

THE RELATIONSHIP BETWEEN INTRA- AND INTERSPECIFIC BROOD AMALGAMATION IN WATERFOWL¹

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Abstract. Interspecific brood amalgamation in waterfowl has been hypothesized to be an extension of intraspecific brood amalgamation behavior that increases the likelihood of successful amalgamation by increasing the range of potential recipients. I tested this hypothesis using recent phylogenetic information. The analysis revealed that the likelihood that a lineage carries the interspecific brood amalgamation state increases significantly when the lineage also carries the intraspecific amalgamation state, thus supporting the hypothesis. The likelihood of a transition to interspecific brood amalgamation was similar across categories of several ecological and life-history factors, including nesting dispersion, nesting substrate, type of brood care, and level of reproductive effort. Nevertheless, several lineages carrying the intraspecific brood amalgamation state failed to show the interspecific counterpart, suggesting that the expression of interspecific brood amalgamation tendencies can be constrained by other factors.

Key words: *comparative ecology, intraspecific brood amalgamation, interspecific brood amalgamation, phylogeny, waterfowl.*

Laying eggs in the nests of other females occurs frequently in waterfowl, both within and among species (Eadie et al. 1988, Rowher and Freeman 1989). Beauchamp (1997) estimated that nearly 60% of the better-known species exhibit intraspecific brood amalgamation (IABA). With respect to interspecific brood amalgamation (IRBA), amalgamation tendencies also are well documented in a number of tribes including the pochards (Aythyini) and stiff-tailed ducks (Oxyurini) (Weller 1959, Lyon and Eadie 1991, Saylor 1992). In waterfowl, IRBA is almost always facultative and occurs before hatching (Lyon and Eadie 1991).

Although the fitness consequences of brood amalgamation for the recipient parents, the donated young, and the donor parents are fairly well understood, the proximate determinants are still unclear. With respect to IABA, a recent phylogenetic study of ecological and life-history correlates indicated that factors that increase the ease with which females can locate potential recipients, for example colonial breeding and hole nesting, likely act as proximate determinants (Beauchamp 1997). However, evolutionary transitions to IABA occurred equally frequently in lineages carrying different life histories, as indexed by reproductive effort, and in lineages carrying different types of brood

care. The proximate determinants of IRBA have yet to be examined within a phylogenetic context.

In this paper, I examine one proximate hypothesis for the occurrence of IRBA in waterfowl, namely that IRBA represents an extension of amalgamation tendencies within a species that allows an increase in the number of potential recipients (Lyon and Eadie 1991). The hypothesis predicts that evolutionary transitions to IRBA should occur more frequently in lineages that carry the IABA state. Support thus far for the prediction comes from the observation that several species that show IABA also tend to exhibit interspecific amalgamation behavior (Lyon and Eadie 1991). However, it is likely that information from tribes with many related species inflated the correlation (Harvey and Pagel 1991). Instead of using species as independent observations, interspecific correlations should thus be evaluated with phylogenetic information. Therefore, I tested the prediction using recent phylogenetic analyses of waterfowl. Because the tendency to exhibit IABA may be linked to several ecological and life-history traits that could influence IRBA on their own, I explored the relationship between IRBA and IABA in a multivariate analysis. The analysis included factors that have been considered potential determinants of IABA, namely nesting dispersion, nesting substrate, type of brood care, and level of reproductive effort (Eadie et al. 1988, Rohwer and Freeman 1989, Saylor 1992).

METHODS

ECOLOGICAL INFORMATION

I surveyed the ornithological literature for evidence of IRBA in waterfowl. For each species where information was available, I evaluated qualitatively whether amalgamation has been reported or not. Evidence of IRBA was inferred when eggs or chicks from a given species occurred in broods of other species. Amalgamation tendencies were treated as unknown, instead of unreported, when the breeding biology of a species was poorly known.

I categorized each ecological and life-history trait into one of two possible states (Appendix 1). For each species, I recorded nesting dispersion as colonial (state = 1) or solitary (state = 0), and treated solitary breeders that occasionally nest in colonies, excluding cases of island breeding, as colonial nesters. I recorded whether individuals nested predominantly in cavities (holes in trees or in the ground; state = 1) or on the ground (state = 0). For the purpose of this analysis, I considered species that occasionally nest in the two types of substrate as cavity nesters. I recorded brood care before hatching as biparental (state = 1) when

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males did not desert the nest early on, or uniparental (state = 0) otherwise. I indexed reproductive effort as the ratio of clutch mass to female body mass (%). For this index, I used the average clutch size produced by females multiplied by the average egg mass. I recorded reproductive effort as either small (state = 1), when the ratio was equal or less than 50%, or large (ratio > 50%; state = 0). Finally, I categorized the occurrence of IABA before hatching as present (state = 1) or absent (state = 0). Evidence of IABA was provided from direct observations of egg laying in the nests of conspecifics, or inferred from indirect sources such as extraordinary rates of laying or larger-than-normal clutch sizes (Beauchamp 1997).

ASSOCIATION TESTS

I investigated whether evolutionary transitions from non-amalgamation (state = 0) to IRBA (state = 1), the two states of the dependent variable, were equally likely to occur under the two states of each ecological and life-history character. A condition of the test is that the characters under scrutiny have been reconstructed over the phylogenetic tree. I used phylogenetic trees for waterfowl tribes that are based upon morphological characters not included in the present analysis (Livezey 1991, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997). For each tribe, I then reconstructed the occurrence of each character on the trees using MacClade 3.06 (Maddison and Maddison 1992).

In the analysis, all branches that maintained the non-amalgamation state are regarded as having the potential for a transition to IRBA. Branches that inherited the IRBA state from an ancestor are not counted because a transition to IRBA cannot take place on these branches. Because branch lengths are not known, another assumption is that state transitions are equally likely for all branches (Sillén-Tullberg 1993). Finally, I restricted the analyses to phylogenetic branches that occur within tribes because evolutionary relationships among tribes are not always clear in all the waterfowl clades (Livezey 1996a). The unit of analysis is thus a branch of the phylogenetic tree and the respective states of each variable associated with it.

I used a logistic regression to explore the relationship between the two states of IRBA and the independent variables. A logistic regression is useful in this context because the dependent variable is binomially rather than normally distributed (Sokal and Rohlf 1995). A further advantage lies in the fact that a logistic regression can be conducted as a multivariate test that takes into account the possible correlations between independent variables. Correlations between life-history and ecological traits are common in animals and can obscure the interpretation of univariate tests (e.g., Martin 1995, Beauchamp 1997).

The logistic regression relates the proportion p of branches where IRBA is present to the states of the independent variables according to the following model:

$$\ln[p(1 - p)^{-1}] = a + \sum_i b_i X_i$$

where a is the intercept and b_i is the slope associated with the independent variable X_i . The effect of each independent variable is evaluated with a χ^2 statistic with one degree of freedom. The χ^2 statistic tests the hypothesis that there is no linear relationship between

the logit, that is $\ln[p(1 - p)^{-1}]$, and the independent variable. A maximum-likelihood method is used to fit the regression line and generate values for the parameters a and b that provide the best fit to the observed values. In this context, a positive slope indicates that the probability p increases as the state of the independent variable switches from 0 to 1. Therefore, a positive slope is associated with an increase in the likelihood that a transition from non-amalgamation to amalgamation occurs in a lineage. In order to evaluate whether each variable should remain in the final model, I fitted two models, one with the variable present and the other with the variable omitted. The log-likelihood ratio is computed for each, and the difference D between the two values is used to test the level of significance of the variable left out. The significance of the difference D is evaluated with a χ^2 statistic with one degree of freedom. The final model was found when the omission of any variable caused a significant increase in the deviance D .

RESULTS

I evaluated the occurrence of IRBA in 163 species. IRBA occurred in 37 species (22.7%; Table 1, Appendix 1). Excluding unknown cases, 18.5% of species exhibited IRBA at least infrequently. The analysis of phylogenetic trees yielded 263 lineages. A total of 106 lineages (40.3%) carried the IABA state and 20 lineages (7.6%) carried the IRBA state. Among the 20 lineages that carried the IRBA state, 18 (90%) also carried the IABA state.

The multiple logistic regression revealed that transitions to IRBA occurred more frequently on lineages carrying the IABA state as suggested by the positive slope associated with this variable (Table 2). However, the final model revealed no effects of ecological and life-history variables on transitions to IRBA once the influence of IABA was taken into account.

DISCUSSION

Interspecific brood amalgamation in birds has been hypothesized to be an extension of intraspecific amalgamation tendencies (Lyon and Eadie 1991). I used a phylogenetic approach to test the prediction that transitions to IRBA in waterfowl occur more frequently in lineages that carry the IABA state. The phylogenetic approach avoids possible biases due to passive inheritance of traits among closely related species. Based on recent phylogenetic evidence, the results presented here indicate that the occurrence of IABA on a phylogenetic branch significantly increases the likelihood that the branch will carry the IRBA state, consistent with the hypothesis. This suggests, therefore, that laying eggs in the nests of other species, in addition to those of conspecifics, may act to increase the chances that a species finds a suitable recipient for brood amalgamation. IABA before hatching also is correlated with the tendency to amalgamate broods after hatching (Beauchamp 1997), suggesting that the window of opportunity for successful amalgamation can also be increased temporally by post-hatching brood amalgamation as well as spatially by laying eggs in the nests of other species. Generally, all these different forms of brood amalgamation can be viewed as different means of achieving the same goal of mixing broods (Eadie et al. 1988).

TABLE 1. Number of species in each tribe exhibiting intra- and interspecific brood amalgamation.

Tribe	Intraspecific brood amalgamation			Interspecific brood amalgamation		
	Unknown	Unreported	Occurs	Unknown	Unreported	Occurs
Anseranatini	—	—	1	—	1	—
Dendrocygnini	2	—	7	—	7	2
Anserini	2	5	8	—	13	2
Cygnini	—	6	2	—	8	—
Cereopsini	—	1	—	—	1	—
Stictonettini	—	—	1	—	1	—
Merganettini	—	5	1	—	6	—
Plectropterini	—	—	2	—	2	—
Tadornini	4	6	4	1	12	1
Malacorhynchini	—	1	1	—	2	—
Anatini	11	27	18	6	42	8
Aythiini	4	1	11	1	8	7
Oxyurini	1	1	7	1	3	5
Mergini	2	3	18	4	7	12

The vast majority of lineages that carry the IRBA state also showed the IABA state, but a large number of lineages carried only the IABA state. Hence, the occurrence of the IABA state on a lineage is necessary for the expression of IRBA, but additional factors must be invoked to account for the lack of expression of IRBA in several lineages that carry the IABA state. The lack of expression of the IRBA state may indicate that laying eggs in the nests of other species is costly (Yamauchi 1995). The onus then is on finding factors that prevent interspecific egg laying. My analysis suggests that the expression of the IRBA state in a lineage is not related to nesting dispersion, nesting substrate, type of brood care, or level of reproductive effort once the effect of IABA is taken into account. Therefore, opportunities to lay eggs in the nests of other species are not facilitated nor inhibited by variations found across these large ecological and life-history categories.

Potential factors that could prevent interspecific egg laying include sparsity of heterospecific recipients, aggressive behavior by the recipient species, and lack of suitable recipients. When the density of heterospecific females is low, females may be unable to locate recipients successfully. This conjecture is supported by the fact that IRBA, and other forms of brood amalgamation, affects clustered nests on islands more frequently than dispersed nests in uplands (Bengtson 1972, Saylor 1992). Aggressive behavior by the recipient species

also may limit the ease with which females can lay eggs in the nests of others (Saylor 1992, Gonzalez-Martin and Ruiz 1996). Finally, recipient species may not be available due to differences in breeding schedules or food and habitat requirements (Saylor 1992). An avenue for future research is to compare closely related species that are known to differ in the expression of IRBA tendencies and to examine which of the above factors might be involved. Identification of the constraints that prevent the expression of IRBA will help us to understand why this state is not more prevalent before hatching and perhaps also why it is almost never observed after hatching (Eadie et al. 1988).

Among the lineages that carry the IRBA state, only 2 lineages (10%) failed to exhibit the IABA state. The two exceptions include *Heteronetta atricapilla* and *Anas discors* (Appendix 1). Only the former is well known for complete reliance on IRBA for reproduction (Johnsgard 1978, Reese and Hillgarth 1984). Because cases of IABA are more difficult to document, the occurrence of IABA is undoubtedly underestimated, and it is possible that IABA is present in *Anas discors* but has not been documented.

The relationship between intra- and interspecific brood amalgamation that I observed in waterfowl may be common in other avian taxa. Although phylogenetic analyses are lacking, the two forms of brood amalgamation have been observed conjointly in other taxa

TABLE 2. Maximum-likelihood estimates of the slope parameters b in a logistic regression including the effects of all variables on the occurrence of interspecific brood amalgamation. The difference D between log-likelihood ratios for models with and without each variable is shown.

	Model with all variables				Final model	
	b	P	D	P	b	P
Nesting dispersion	1.33	0.13	2.36	>0.10	—	—
Nesting substrate	-0.011	0.99	0.00	>0.90	—	—
Reproductive effort	-0.70	0.35	1.30	>0.10	—	—
Brood care	-0.93	0.13	3.16	>0.05	—	—
IABA ^a	1.73	0.043	10.21	<0.005	2.44	<0.005

^a Intra-specific brood amalgamation.

including pheasants (Weller 1959), cuckoos (Hughes 1996), shrubsteppe passerines (Yanes et al. 1996), and herons (Gonzales-Martin and Ruiz 1996). Therefore, it may not be surprising that in these other taxa IRBA also represents a carryover of IABA that extends the range of potential recipients.

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APPENDIX 1. Occurrence of intra- (IABA) and interspecific (IRBA) brood amalgamation in waterfowl.

Species ^a	Nesting ^b	RCM ^c	PPDI ^d	IABA	IRBA	Source ^e
Tribe Anseratini						
<i>Anseranas semipalmata</i>	E, C	55.6	O	O	—	1, 2, 3, 4
Tribe Dendrocygnini						
<i>Dendrocygna viduata</i>	E/U, S	54.4	O	O	—	1, 5, 6
<i>D. autumnalis</i>	H, S/C	73.4	O	O	O	1, 7, 8, 9, 10
<i>D. guttata</i>	H, S?	61.3	O	?	—	1
<i>D. arborea</i>	H, S	62.2	O	?	—	1
<i>D. arcuata</i>	U, S	54.6	O	O	—	1, 2, 11
<i>D. javanica</i>	H, S	70.0	O	O	—	1
<i>D. eytoni</i>	U, S	50.5	O	O	—	1, 2, 11
<i>D. bicolor</i>	E, S/C	72.5	O	O	O	1, 7, 9, 12
<i>Thalassornis leuconotos</i>	E, S	69.4	O	O	—	1
Tribe Cygnini						
<i>Cygnus olor</i>	E/U, S/C	19.1	O	O	—	1, 7, 9, 13, 14
<i>C. atratus</i>	E/U, S/C	29.4	O	O	—	1, 2, 11
<i>C. melanocoryphus</i>	E, S	37.1	O	—	—	1
<i>C. buccinator</i>	E, S	17.3	O	—	—	1, 7, 11, 15, 16
<i>C. columbianus</i>	U, S	18.1	O	—	—	1, 9, 13
<i>C. cygnus</i>	U, S	20.4	O	—	—	1, 13
<i>C. bewickii</i>	U, S	15.6	O	—	—	1, 13
<i>Coscoroba coscoroba</i>	E/U, S	15.6	O	—	—	1
Tribe Anserini						
<i>Anser cygnoides</i>	U, S	24.2	O	—	—	1
<i>A. (f.) fabalis</i>	U, S/C	25.7	O	?	—	1, 13
<i>A. (f.) brachyrhynchus</i>	U, S/C	16.7	O	—	—	1, 7, 13
<i>A. (a.) albifrons</i>	U, S	26.2	O	—	—	1, 13, 17, 18
<i>A. erythropus</i>	U, S	29.4	O	—	—	1, 13, 19
<i>A. indicus</i>	U/E, S/C	22.6	O	O	—	1, 20
<i>A. anser</i>	U, S/C	25.8	O	O	—	1, 13
<i>A. caerulescens</i>	U, C	25.2	O	O	O	1, 7, 9, 21, 22, 23
<i>A. rossii</i>	U, C	30.7	O	O	—	1, 7, 9
<i>A. canagicus</i>	U, S/C	21.7	O	O	—	1, 7, 9, 24
<i>Branta sandvicensis</i>	U, S	34.4	O	—	—	1, 25
<i>B. canadensis</i>	E/U, S/C	18.1	O	O	O	1, 2, 7, 9, 13, 23, 26
<i>B. leucopsis</i>	U, C	35.7	O	O	—	1, 7, 9, 13, 27, 28
<i>B. bernicla</i>	U, C	22.7	O	O	—	1, 7, 9, 13, 29, 30
<i>B. ruficollis</i>	U, C	39.7	O	?	—	1
Tribe Cereopsini						
<i>Cereopsis novaehollandiae</i>	U, S	18.2	O	—	—	1, 2, 11
Tribe Stictonettini						
<i>Stictonetta naevosa</i>	E, S	54.9	—	O	—	1, 2, 11, 31
Tribe Merganettini						
<i>Hymenolaimus malacorhynchus</i>	H, S	52.6	O	—	—	1, 2, 32
<i>Tachyeres patachonicus</i>	U, S	30.8	O	—	—	1, 33
<i>T. pteneres</i>	U, S	24.4	O	—	—	1, 33
<i>T. leucocephalus</i>	U, S	?	?	—	—	1, 33
<i>T. brachypterus</i>	U, S	25.9	O	O	—	1, 33
<i>Merganetta armata</i>	H, S	71.1	O	—	—	1, 34
Tribe Plectropterini						
<i>Plectropterus gambensis</i>	U/H, S	28.0	—	O	—	1, 35
<i>Sarkidiornis melanotos</i>	H/U, S	24.3	—	O	—	1, 36, 37
Tribe Tadornini						
<i>Cyanochen cyanopterus</i>	U, S?	39.1	?	?	?	1
<i>Chloephaga melanoptera</i>	U, S?	30.6	O	—	—	1
<i>C. picta</i>	U, S	24.2	O	—	—	1
<i>C. hybrida</i>	U, S	41.7	O	—	—	1

APPENDIX 1. Continued.

Species ^a	Nesting ^b	RCM ^c	PPDI ^d	LABA	IRBA	Source ^e
<i>C. poliocephala</i>	U, S	20.2	O	—	—	1
<i>C. rubidiceps</i>	U, S	27.0	O	—	—	1, 38
<i>Neochen jubata</i>	H, S	40.3	O	?	—	1
<i>Alopochen aegyptiacus</i>	U/H, S	41.2	O	—	—	1, 13
<i>Tadorna ferruginea</i>	H, S	69.2	O	O	—	1, 13
<i>T. cana</i>	H, S	58.6	O	?	—	1
<i>T. tadornoides</i>	H, S	86.4	O	O	—	1, 3, 11, 13, 39
<i>T. variegata</i>	H, S	56.0	O	O	—	1, 2, 40
<i>T. tadorna</i>	H, S	70.0	O	O	O	1, 13, 41, 42, 43
<i>T. radjah</i>	H, S	63.3	O	?	—	1, 2, 11
Tribe Malacorhynchini						
<i>Malacorhynchus membranaceus</i>	H, S	63.1	O	O	—	1, 2, 11
<i>Salvadorina waigiuiensis</i>	U, S	37.1	O	—	—	1, 44, 45
Tribe Anatini						
<i>Cairina moschata</i>	H/E, S	74.0	—	O	—	1
<i>C. scutulata</i>	H/U, S?	35.6	?	?	?	1
<i>Pteronetta hartlaubii</i>	H, S	45.3	O	?	—	1
<i>Aix sponsa</i>	H, S	114.3	O	O	O	1, 7, 9, 46, 47
<i>A. galericulata</i>	H, S	77.9	O	O	—	1, 13, 89
<i>Chenonetta jubata</i>	H, S	67.5	O	O	—	1, 2, 11, 48, 49
<i>Nettapus auritus</i>	H, S	79.6	—	?	—	1
<i>N. coromandelianus</i>	H, S	71.1	?	O	—	1, 2, 11
<i>N. pulchellus</i>	H, S	98.7	O	O	—	1, 2, 11
<i>Amazonetta brasiliensis</i>	E/H, S	37.4	O	?	—	1
<i>Callonetta leucophrys</i>	H, S?	115.2	O	?	—	1, 50
<i>Lophonetta specularioides</i>	U, S	40.4	O	—	—	1, 51
<i>Speculanus specularis</i>	U, S	39.1	?	—	—	1
<i>Mareca capensis</i>	U, S	59.2	O	—	—	1, 59, 90
<i>M. strepera</i>	U, S	51.8	O	O	O	1, 7, 9, 12, 13, 46, 52
<i>M. falcata</i>	U, S	67.0	O	—	—	1
<i>M. sibilatrix</i>	U, S	41.6	O	—	—	1
<i>M. penelope</i>	U, S	61.9	—	O	—	1, 13, 53
<i>M. americana</i>	U, S	50.6	O	—	—	1, 7, 9, 46
<i>Anas sparsa</i>	U/H, S	40.1	O	—	—	1, 90
<i>A. rubripes</i>	U, S	51.6	O	O	—	1, 7, 46
<i>A. (p.) fulvigula</i>	U, S	55.8	—	O	—	1, 7, 9, 54
<i>A. (p.) diazi</i>	U, S	?	—	—	—	1, 7, 9, 46
<i>A. (p.) platyrhynchos</i>	U, S	50.4	—	O	O	1, 2, 7, 9, 12, 13, 46, 53, 55
<i>A. (p.) wyvilliana</i>	U, S	62.3	—	?	?	1
<i>A. (p.) laysanensis</i>	U, S	?	—	?	?	1, 56
<i>A. luzonica</i>	U, S	65.5	?	—	—	1
<i>A. (p.) superciliosa</i>	U/H, S	60.0	—	O	O	1, 2, 57
<i>A. (p.) poecilorhyncha</i>	U/H, S	48.0	O	?	?	1
<i>A. (p.) zonorhyncha</i>	U/H, S	?	?	?	?	1
<i>A. undulata</i>	U, S	53.9	O	—	—	1, 90
<i>A. melleri</i>	U, S	?	O	?	—	1, 58
<i>A. discors</i>	U, S	87.3	O	—	O	1, 7, 9, 12, 46
<i>A. cyanoptera</i>	U, S	88.4	O	O	O	1, 7, 12, 46, 61
<i>A. smithii</i>	U, S	75.4	O	—	—	1, 59, 90
<i>A. platalea</i>	U, S?	57.2	?	—	—	1, 88
<i>A. rhynchotis</i>	U, S	64.7	—	—	—	1, 2
<i>A. clypeata</i>	U, S	72.7	O	O	O	1, 7, 12, 13
<i>A. bernieri</i>	U, S	?	?	?	?	1, 60
<i>A. gibberifrons</i>	U/H, S	55.4	O	O	—	1, 2, 11, 57
<i>A. castanea</i>	U/H, S	70.5	O	O	—	1, 2, 11, 62
<i>A. chlorotis</i>	U, S	77.0	O	—	—	1, 2, 87
<i>A. aucklandica</i>	U, S	58.3	O	—	—	1, 2
<i>A. bahamensis</i>	U, S	?	O	—	—	1, 7, 63

APPENDIX 1. Continued.

Species ^a	Nesting ^b	RCM ^c	PPD ^d	IABA	IRBA	Source ^e
<i>A. erythrorhyncha</i>	U, S	68.9	O	—	—	1, 90
<i>A. flavirostris</i>	H/U, S	64.3	O	—	—	1, 88
<i>A. georgica</i>	U, S	41.7	O	—	—	1, 88
<i>A. (a.) acuta</i>	U, S	40.6	—	—	O	1, 7, 9, 13, 64
<i>A. (a.) eatoni</i>	U, S	28.9	—	—	—	1, 2, 65
<i>A. querquedula</i>	U, S	81.0	—	O	—	1, 11, 13
<i>A. formosa</i>	U, S	53.9	?	—	—	1
<i>A. (c.) crecca</i>	U, S	80.3	—	—	—	1, 13, 53, 66
<i>A. (c.) carolinensis</i>	U, S	81.5	—	O	—	1, 7, 9, 46
<i>A. (v.) puna</i>	U, S	?	?	—	—	1
<i>A. (v.) versicolor</i>	U, S	72.9	O	—	—	1, 88
<i>A. hottentota</i>	U/E, S	72.9	O	—	—	1, 90
Tribe Aythiini						
<i>Marmaronetta angustirostris</i>	U, S/C	77.5	—	O	—	1, 13
<i>Netta rufina</i>	U/E, S	52.1	O	O	O	1, 13, 67, 86
<i>Metopiana erythrophthalma</i>	U/E, S	70.8	?	?	—	1
<i>M. peposaca</i>	E, S	59.8	—	O	—	1
<i>Aythya valisineria</i>	E, S	58.9	—	O	O	1, 7, 9, 12, 68
<i>A. ferina</i>	E, S	55.8	O	O	O	1, 13
<i>A. americana</i>	E, S	44.2	O	O	O	1, 7, 9, 12, 69, 70
<i>A. australis</i>	E, S	71.6	—	O	—	1, 2, 11
<i>A. baeri</i>	E, S	56.9	?	?	—	1
<i>A. nyroca</i>	E/U, S	74.4	O	O	—	1, 13
<i>A. innotata</i>	E, S	?	?	?	?	1, 71
<i>A. novaeseelandiae</i>	U/E, S/C	67.1	—	?	—	1, 2
<i>A. fuligula</i>	E, S	53.3	—	O	O	1, 13, 53
<i>A. collaris</i>	E, S	59.1	O	—	—	1, 7, 9
<i>A. marila</i>	U, S/C	67.0	—	O	O	1, 7, 9, 12, 13, 53
<i>A. affinis</i>	U/S	55.0	O	O	O	1, 7, 9, 12, 72
Tribe Oxyurini						
<i>Heteronetta atricapilla</i>	E, S	?	—	—	O	1, 73
<i>Nomonyx dominica</i>	E, S	76.7	—	O	—	1, 7
<i>Oxyura ferruginea</i>	E, S	?	?	?	?	74
<i>O. jamaicensis</i>	E, S	116.8	—	O	O	1, 7, 9, 13, 46, 75
<i>O. vittata</i>	E, S	61.4	—	O	—	1
<i>O. australis</i>	E, S	58.1	—	O	O	1, 2, 11, 76
<i>O. maccoa</i>	E, S	80.0	—	O	O	1
<i>O. leucocephala</i>	E, S	100.0	—	O	—	1, 13
<i>Biziura lobata</i>	E, S	16.5	O	O	O	1, 2, 11, 76
Tribe Mergini						
<i>Polystica stelleri</i>	U, S	50.6	O	—	—	1, 7, 9, 13, 46
<i>Somateria fischeri</i>	U, S	17.9	—	O	O	1, 7, 9, 46
<i>S. spectabilis</i>	U, S	20.9	—	O	—	1, 7, 9
<i>S. (m.) v-nigrum</i>	U, C	21.6	—	?	?	1, 77
<i>S. (m.) dresseri</i>	U, C	23.5	—	O	O	1, 7, 9, 46, 77, 78
<i>S. (m.) borealis</i>	U, C	30.7	—	O	?	1, 23, 77, 79, 80
<i>S. (m.) mollissima</i>	U, C	18.1	—	O	—	1, 13
<i>Histrionicus histrionicus</i>	U, S	58.9	—	O	—	1, 7, 9, 13
<i>Melanitta perspicillata</i>	U, S	53.3	—	—	—	1, 9
<i>M. (f.) fusca</i>	U, S	53.2	—	O	O	1, 13
<i>M. (f.) deglandi</i>	U, S	62.4	—	O	O	1, 7, 9, 12, 82
<i>M. (n.) nigra</i>	U, S	56.9	—	O	—	1, 13, 53
<i>M. (n.) americana</i>	U, S	45.5	—	O	—	1, 7, 9, 46
<i>Clangula hyemalis</i>	U, S	43.0	—	O	O	1, 7, 9, 13, 46, 53
<i>Bucephala albeola</i>	H, S	95.3	—	O	O	1, 9, 46, 81
<i>B. clangula</i>	H, S	87.5	—	O	O	1, 9, 46, 47
<i>B. islandica</i>	H, S	71.3	—	O	O	1, 9, 12, 46, 53
<i>Mergellus albellus</i>	H, S	50.4	—	O	O	1, 13

APPENDIX 1. Continued.

Species ^a	Nesting ^b	RCM ^c	PPDI ^d	IABA	IRBA	Source ^e
<i>Lophodytes cucullatus</i>	H, S	111.1	—	O	O	1, 7, 9, 46, 47
<i>M. octosestaceus</i>	H, S?	?	O	?	?	1, 83
<i>M. merganser</i>	H, S	73.9	—	O	O	1, 7, 9, 46
<i>M. serrator</i>	U, S	64.9	—	O	O	1, 7, 9, 12, 46, 84
<i>M. squamatus</i>	H, S	?	—	—	—	1, 85

^a Based on the tribal classification of Johnsgard (1978) and Livezey (1991, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997).

^b E = emergent vegetation; U = upland; H = hole or cavity; S = solitary breeder; C = colonial breeder; S/C = solitary to colonial breeder.

^c RCM = relative clutch mass.

^d PPDI = paternal presence during incubation; ? = not known; — = not reported; O = occurs.

^e (1) Johnsgard 1978, (2) Marchant and Higgins 1990, (3) Whitehead and Tschirmer 1991, (4) Horn et al. 1996, (5) Clark 1976, (6) Siegfried 1973, (7) Palmer 1976, (8) Bergman 1994, (9) Bellrose 1978, (10) McCamant and Bolen 1979, (11) Frith 1967, (12) Weller 1959, (13) Cramp and Simmons 1977, (14) Perrins et al. 1994, (15) Henson and Cooper 1992, (16) Henson and Cooper 1994, (17) Fox et al. 1995, (18) Van Impe 1996, (19) Tegelstrom and Vonessen 1996, (20) Weigmann and Lamprecht 1991, (21) Williams 1994, (22) Lank et al. 1991, (23) Prevett et al. 1972, (24) Eisenhower and Kirkpatrick 1977, (25) Banko 1992, (26) Seddon and Nudds 1994, (27) Choudhury et al. 1993, (28) Forslund and Larson 1995, (29) Bregnballe and Madsen 1990, (30) Spaans et al. 1993, (31) Fullagar et al. 1990, (32) Veltman and Williams 1990, (33) Livezey and Humphrey 1992, (34) Moffett 1970, (35) Clark 1980, (36) Ali and Ripley 1968, (37) Wilson and Wilson 1980, (38) Vuilleumier 1994, (39) Riggert 1977, (40) Williams 1979, (41) Hori 1969, (42) Patterson et al. 1982, (43) Fox and Salmon 1994, (44) Kear 1975, (45) Hallstrom 1956, (46) Johnsgard 1975, (47) Bouvier 1974, (48) Briggs 1991, (49) Kingsford 1990, (50) Brewer 1989, (51) Buitron and Nuechterlein 1989, (52) Duebber et al. 1983, (53) Bengtson 1972, (54) Johnson et al. 1996, (55) Titman and Lowther 1975, (56) Moulton and Weller 1984, (57) Cunningham and Welch 1955, (58) Young 1995, (59) Heyl 1994, (60) Green et al. 1994, (61) Hohman and Anckey 1994, (62) Norman and McKinney 1987, (63) Sorenson et al. 1992, (64) Esler and Grand 1994, (65) Stahl et al. 1994, (66) Nummi and Pöysä 1995, (67) Amat 1991, (68) Sorenson 1993, (69) Bouffard 1983, (70) Sorenson 1991, (71) Wilme 1994, (72) Hines and Mitchell 1984, (73) Reese and Hillgarth 1984, (74) Livezey 1995b, (75) Joyner 1983, (76) Briggs 1988, (77) Alisaukas and Anckey 1992, (78) Robertson et al. 1992, (79) Bjorn and Erikstad 1994, (80) Butnes and Erikstad 1991, (81) Gauthier 1987, (82) Brown and Brown 1981, (83) Bartmann 1988, (84) Pelz 1971, (85) Zhengjie et al. 1995, (86) Amat 1985, (87) Dumbell 1986, (88) McKinney and Brewer 1989, (89) Davies and Baggott 1989, (90) Siegfried 1974.

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FIRST BREEDING RECORDS OF WHOOPER SWAN AND BRAMBLING IN NORTH AMERICA AT ATTU ISLAND, ALASKA¹

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Abstract. We document the first breeding records of Whooper Swan (*Cygnus cygnus*) and Brambling (*Fringilla montifringilla*) in Alaska and North America on Attu Island in the Western Aleutians in the spring of 1996. Five cygnets were seen with adults and the nest located, and a territorial pair of Bramblings was observed and a nest with eggs found.

Key words: *Alaska, Attu Island, Brambling, breeding record, Cygnus cygnus, Fringilla montifringilla, Whooper Swan.*

A pair of adult Whooper Swans (*Cygnus cygnus*) and what was suspected to be a nest were discovered by D. J. Trochlell and R. A. Wilt on 19 May 1996 near Lake Nicholas (165 ha) in lower Siddens Valley, Attu

Island, Western Aleutians, Alaska. Attu (67 km long, 28 km wide, 888 km²) is treeless and mountainous, and lies 700 km east of the Kamchatka Peninsula, Russia. D. Sonneborn et al. observed five small cygnets swimming with two adult *C. cygnus* on a lake SE of Lake Nicholas on 5 June. On 8 June D. D. Gibson confirmed a swan nest on an islet in a small pond (different from where cygnets were seen) SE of Lake Nicholas. A white flank feather and a few white breast feathers, all in fresh condition, and eggshell fragments were collected from the nest by D. D. Gibson (all material, University of Alaska Museum: UAM 6988). R. C. Laybourne, National Museum of Natural History, confirmed the identity of the feathers. This *C. cygnus* nesting site (52°52'13"N, 173°15'45"E) was on a narrow 1-ha pond 0.5 km SE of Lake Nicholas. The nesting islet was 6 m from the nearest point on shore (D. D. Gibson, pers. comm.), and one of the few places safe from terrestrial predators—primarily the intro-

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