitted with nasal disks or marked with colour paint on the back of the head (Morrier *et al.* 1997). Clutch size in Surf Scoters averaged 7.5 ± 0.2 eggs, n=14; range (six to nine eggs). Most nests had either seven or eight eggs, only one nest had six eggs and only one nine eggs (Morrier *et al.* 1997). Because most marked clutches (4 of 5) lost young before they were first seen on the lake we considered broods with ≥ 9 young as amalgamated broods.

The behaviour of hens and broods was observed with a spotting scope and binoculars from blinds hidden on shore or on the islands. In 1994, brood behaviour was recorded incidentally to time budget data but in 1995 and 1996 broods were observed solely to record agonistic interactions. For each interaction we noted the identity of the aggressor and the victim, and the intensity of the interaction. Interactions were classified as threat only, or as threat with a rush toward the victim. Complex interactions such as brood mixing were often recorded on tape and later transcribed so as to better focus on the interaction. Over the three years of the study we accumulated 118 hours of brood observations and witnessed several occurrences of brood mixing and amalgamation. Brood surveys were conducted by boat at Lake Malbaie (every two days in 1994, daily in 1995-96), noting marked females and recording the number of ducklings and their approximate age (Lesage *et al.* 1996) in each brood.

In the remote north-central study area our observations were limited to brood surveys. A survey was conducted by helicopter on 11-21 July 1995, covering all wetlands in ten 10 x 10 km plots (Bergeron *et al.* 1996).

Results

Brood amalgamation, as indicated by the occurrence of abnormally large broods (≥ 9 ducklings), was frequent on Lake Malbaie, especially in 1995 when brood density was high (**Table 1**) but was also observed in 1994 and 1996 at lower density. In our high boreal forest study area, where brood densities were low, only 3% of 33 broods observed in 1995 were classified as amalgamated (**Table 1**).

Although the presence of these large broods is a good indication that brood amalgamation occurred, it underestimates the true frequency of exchange of young between broods because even small broods may contain young from more than one family. At Lake Malbaie, we witnessed at least five brood mixings that

Table 1. Abundance of Surf Scoter broods and frequency of amalgamation at Lake Malbaie and a more northerly study area in Québec during the month of July.

	Lake Malbaie			North-Central Québec
	1994	1995	1996	1995
Maximum number of broods seen during a given survey	11	29	12	33[1]
Maximum number of broods seen with more than 8 young	2	10	3	1
% amalgamated	18	34	25	3
Maximum number of young seen	79	233	71	143
Mean number of young per survey (*n* = number of surveys ; ± standard error)	63.5±2.3 n= 5	165.9±14.4 n = 14	45.2±5.3 n = 6	143 n=1
Maximum number of lone females	65	44	64	9
Mean number of lone females per survey (n = number of surveys)	55.0±3.5 n = 5	34.9±2.0 n = 14	59.1±2.2 n = 6	9 n=1

During a single survey, 33 broods were observed on 28 different lakes and ponds.

resulted in the exchange of only one or two ducklings between broods. During surveys of the lake, we recorded considerable day-to-day variation in the number of broods and young (**Table 2**), suggesting also that exchange of young occurred frequently. Exchange of young between broods occurred in young and old broods (**Tables 2-3**). Production of young on the lake varied considerably among the three years of the study and amalgamation was most prevalent in 1995 when brood density and abundance of young were highest. The number of young observed in broods with more than eight young represented a maximum of 53% of the young in 1994, 66% in 1995 and 64% in 1996.

During the three years of study we followed 10 broods with marked females (**Table 3**). They revealed a variety of amalgamations and confirmed the high frequency of exchange of young in some broods as well as the stability in others. Because of the frequency of brood surveys, we can safely assume that our initial observation of these broods occurred within two days of hatching.

Female B in 1994 was quite unusual. She hatched seven young and a few days later on 11 July had 12 young, 15 on 13 July and 33 on 15 and 18 July. That female was unusually aggressive and showed stronger maternal bonds than several other females with young that we attempted to drive trap. Females C and G in 1995 and J in 1996 are examples of females that apparently raised single (presumably their own), normal-sized (accounting for natural attrition) broods. Most frequently, amalgamations occurred within the first week following hatching (Female B, E, H, I, **Table 3**) although the exchange of young between

Table 2. Variations in productivity, brood numbers and brood sizes between years and between surveys at Lake Malbaie, Québec.

		Broods with 1-8 young		Broods with >8 young			
Survey Date	Total No Young	No of broods	No of young	No of broods	No of young	Actual brood size	% young amalgamated
1994							
7 July	8	1	8				0
8 July	20	4	20				0
11 July	57	8	45	1	12	12	21
18 July	79	9	37	2	42	9-33	53
26 July	58	9	33	1	25	25	43
3 August	74	9	43	1	31	31	42
9 August	74	7	45	1	29	29	39
1995							
4 July	51	8	42	1	9	9	18
5 July	103	10	56	4	47	9-10-13-15	46
8 July	146	15	71	6	75	10-11-11-12-15-16	51
11 July	215	14	73	10	142	9-9-9-9-10-12-17-17-18-32	66
14 July	233	19	81	10	152	9-9-10-11-12-12-13-16-20-40	65
16 July	221	17	87	8	134	11-11-12-13-13-14-20-20	61
19 July	199	15	76	8	123	9-9-10-11-14-14-21-35	62
22 July	201	21	92	7	109	10-11-11-16-17-22-22	54
1996							
10 July	14	2	14				0
12 July	23	5	23				0
14 July	42	5	27	1	15	15	36
15 July	71	9	38	2	33	14-19	46
17 July	56	10	32	2	24	10-14	43
19 July	43	5	19	2	24	9-15	56
29 July	48	6	21	2	27	11-16	56
31 July	59	7	21	3	38	10-11-17	64

broods continued throughout the season (**Table 2**).

Broods were always tended by a single female whether they had amalgamated or not. At Lake Malbaie, females with broods were not territorial but tended to concentrate their activities in a given area of the lake for weeks at a time. Several broods used the same sectors simultaneously. Nevertheless aggression between females with broods was rare and broods tended to tolerate each other. When two broods came in close proximity, aggression of the female was usually directed at the intruding young rather than at the other female. However a female would sometimes attack a female that had attacked her young, limiting the attack to a simple chase rarely accompanied by physical contact. The most aggressive encounter we witnessed was with a female Common Goldeneye *Bucephala clangula* with young that had attacked one of the Surf Scoter young. The female scoter rushed the female goldeneye on several occasions before leaving the goldeneye territory.

Table 3. Marked Surf Scoter females with young in Lake Malbaie, Québec: changes in brood size throughout the season.

	1994A		1994B		1995C		1995D		1995E		1995F		1995G		1996H		1996I		1996J	
No. of eggs hatching	?		7		?		8		8		?		6		8		8		9	
	Date	No of young	Date	No of young	Date	No of young	Date	No of young	Date	No of young	Date	No of young	Date	No of young	Date	No of young	Date	No of young	Date	No of young
	7/7	7	14/7	12	8/8	3	4/7	7	6/7	8	13/7	11	7/7	5	9/7	0	12/7	7	14/6	7
	18/7	7	14/8	12	8/8	3	4/7	7	6/7	8	13/7	11	7/7	5	9/7	0	12/7	7	14/7	7
	19/7	7	15/7	33	11/8	2	6/7	7	8/7	4	15/7	8	10/7	4	15/7	14	12/7	5	16/7	4
	20/7	7	18/7	33	12/8	2	7/7	6	10/7	15	16/7	7	11/7	6	17/7	14	15/7	6	17/7	4
	22/7	7	20/7	31	14/8	2	8/7	12	11/7	5	17/7	9	12/7	0	18/7	14	17/7	5	18/7	4
	1/8	7	26/7	25	15/8	2	10/7	7	12/7	21	18/7	7	13/7	4	19/7	15	18/7	6	19/7	3
	2/8	6	27/7	25	16/8	2	11/7	8	13/7	22	18/7	6	14/7	4	29/7	16	18/7	9	25/7	3
	3/8	8	30/7	25	17/8	2	12/7	9	14/7	11	22/7	7	15/7	4	31/7	17	25/7	11	31/7	3
	3/8	7	2/8	26	18/8	2	13/7	7	15/7	16	25/7	7	18/7	4	6/8	17	29/7	11		
	4/8	3	3/8	31	19/8	2	14/7	5	16/7	8	27/7	2	19/7	4			31/7	11		
	5/8	8	4/8	31	21/8	2	15/7	7	17/7	9	28/7	7	21/7	4			6/8	11		
	9/8	7	9/8	29	22/8	2	16/7	8	18/7	11	1/8	6	24/7	4						
	11/8	6	11/8	27	24/8	3	17/7	8	21/7	3	2/8	7	25/7	4						
	15/8	8	15/8	8	25/8	2	19/7	3	22/7	3	3/8	7	26/7	4						
	18/8	7	18/8	19	26/8	2	22/7	11	24/7	5	4/8	7	27/7	4						
	22/8	6	25/8	2	27/8	2	24/7	7	25/7	4	7/8	7	28/7	4						
	25/8	6	26/8	24	28/8	2	25/7	8	26/7	3	9/8	7	31/7	4						
	26/8	7			31/8	2	26/7	6	27/7	12	10/8	7	1/8	4						
					1/9	2	27/7	6	31/7	2			4/8	4						
					2/9	2	28/7	6	1/8	2			7/8	5						
							1/8	6	4/8	1			8/8	3						
							2/8	5					8/8	4						
							3/8	6					10/8	3						
							4/8	6					14/8	4						
							8/8	6					18/8	3						
							9/8	6					23/8	4						
							10/8	7												

Table 4. Aggressive behaviour of Surf Scoters during brood rearing at Lake Malbaie, Québec.

Year		1994		1995		1996		TOTAL	
Length of observations (hours)		67[1]		27		24			
Aggressor	Victim	T[2]	A[3]	T	A	T	A	T	A
Female with young	Female with young	1	3	18	7		2	19	12
	Lone female	5	42	14	11	73	72	92	125
	Young		27	48	93	8	3	56	123
Lone female	Female with young			1				1	
	Lone female			1				1	
	Young	3	12	6	13	10	36	19	61

[1] Brood time budgets were done in 1994 so that most observations dealt with single brood whereas in 1995 and 1996 observations were directed at aggressive interactions. This likely explains the low number of interactions observed in 1994.

[2] Simple threat.

[3] Threat followed by an attack.

We observed 509 aggressive interactions during 118 hours of observations of Surf Scoter broods at Lake Malbaie (**Table 4**). Attacks varied in intensity from short chases to physical contacts. Physical contacts occurred mostly during encounters between females and young where the female would try to grab and shake the young. All attacks involving young resulted in no obvious injury to young. Females with broods were especially aggressive toward strange young, sometimes attempting to drown them. Lone females were less aggressive towards young, usually just jabbing at them.

Females with young were aggressive towards lone females (females without young, **Table 4**). These lone females were observed in groups of two to 15 and spent most of their time resting. Some females associated occasionally with broods for short periods of time (<1 min.) sometimes being tolerated by the female of the brood but most often being chased away. These females had an ambivalent attitude towards young, either tolerating or attacking them. Attacks usually provoked a reaction from the attending female. Aggression of lone females towards young occurred usually when the young of a brood would attempt to use a resting spot already used by lone females or when, following a disturbance, confused young would mistakenly follow one or several lone females.

At Lake Malbaie, interactions between females, and between females and young, were apparently density dependent (**Tables 1-4**). In 1994 and 1996 when the density of lone females was high and that of broods low (**Table 1**), females with young interacted mostly with lone females (**Table 4**). In 1995, when the reverse occurred, they interacted mostly with young. Lone females interacted mostly with young and were rarely aggressive towards other females.

Brood mixing occurred frequently whenever several broods used the same area for resting or feeding. It was often precipitated by disturbance by anglers (at least 10 boats active daily for the summer) or by Common Loons *Gavia immer*, the latter always provoking panic among broods. In nearly 120 hours of observations we did not witness any direct attempts by a female to abandon her young to the care of another female.

Discussion

Brood amalgamation has been documented in several species of waterfowl (Eadie *et al.* 1988, Patterson *et al.* 1982, Beauchamp 1997) and is particularly common in the Tribe Mergini (Hilden 1964, Kehoe 1986, 1989, Munro & Bédard 1977a, Savard 1987). It has been well studied in the Common Eider (Munro & Bédard 1977a, Bédard & Munro 1977, Gorman & Milne 1972, Bustness & Erickstad 1991, Schmutz *et al.* 1982) and several similarities can be seen in brood amalgamation of eiders and Surf Scoters: 1) Aggressiveness and broodiness of females varies among individual females; 2) Lone females associate sometimes with a brood for a short period of time and show ambivalent behaviour towards young sometimes being broody sometimes aggressive; 3) Females with young are aggressive towards strange young and other females; 4) No behaviour indicating voluntary abandonment of the brood has been described in either species. The major difference between Common Eiders and Surf Scoters is that in eiders, more than one female can associate closely with an amalgamated brood whereas this has not been observed in scoters where the association of a lone female with a brood was always of short duration. At the other extreme in highly territorial goldeneyes, no other female is tolerated near the brood (Savard 1987, 1988). It is interesting to note the similarities between brood amalgamation of Common Eiders and Surf Scoters given that eiders nest colonially and that Surf Scoters never do so, breeding usually at quite low densities in most parts of their range (Savard *et al.* 1998, Savard & Lamothe 1991).

Several hypotheses have been proposed to explain post-hatch brood amalgamation in waterfowl (Eadie *et al.* 1988, Beauchamp 1997). It is likely that there are several causes and functions to brood amalgamation so that it may be difficult to single out unambiguously a single hypothesis. There is mounting evidence that this behaviour is not genetically based (Bustness & Erikstad 1991, Eadie 1989) but rather related to local conditions, especially mortality rates (Poysa 1992, Poysa *et al.* 1997, Eadie & Lyon 1998) and crowding conditions (Munro & Bedard 1977a, Patterson *et al.* 1982, Savard 1987).

Accidental mixing of broods resulting in partial or complete amalgamation of broods has been reported in most species studied to date (Munro & Bedard 1977a, 1977b, Williams 1974, Patterson *et al.* 1982, Savard 1987) especially in crowded situations. It is thought to be facilitated by weak mother-young bonds at hatching and by the strong attraction between young of similar age (Savard 1987). The dominance of one of the females in terms of aggressiveness and broodiness excludes the other female (Munro & Bédard 1977a, Savard 1987). Whether or not it is the only factor leading to brood amalgamation is strongly debated (Eadie *et al.* 1988, Poysa *et al.* 1997, Eadie & Lyon 1998). The other main hypothesis is the salvage strategy hypothesis which assumes that females consciously abandon their young to the care of an other females to further their own survival and or that of their young (Eadie et al, 1988, Afton & Paulus 1992, Hori 1964a, 1964b, 1969, Gorman & Milne 1972). Bustness & Erikstad (1995) argued that brood abandonment was a conscious decision made by the female prior to hatching, a decision based on her condition (salvage strategy hypothesis) whereas Poysa (1995) argued that brood abandonment was decided after females had assessed the survival chances of their young (brood success hypothesis). We consider these theories premature as no evidence was provided that females voluntarily abandon their young to the care of other females. To the contrary, available descriptive accounts of brood amalgamation in the Tribe Mergini indicate that females do not abandon their young voluntarily to the care of another female but rather lose them to the other female.

Eadie & Lyon (1998) argued that in Barrow's Goldeneye, crèching behaviour is driven by selection on adults to abandon their young when the benefits of continued investment are outweighed by the reduction in future reproduction and by selection on deserted ducklings to join other broods. They present good experimental evidence that Barrow's Goldeneye do in fact often desert reduced broods as Poysa 1992 and Poysa *et al.* 1997 had shown in Common Goldeneye. Eadie & Lyon (1998) also showed that some of the deserted young were subsequently adopted in other broods and that the success of adoption was greatly influenced by similarities in duckling age between deserted ducklings and ducklings of the adopting female.

However, in Barrow's Goldeneye and in most of the other species studied to date, deserted broods comprised only a small fraction of brood amalgamation cases. In most studies, amalgamation resulted from encounters between broods with females and amalgamation occurred following eviction of one female and/or mixing of all or part of the brood. In our study, all observed brood mixing and amalgamation involved broods with females. Single ducklings lost were usually successfully driven away by the female. Whether brood amalgamation is adaptive or not remains to be demonstrated.

Most of the confusion in the current literature is with the term abandon. We would argue that most observations indicate that females are usually forced to abandon their young to a more aggressive female and that this is not their initial intent. Females in poor conditions and/or which have suffered heavy mortality in their brood may not be able to strengthen their mother-duckling bonds. Thus, they are more likely to lose their ducklings in the event of an aggressive encounter with another brood where mixing of young occurs. This may be advantageous in the long term to the female if it increases her chance of survival without affecting too much the survival of her young.

Proximal causes of amalgamation seemed diverse with partial amalgamation occurring quite frequently. Factors affecting the strength of mother-duckling bonds, the level of attraction between young, the aggressiveness of the female and chance events all contribute to partial or complete brood amalgamation. In all species studied, the adopting parent displays initial aggression towards strange ducklings which, in highly territorial Goldeneyes, can lead to duckling death (Savard 1987, Savard et *al.* 1991, Einarsson 1988, 1990). Acceptance of young is likely related to the ability of the female to properly identify her own young which could explain why most amalgamated broods are of similar age (Savard 1987, Eadie & Lyon 1998).

The existence of an adaptive function of brood amalgamation which has a genetic basis has yet to be demonstrated. It may be extremely difficult to prove, especially if no proximal adaptation accompanies it. Also, given that an important portion of brood amalgamation is fortuitous, large sample sizes will be needed to separate the two occurrences. In the absence of a genetic basis for brood amalgamation there might still be an adaptive function to brood amalgamation. However, our review yielded no evidence of conscious abandonment of young to another female. To the contrary, it stressed the prevalence of accidental mixing and the importance of chance events in brood amalgamations. If a behaviour is not genetically programmed and not consciously performed can we talk about an adaptive behaviour? or even a behaviour? or a strategy? Better care is needed in choosing our vocabulary to describe a given occurrence. To date accidental mixing has been shown to occur in most species studied. Whether or not purposeful abandonment of young occurs, in the context of brood amalgamation, it has yet to be conclusively demonstrated.

However, even if voluntary abandonment of young by a female is not prevalent in most brood amalgamations, brood amalgamation may still be advantageous for some of the birds involved. Such advantages may not be so great as to lead to the evolution of behaviour favouring brood amalgamation. Variation in hormonal levels related to female condition and to the level of stimulation by her young is a possible mechanism that could affect female-ducklings bonds and indirectly lead to brood amalgamation. Such a mechanism does not require a genetic basis or a conscious decision from the female. More detailed observations of proximal mechanisms leading to brood amalgamation as well as better quantification of its impact on the survival of the birds involved are greatly needed to fully understand this phenomenon so common in waterfowl.

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