

## DETERMINANTS OF INTRASPECIFIC BROOD AMALGAMATION IN WATERFOWL

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**ABSTRACT.**—Intraspecific brood amalgamation in waterfowl can occur before hatching, when females lay eggs in the nests of conspecifics, or after hatching, when females abandon their young to the care of other conspecific families. Using phylogenetic information, I examined whether evolutionary transitions to intraspecific prehatching and posthatching brood amalgamation in waterfowl can be associated with certain life-history and ecological variables. Transitions to intraspecific prehatching brood amalgamation occurred more frequently in lineages carrying the colonial-breeding state and the cavity-nesting state. However, such transitions occurred equally frequently in lineages carrying different life histories as indexed by the ratio of clutch mass to female body mass. The results support the view that opportunities for successful amalgamation, which are thought to be higher in colonial-nesting and cavity-nesting species, act as a proximate determinant of prehatching brood amalgamation. Transitions to posthatching brood amalgamation occurred most often in lineages carrying the prehatching brood-amalgamation state, which suggests that amalgamation after hatching represents an extension of amalgamation before hatching that temporally increases the window of opportunity for brood mixing. *Received 27 October 1995, accepted 16 July 1996.*

AS A RESULT of intraspecific brood amalgamation, parents provide care to unrelated young in many species of mammals (Packer et al. 1992), birds (Eadie et al. 1988), fishes (Johnston 1994, Fraser and Keenleyside 1995), and insects (Mappes et al. 1995, Petanidou et al. 1995, Premoli and Sella 1995). Initially a puzzling case for classic evolutionary theory, intraspecific brood amalgamation can increase reproductive success of adoptive parents, adopted young, and/or genetic parents (Riedman 1982, Eadie et al. 1988, Sayler 1992).

Among birds, intraspecific brood amalgamation arises in two ways. Prehatching brood amalgamation (preHBA) occurs when one female lays eggs in the nest of a conspecific that incubates the clutch and subsequently raises the offspring. Posthatching brood amalgamation (postHBA) occurs when the young from one family mix permanently with offspring from another conspecific family. The two types of intraspecific brood amalgamation are common in species that have self-feeding young, such as waterfowl. Nevertheless, the determinants of

intraspecific brood amalgamation in waterfowl are poorly known (Eadie et al. 1988, Rohwer and Freeman 1989, Afton and Paulus 1992, Sayler 1992).

Various life-history and ecological determinants of intraspecific preHBA and postHBA in waterfowl have been suggested on the basis of comparative studies that commonly use individual species or genera as independent units of analysis. The validity of these claims is questionable, however, because phylogenetic information rarely is used. For example, it is conceivable that information from tribes with many species inflated some life-history and ecological correlations (Harvey and Pagel 1991). Consequently, I examined whether evolutionary transitions to intraspecific preHBA and postHBA in waterfowl are associated with certain life-history and ecological variables using the phylogenetic classification proposed by Livezey (1991; 1995a, b, c; 1996). Below, I review the non-phylogenetically based determinants of intraspecific brood amalgamation that have been suggested in earlier waterfowl studies.

*Determinants of preHBA.*—Discussions of the determinants of intraspecific preHBA have focused on nest visibility, nest density, parental behavior, and reproductive effort. Nest visibility and nest density may reflect the ease with

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which parasitic females can locate potential nests. Compared with cavity nests, ground nests are scattered widely and are fairly cryptic, making them less easy to find. Hence, opportunities for preHBA should be more frequent in cavity-nesting versus ground-nesting species (except on islands). Opportunities for preHBA also should be more frequent in species that nest colonially versus solitarily because the number of potential nests increases with nest density (Eadie et al. 1988, Rohwer and Freeman 1989, Sayler 1992).

Parental behavior potentially can influence the occurrence of preHBA. PreHBA may occur less often in species with biparental rather than uniparental care because pairs could defend nests more effectively against intruders than could single individuals (Sayler 1992). Reproductive effort also may influence the occurrence of preHBA. Sayler (1992) suggested that preHBA should be more frequent in species with relatively high reproductive effort as indexed by the ratio of clutch mass to female body mass. In species with high reproductive effort, females might benefit from being able to salvage some reproductive success by laying eggs in the nests of others when faced with difficult environmental conditions that preclude normal clutch production and incubation.

*Determinants of postHBA.*—Nest density, parental behavior, and reproductive effort also may influence the occurrence of intraspecific postHBA. Afton and Paulus (1992) suggested that postHBA should be more frequent in species that nest colonially rather than solitarily because of the greater likelihood of brood encounters after hatching. Species with biparental care probably maintain family cohesion and protect the family against intruders more easily than species with uniparental care, which might reduce the occurrence of postHBA (Afton and Paulus 1992).

The energetic cost of egg laying and incubation may place a strain on breeding females that could affect future reproductive success. Brood desertion could be used by females to salvage some reproductive success when faced with detrimental environmental conditions. In this context, amalgamation from the point of view of the donor female potentially increases lifetime reproductive success at the expense of only one breeding effort. As noted for preHBA, species with relatively high reproductive effort should be more likely to exhibit postHBA than

species that invest less in each breeding episode.

## METHODS

*Ecological information.*—I searched the literature for evidence of intraspecific brood amalgamation in waterfowl and evaluated amalgamation based on whether or not it had been reported for the species in question. A more quantitative description is difficult because the proportion of families involved in amalgamation activities frequently is not recorded. Evidence of preHBA was provided from direct observations of amalgamation (e.g. Forslund and Larsson 1995) or inferred from a variety of indirect sources, including larger-than-normal clutches, clutches laid at extraordinary rates (e.g. more than one egg/day), and eggs added to nests during incubation (i.e. after the normal laying period). Evidence of postHBA was provided from direct observations of brood mixing before fledging.

Several life-history and ecological variables were analyzed and categorized in one of two possible states (Appendix). For each species, I recorded whether individuals predominantly nested in cavities or on the ground. Cavity nesters included species that nest in holes in trees or in the ground, whereas ground nesters included species that build their nests in uplands or on emergent substrates. I considered species that build nests in both types of locations as cavity nesters. I recorded whether species were colonial or solitary breeders, and considered solitary breeders that occasionally nest in colonies (excluding cases of island breeding) as colonial nesters.

I noted whether males remained near the nest during the incubation period and participated in rearing after hatching in order to characterize families as biparental or uniparental at each of these stages. I indexed reproductive effort as the ratio of clutch mass to female body mass (%). In order to calculate clutch mass for each species, I used the average clutch size produced by females multiplied by the average egg mass. I recorded reproductive effort as either small, when the ratio of clutch mass to female body mass was less than 50%, or large (>50%).

*Phylogenetic information.*—I used the phylogenetic classification of the following waterfowl tribes: Dendrocygnini (Livezey 1995a), Tachyerini (Livezey and Humphrey 1992), Anatini (which formerly included the Cairini; Livezey 1991), Aythyini (Livezey 1996), Oxyurini (Livezey 1995b), and Mergini (Livezey 1995c). These phylogenies were derived using characters other than those used in the present analysis. Tribes that include only one species were assumed to be evolutionarily independent from the others.

*Association tests.*—I used the contingent-states test to examine the association between ecological and life-history variables and the occurrence of preHBA and postHBA (Sillén-Tullberg 1993). This univariate

test is particularly suitable to investigate the relationship between two characters, each having two potential states. I investigated whether evolutionary transitions from non-amalgamation to amalgamation, the two states of the first character, were equally likely to take place under the two states for each life-history and ecological character. I then considered the occurrence or non-occurrence of preHBA or postHBA as a dependent variable, using all of the aforementioned life-history and ecological factors as independent variables. A condition of this test is that the two characters under investigation have been reconstructed over the phylogenetic tree. For each tribe with a phylogenetic tree, I reconstructed the occurrence of each character under the assumption that the following traits are ancestral: non-occurrence of amalgamation, ground nesting, solitary breeding, uniparental care, and large reproductive effort (see Livezey 1995a, b, c; 1996).

As an illustration of the test, consider whether transitions to preHBA are equally likely to take place on branches carrying the cavity-nesting or the ground-nesting state. For each state, I counted the number of branches with transitions to preHBA and the number of branches that maintain non-amalgamation. All branches that have maintained the non-amalgamation state are regarded as having the potential for a transition to preHBA. Branches that carry the preHBA state and those where a reversal of state occurred from amalgamation to non-amalgamation were left out of the analysis because a transition to preHBA cannot take place on such branches. Moreover, I left out branches where the state of the dependent and independent variables could not be assigned. The resulting frequencies for each tribe were combined in a  $2 \times 2$  table. Because branch lengths are unknown, the test assumes that state transitions are equally probable for all branches.

Reversals involve branches where an evolutionary transition occurred from a more recently acquired state back to the ancestral state. When studying characters that are difficult to observe in the field, such as the occurrence of brood amalgamation in lesser-known species, a more parsimonious interpretation of reversals is that the more recently acquired state is present but has not yet been observed. Whether or not the more recent state is present, it is not advisable to include those branches in the contingency table.

Tribes for which no phylogenetic information is available can only be used indirectly for this test. Under the assumption that each branch carrying the non-amalgamation state has the potential for a transition to amalgamation, each species for which amalgamation is not reported can be included in the table as an instance of maintenance of the ancestral state. A problem arises in tribes that include several species carrying the amalgamation trait. In this case, it is impossible to ascertain whether the trait arose independently in each species, or once in a common ancestor.

Therefore, only one independent origin of the state can be tallied in each tribe that includes more than one species with the amalgamation state.

The test is sensitive to biased inclusion of taxa. Therefore, it is important to consider whether the exclusion of certain branches from analyses due to incomplete phylogenetic information can bias the results with respect to the hypotheses being tested. Phylogenetic information was not available in two tribes (Anserini and Tadornini) that are well known for the frequent occurrence of preHBA and postHBA (see Appendix). The partial exclusion of geese and swans is more problematic because the Anserini includes several branches carrying rare states such as colonial breeding and small reproductive effort (Appendix). However, several species in the tribe show similar amalgamation tendencies, which suggests that amalgamation did not arise independently in each species but instead arose a few times in common ancestors, thereby lessening any effects related to the partial exclusion of certain branches from the analysis.

## RESULTS

*Occurrence of brood amalgamation.*—Intraspecific preHBA and postHBA occur commonly among the 162 species of waterfowl included in the analysis (Table 1, Appendix). PreHBA was reported in 76 species, and excluding unknown cases, 57% of species exhibited preHBA at least infrequently. PostHBA occurred less often and was reported in 48 species. Excluding unknown cases, 38% of species exhibited postHBA, at least infrequently. Both types of brood amalgamation were exhibited by 44 species, 26 species exhibited only preHBA, and 3 species exhibited only postHBA. Because information was not available for several species, the occurrence of brood amalgamation undoubtedly was underestimated.

*Determinants of preHBA.*—I found that transitions to amalgamation were more frequent on branches carrying the: (1) colonial- rather than solitary-breeding state, (2) cavity- rather than ground-nesting state, and (3) large- rather than small-reproductive-effort state (Table 2). Transitions to amalgamation arose as frequently on branches carrying the biparental-care state as on those carrying the uniparental-care state (Table 2).

Nest-site location is a potential confounding factor in the analysis of coloniality because most colonial species nest on the ground, in contrast to noncolonial species (Appendix). Hence, I excluded branches carrying the cavity-nesting state

TABLE 1. Number of species in each tribe exhibiting prehatching and posthatching brood amalgamation.

Tribe	Prehatching brood amalgamation			Posthatching brood amalgamation		
	Unknown	Unreported	Occurs	Unknown	Unreported	Occurs
Anseranatini	—	—	1	—	1	—
Dendrocygnini	2	1	6	5	2	2
Anserini	3	10	10	1	14	8
Cereopsini	—	1	—	—	1	—
Stictonettini	—	—	1	—	1	—
Tadornini	4	6	4	4	6	4
Tachyerini	—	3	1	—	4	—
Merganettini	—	1	—	—	1	—
Anatini	11	32	17	16	36	8
Aythiini	4	1	10	4	4	7
Mergini	4	2	18	4	3	17
Oxyurini	1	—	8 <sup>a</sup>	1	5	2

<sup>a</sup> One species is an obligate interspecific parasite.

and found that transitions to amalgamation in the subset of branches carrying the ground-nesting state were still more likely to occur in colonial branches ( $G_{adj} = 4.98, n = 107, P < 0.05$ ). Similarly, reproductive effort is a potential confounding factor in the analysis of nest-site location because cavity nesters tend to invest relatively more in their offspring than do ground nesters (Appendix). I excluded branches carrying the small-reproductive-effort state from the analysis of nest-site location and found that transitions to amalgamation in the subset of branches carrying the large-reproductive-effort

state still were more likely to occur in cavity-nesting lineages ( $G_{adj} = 5.17, n = 86, P < 0.025$ ). Species that are characterized by the small-reproductive-effort state also tend to be ground nesters. In contrast to the previous finding, I found that transitions to amalgamation in the subset of branches carrying the ground-nesting state were equally likely to occur on branches carrying the small- or large-reproductive-effort state ( $G_{adj} = 1.51, n = 101, P > 0.10$ ).

*Determinants of postHBA.*—Transitions to postHBA were equally likely to occur on branches carrying the: (1) colonial- or solitary-breeding state, and (2) biparental- or uniparental-care state. However, such transitions occurred more frequently on branches carrying the large- rather than small-reproductive-effort state (Table 3). The occurrence of postHBA was strongly associated with the occurrence of preHBA on the same branch (Table 3).

I did not find an association between coloniality and reproductive effort, because an equal number of colonial species was characterized by a small or large value of the reproductive-effort index (Appendix). This reduces the likelihood that coloniality was a confounding factor in the analysis of reproductive effort.

## DISCUSSION

The usefulness of phylogenetic information in comparative analyses is widely recognized (Harvey and Pagel 1991). The subject of more recent discussions centers around how the information should be used. The contingent-states test was devised to investigate the correlation between two discrete characters and has been

TABLE 2. Transition to prehatching brood amalgamation or maintenance of non-amalgamation as function of contrasting life-history and ecological traits in waterfowl.

Trait	Transition to	
	Prehatching brood amalgamation	Maintenance of non-amalgamation
<b>Nesting dispersion (<math>G = 4.73^*</math>)<sup>a</sup></b>		
Colonial	2	0
Solitary	22	104
<b>Nesting substrate (<math>G = 6.61^{**}</math>)</b>		
Ground	16	95
Cavity	2	11
<b>Reproductive effort (<math>G = 4.28^*</math>)</b>		
Small	3	31
Large	21	64
<b>Brood care (<math>G = 0.20^{ns}</math>)</b>		
Biparental	12	56
Uniparental	11	39

<sup>ns</sup>,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ .

<sup>a</sup>  $G$ -tests adjusted with Williams' correction.

used in recent studies of the evolution of aposomatic coloration in insects and of mating systems in birds (Sillén-Tullberg 1993, Temrin and Sillén-Tullberg 1995). I used the test to investigate the pattern of association between the occurrence of intraspecific preHBA and postHBA and the possible states of a series of life-history and ecological variables. The analysis adds a new dimension to comparative studies of the determinants of intraspecific brood amalgamation in waterfowl and confirms or challenges several earlier hypotheses.

*Determinants of preHBA.*—The analysis shows that the occurrence of preHBA is associated with coloniality and cavity nesting, two factors thought to increase opportunities for laying eggs in the nests of conspecifics (Eadie et al. 1988, Rohwer and Freeman 1989, Sayler 1992). Moreover, these two factors can influence the occurrence of amalgamation independently of each other. The relative detectability of nests, therefore, can be considered a proximate cause of preHBA in waterfowl.

The type of parental care was not correlated with the occurrence of amalgamation. Although the presence of males during incubation can deter females from laying eggs in the nests of others (e.g. Mineau 1978, Chronister 1985), preHBA was equally likely to occur on branches carrying the biparental-care or the uniparental-care state. It is therefore possible that the presence of two parents has only marginal effects on the prevention or avoidance of preHBA.

I failed to find an association between life history, as classified by reproductive effort, and the occurrence of preHBA. In a study of the frequency of preHBA in North American Anatidae, Eadie et al. (1988) found little evidence for an association between life history, classified along the  $r$  and  $K$  continuum, and amalgamation using genera as independent units of analysis. Sayler (1992), however, used species as independent units of analysis and showed that species under selection for a high reproductive effort were more likely to exhibit amalgamation tendencies. I suggest that this result is an artifact of biased inclusion of taxa. After controlling for phylogeny and taking into account nest-site location, the association between reproductive effort and brood amalgamation disappeared in a subset of the total data set. The results suggest that parental behavior and reproductive effort are less important as a

TABLE 3. Transition to posthatching brood amalgamation or maintenance of non-amalgamation as function of contrasting life-history and ecological traits in waterfowl.

Trait	Transition to	
	Posthatching brood amalgamation	Maintenance of non-amalgamation
<b>Nesting dispersion (<math>G = 0.47^{ns}</math>)<sup>a</sup></b>		
Colonial	2	9
Solitary	16	138
<b>Reproductive effort (<math>G = 5.02^*</math>)</b>		
Small	1	39
Large	17	104
<b>Brood care (<math>G = 1.73^{ns}</math>)</b>		
Biparental	6	67
Uniparental	12	67
<b>Prehatching amalgamation (<math>G = 21.42^{***}</math>)</b>		
Present	16	47
Absent	2	97

<sup>ns</sup>,  $P > 0.05$ ; <sup>\*</sup>,  $P < 0.05$ ; <sup>\*\*\*</sup>,  $P < 0.001$ .

<sup>a</sup>  $G$ -tests adjusted with Williams' correction.

proximate determinant of preHBA than opportunities for successful amalgamation. The logic that species under selection for high reproductive effort might benefit more from intraspecific brood amalgamation probably needs to be re-considered.

*Determinants of postHBA.*—I failed to find an association between postHBA and coloniality because several noncolonial species exhibited postHBA (Afton and Paulus 1992). One potential reason is that solitary breeders will sometimes nest at densities that are sufficiently high to favor encounters between families and, thus, potential brood amalgamation in areas with limited brood habitats. Indeed, postHBA was thought to be an artifact of high brood density in noncolonial Mallards (*Anas platyrhynchos*; Titman and Lowther 1975) Common Shelducks (*Tadorna tadorna*; Patterson et al. 1982), and Canada Geese (*Branta canadensis*; Warhurst and Bookhout 1983). Therefore, a relative index of nest density that goes beyond the usual colonial-solitary breeding dichotomy may be more appropriate to examine the effect of brood density on amalgamation tendencies.

Involvement of the male parent during brood rearing was not associated with the occurrence of postHBA, contrary to the hypothesis that biparental-care species would be able to maintain family cohesion and protect the family to a greater extent than would uniparental species

(Afton and Paulus 1992). In parallel to the conclusion reached at the prehatching stage, the presence of two parents apparently has only marginal effects on the prevention or avoidance of postHBA.

The finding that postHBA is prevalent on branches carrying the high-reproductive-effort state must be interpreted with caution because the small sample size makes this test more sensitive to the partial exclusion of the Anserini from the analysis. More interesting is the general correlation between the occurrence of brood amalgamation before and after hatching. Indeed, the results show that the majority of species that exhibit postHBA also exhibit preHBA. Therefore, it is conceivable that the factors promoting the occurrence of amalgamation early in the breeding cycle, such as constraints on parental breeding (Sayler 1992), also favor amalgamation after hatching. In this case, postHBA may represent an extension of preHBA that increases the window of opportunity for amalgamation on a temporal scale. My study supports the idea proposed by Eadie et al. (1988) that in several species amalgamation before versus after hatching represent different means of achieving the same goal of mixing broods.

*Directions for future study.*—Phylogenetic studies could be extended to cases of interspecific brood amalgamation. Several species of waterfowl lay eggs in the nests of other species (Eadie et al. 1988, Lyon and Eadie 1991). The hypothesis that interspecific preHBA represents an extension of intraspecific preHBA that increases the potential number of available nest sites could be investigated easily with the contingent-states test (Lyon and Eadie 1991).

Although the analysis focused on broad patterns of variation across species, the pattern of occurrence of brood amalgamation across ecological categories in any given species should follow the patterns uncovered at the coarser phylogenetic level. With respect to the effect of nest density for instance, preHBA within a species is already known to affect clustered nests on islands more often than widely scattered nests in uplands (Rohwer and Freeman 1989, Sayler 1992). Similarly, the pattern of occurrence of intraspecific preHBA should vary within a species as a function of nest-site location; i.e. populations that use cavities should exhibit preHBA more frequently than populations that nest on the ground.

A challenge for future studies is to quantify

both the occurrence of intraspecific brood parasitism and the various ecological variables that act as determinants. A more quantitative analysis would be important in understanding the variation across species in the extent to which intraspecific brood parasitism occurs.

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APPENDIX. Occurrence of prehatching (preHBA) and posthatching (postHBA) brood amalgamation in waterfowl.

Species <sup>a</sup>	Nesting <sup>b</sup>	RCM <sup>c</sup>	PPDI <sup>d</sup>	PPDR	Pre-HBA	Post-HBA	Source <sup>e</sup>
<b>Tribe Anseranatini</b>							
<i>Anseranas semipalmata</i>	E, C	55.6	0	0	0	—	1, 2, 3, 8
<b>Tribe Dendrocygnini</b>							
<i>Dendrocygna viduata</i>	E, U, S	54.4	0	0	0	?	1, 2
<i>D. autumnalis</i>	H, S/C	73.4	0	0	0	0	1, 2, 5, 9, 11, 24
<i>D. guttata</i>	H, S?	61.3	0	?	?	?	1
<i>D. arborea</i>	H, S	62.2	0	?	?	?	1
<i>D. arcuata</i>	U, S	54.6	0	0	0	0	1, 3
<i>D. javanica</i>	H, S	70.0	0	0	0	?	1
<i>D. eytoni</i>	U, S	50.5	0	0	—	—	1, 3
<i>D. bicolor</i>	E, S/C	72.5	0	0	0	—	1, 2, 5, 11
<i>Thalassornis leucotis</i>	E, S	69.4	0	?	0	?	1, 2
<b>Tribe Anserini</b>							
<i>Cygnus olor</i>	E, U, S/C	19.1	0	0	0	—	1, 5, 6, 11, 36
<i>C. atratus</i>	E, U, S/C	29.4	0	0	0	0	1, 2, 3
<i>C. melanocorynphus</i>	E, S	37.1	0	0	—	—	1
<i>C. buccinator</i>	E, S	17.3	0	0	—	—	1, 5, 11, 33
<i>C. columbianus</i>	U, S	18.1	0	0	—	—	1, 11
<i>C. cygnus</i>	U, S	20.4	0	0	—	—	1, 6



## APPENDIX. Continued.

Species <sup>a</sup>	Nesting <sup>b</sup>	RCM <sup>c</sup>	PPDI <sup>d</sup>	PPDR	Pre-HBA	Post-HBA	Source <sup>e</sup>
<i>C. bewickii</i>	U, S	15.6	0	0	—	—	1, 6
<i>Coscoroba coscoroba</i>	E, U, S	15.6	0	0	—	—	1
<i>Anser cygnoides</i>	U, S	24.2	0	0	—	—	1, 2
<i>A. (f.) fabalis</i>	U, S/C	16.7	0	0	?	—	1, 2, 5
<i>A. (f.) brachyrhynchus</i>	U, S/C	16.7	0	0	?	0	1, 6
<i>A. albifrons frontalis</i>	U, S	28.1	0	0	—	—	1, 5, 11
<i>A. erythropus</i>	U, S	29.4	0	0	—	—	1, 6
<i>A. indicus</i>	U, E, S/C	22.6	0	0	0	0	1, 26
<i>A. anser</i>	U, S/C	25.8	0	0	0	?	1, 2, 6
<i>Chen caerulescens</i>	U, C	25.2	0	0	0	0	1, 2, 5, 11, 27, 28
<i>C. rossii</i>	U, C	30.7	0	0	0	0	1, 5, 11
<i>C. canagica</i>	U, S/C	21.7	0	0	0	0	1, 5, 11
<i>Branta sandvicensis</i>	U, S	34.4	0	0	—	—	1, 34
<i>B. canadensis</i>	E, U, S/C	18.1	0	0	0	0	1, 2, 3, 5, 6, 11
<i>B. leucopsis</i>	U, C	35.7	0	0	0	0	1, 5, 6, 11, 29, 30
<i>B. bernicla</i>	U, C	22.7	0	0	0	—	1, 5, 6, 11, 38
<i>B. ruficollis</i>	U, C	39.7	0	0	?	—	1
<b>Tribe Cereopsini</b>							
<i>Cereopsis novaehollandiae</i>	U, S	18.2	0	0	—	—	1, 3
<b>Tribe Stictonettini</b>							
<i>Stictonetta naevosa</i>	E, S	54.9	—	—	0	—	1, 3
<b>Tribe Tadornini</b>							
<i>Cyanochen cyanopterus</i>	U, S?	39.1	?	?	?	?	1
<i>Chloephaga melanoptera</i>	U, S?	30.6	0	0	—	—	1
<i>C. picta</i>	U, S	24.2	0	0	—	—	1
<i>C. hybrida</i>	U, S	41.7	0	0	—	—	1
<i>C. poliocephala</i>	U, S	20.2	0	0	—	—	1
<i>C. rubidiceps</i>	U, S	27.0	0	0	—	—	1
<i>Neochen jubata</i>	H, S	40.3	0	0	?	?	1
<i>Alopochen aegyptiacus</i>	U, H, S	41.2	0	0	—	—	1, 6
<i>Tadorna ferruginea</i>	H, S	69.2	0	0	0	0	1, 6
<i>T. cana</i>	H, S	58.6	0	0	?	?	1
<i>T. tadornoides</i>	H, S	86.4	0	0	0	0	1, 2, 3, 22
<i>T. variegata</i>	H, S	56.0	0	0	0	0	1, 3
<i>T. tadorna</i>	H, S	70.0	0	0	0	0	1, 2, 6, 23, 25
<i>T. radjah</i>	H, S	63.3	0	0	?	?	1, 3
<b>Tribe Tachyerini</b>							
<i>Tachyeres patachonicus</i>	U, S	30.8	0	0	—	—	1, 7
<i>T. pteneres</i>	U, S	24.4	0	0	—	—	1, 7
<i>T. leucocephalus</i>	U, S	?	?	?	—	—	1, 7
<i>T. brachypterus</i>	U, S	25.9	0	0	0	—	1, 7
<b>Tribe Merganettini</b>							
<i>Merganetta armata</i>	H, S	71.1	0	0	—	—	1
<b>Tribe Anatini</b>							
<i>Hymenolaimus malacorhynchus</i>	H, S	52.6	0	0	—	—	1, 3, 39
<i>Salvadorina waigiuiensis</i>	U, S	37.1	0	0	—	—	1
<i>Cairina moschata</i>	H, E, S	74.0	—	—	0	?	1
<i>C. scutulata</i>	H, U, S?	35.6	?	?	?	?	1
<i>Pteronetta hartlaubi</i>	H, S	45.3	0	0	?	—	1
<i>Aix sponsa</i>	H, S	114.3	0	—	0	0	1, 2, 4, 5, 11
<i>A. galericulata</i>	H, S	77.9	0	—	—	—	1, 6
<i>Chenonetta jubata</i>	H, S	67.5	0	0	0	0	1, 3, 10, 40
<i>Nettion auritus</i>	H, S	79.6	—	?	?	?	1
<i>N. coromandelianus</i>	H, S	71.1	?	?	0	—	1, 3
<i>N. pulchellus</i>	H, S	98.7	0	0	0	—	1, 3
<i>Amazonetta brasiliensis</i>	E, H, S	37.4	0	0	?	?	1

## APPENDIX. Continued.

Species <sup>a</sup>	Nesting <sup>b</sup>	RCM <sup>c</sup>	PPDI <sup>d</sup>	PPDR	Pre-HBA	Post-HBA	Source <sup>e</sup>
<i>Callonetta leucophrys</i>	H, S?	115.2	O	O	?	—	1, 41
<i>Lophonetta specularioides</i>	U, S	40.4	O	O	—	—	1, 42
<i>Specularias specularis</i>	U, S	39.1	?	?	—	—	1
<i>Mareca capensis</i>	U, S	59.2	O	O	—	—	1
<i>M. strepera</i>	U, S	51.8	O	—	O	O	1, 2, 4, 5, 6, 11
<i>M. falcata</i>	U, S	67.0	O	—	—	?	1
<i>M. sibilatrix</i>	U, S	41.6	O	O	—	—	1
<i>M. penelope</i>	U, S	61.9	—	—	O	—	1, 6
<i>M. americana</i>	U, S	50.6	O	—	—	—	1, 4, 5, 11
<i>Anas sparsa</i>	U, H, S	40.1	—	—	—	—	1
<i>A. rubripes</i>	U, S	51.6	O	—	O	—	1, 4, 5
<i>A. (p.) fulvigula</i>	U, S	55.8	—	—	—	—	1, 5, 11
<i>A. (p.) diazi</i>	U, S	—	—	—	—	—	1, 4, 11
<i>A. (p.) platyrhynchos</i>	U, S	50.4	—	—	O	O	1, 2, 3, 4, 6, 11, 44
<i>A. (p.) wyvilliana</i>	U, S	62.3	—	—	?	?	1
<i>A. (p.) laysanensis</i>	U, S	—	—	—	?	?	1
<i>A. luzonica</i>	U, S	65.5	?	?	—	?	1
<i>A. (p.) superciliosa</i>	U, H, S	60.0	—	—	O	—	1, 3
<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
<i>A. melleri</i>	U, S	—	?	?	?	?	1
<i>A. discors</i>	U, S	87.3	O	—	—	—	1, 4, 5, 11
<i>A. cyanoptera</i>	U, S	88.4	O	—	—	—	1, 4, 5
<i>A. smithii</i>	U, S	75.4	O	—	—	—	1
<i>A. platalea</i>	U, S?	57.2	?	?	—	—	1
<i>A. rhynchotis</i>	U, S	64.7	?	?	—	—	1, 3
<i>A. clypeata</i>	U, S	72.7	O	—	O	O	1, 5, 6
<i>A. bernieri</i>	U, S	—	?	?	?	?	1, 37
<i>A. gibberifrons</i>	U, H, S	55.4	?	?	O	—	1, 2, 3
<i>A. castanea</i>	U, H, S	70.5	O	O	O	—	1, 3
<i>A. chlorotis</i>	U, S	60.9	O	?	—	—	1, 3
<i>A. aucklandica</i>	U, S	58.3	O	?	—	—	1, 3
<i>A. bahamensis</i>	U, S	—	O	?	—	?	1, 35
<i>A. erythrorhyncha</i>	U, S	68.9	O	—	—	—	1
<i>A. flavirostris</i>	H, U, S	64.3	O	O	—	—	1
<i>A. georgica</i>	U, S	41.7	O	O	—	—	1, 2
<i>A. (a.) acuta</i>	U, S	40.6	—	—	—	—	1, 5, 6, 11
<i>A. (a.) eatoni</i>	U, S	—	—	—	—	—	1, 3
<i>A. querquedula</i>	U, S	81.0	—	—	O	—	1, 6
<i>A. formosa</i>	U, S	53.9	?	?	—	?	1
<i>A. (c.) crecca</i>	U, S	—	—	—	—	—	1, 6
<i>A. (c.) carolinensis</i>	U, S	81.5	—	—	O	O	1, 4, 5, 11
<i>A. (v.) versicolor</i>	U, S	72.9	?	?	—	?	1, 2
<i>A. (v.) puna</i>	U, S	—	?	?	—	?	1, 2
<i>A. hottentota</i>	U, E, S	72.9	O	—	—	—	1
<i>Malacorhynchos membranaceus</i>	H, S	63.1	O	O	O	O	1, 3
<b>Tribe Aythyini</b>							
<i>Marmaronetta angustirostris</i>	U, S/C	77.5	—	—	O	—	1, 6
<i>Netta rufina</i>	U, E, S	52.1	O	O	O	—	1, 6
<i>Metopiana erythrophthalma</i>	U, E, S	70.8	?	?	?	?	1, 2
<i>M. peposaca</i>	E, S	59.8	—	—	O	O	1
<i>Aythya valisineria</i>	E, S	58.9	—	—	O	O	1, 5, 11, 31
<i>A. ferina</i>	E, S	55.8	O	—	O	O	1, 6
<i>A. americana</i>	E, S	44.2	O	—	O	O	1, 5, 11, 32
<i>A. australis</i>	E, S	71.6	—	—	O	?	1, 3
<i>A. baeri</i>	E, S	56.9	?	?	?	?	1
<i>A. nyroca</i>	E, U, S	74.4	O	—	O	—	1, 6
<i>A. innotata</i>	E, S	—	?	?	?	?	1
<i>A. novaeseelandiae</i>	U, E, S/C	67.1	—	—	?	—	1, 3

## APPENDIX. Continued.

Species <sup>a</sup>	Nesting <sup>b</sup>	RCM <sup>c</sup>	PPDI <sup>d</sup>	PPDR	Pre-HBA	Post-HBA	Source <sup>e</sup>
<i>A. fuligula</i>	E, S	53.3	—	—	O	O	1, 6
<i>A. collaris</i>	E, S	59.1	O	—	—	—	1, 5, 11
<i>A. marila</i>	U, S/C	67.0	—	—	O	O	1, 2, 5, 6, 11
<i>A. affinis</i>	U, S	55.0	O	—	O	O	1, 2, 5, 11
<b>Tribe Oxyurini</b>							
<i>Heteronetta atricapilla</i>	E, S		—	—	—	—	1, 12
<i>Nomonyx dominicus</i>	E, S	76.7	—	—	O	—	1, 2
<i>Oxyura ferruginea</i>	E, S		?	?	?	?	12
<i>O. jamaicensis</i>	E, S	116.8	—	—	O	O	1, 2, 4, 5, 6
<i>O. vittata</i>	E, S	61.4	—	—	O	—	1
<i>O. australis</i>	E, S	58.1	—	—	O	O	1, 3
<i>O. maccoa</i>	E, S	80.0	—	—	O	—	1, 2
<i>O. leucocephala</i>	E, S	100.0	—	—	O	—	1, 6
<i>Biziura lobata</i>	E, S	16.5	O	O	O	—	1, 3
<b>Tribe Mergini</b>							
<i>Polysticta stelleri</i>	U, S	50.6	O	—	—	O	1, 4, 5, 6, 11
<i>Somateria fischeri</i>	U, S	17.9	—	—	O	O	1, 4, 5, 11
<i>S. spectabilis</i>	U, S	20.9	—	—	O	O	1, 5, 11
<i>S. (m.) v-nigrum</i>	U, C	21.6	—	—	?	?	1, 45
<i>S. (m.) dresseri</i>	U, C	23.5	—	—	O	O	1, 4, 5, 11, 13, 14, 45
<i>S. (m.) borealis</i>	U, C	30.7	—	—	O	O	1, 15, 16, 45
<i>S. (m.) mollissima</i>	U, C	18.1	—	—	O	O	1, 6, 17, 18
<i>Histrionicus histrionicus</i>	U, S	58.9	—	—	O	O	1, 5, 6, 11
<i>Melanitta perspicillata</i>	U, S	53.3	—	—	—	O	1, 11
<i>M. (f.) fusca</i>	U, S	53.2	—	—	O	O	1, 6
<i>M. (f.) deglandi</i>	U, S	62.4	—	—	O	O	1, 5, 11, 19
<i>M. (n.) nigra</i>	U, S	56.9	—	—	O	O	1, 2, 6
<i>M. (n.) americana</i>	U, S	45.5	—	—	O	—	1, 4, 5, 11
<i>Clangula hyemalis</i>	U, S	43.0	—	—	O	O	1, 4, 5, 6, 11
<i>Bucephala albeola</i>	H, S	95.3	—	—	O	O	1, 2, 4, 11, 20
<i>B. clangula</i>	H, S	87.5	—	—	O	O	1, 2, 4, 11
<i>B. islandica</i>	H, S	71.3	—	—	O	O	1, 2, 4, 11, 20
<i>Mergellus albellus</i>	H, S	50.4	—	—	O	—	1, 6
<i>Lophodytes cucullatus</i>	H, S	111.1	—	—	O	—	1, 4, 5, 11, 21
<i>Mergus australis</i>	?		?	?	?	?	1
<i>M. octoetaceus</i>	H, S?		O	O	?	?	1, 43
<i>M. merganser</i>	H, S	73.9	—	—	O	O	1, 4, 5, 11
<i>M. serrator</i>	U, S	64.9	—	—	O	O	1, 2, 4, 5, 11
<i>M. squamatus</i>	H, S		?	?	?	?	1, 2

<sup>a</sup> Based on tribal classifications of Johnsgard (1978) and Livezey (1991; 1995a, b, c; 1996).

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

<sup>c</sup> RCM = relative clutch mass; PPDI = paternal presence during incubation; PPDR = paternal presence during brood rearing.

<sup>d</sup> ? = not known; — = not reported; O = occurs.

<sup>e</sup> (1) Johnsgard 1978; (2) Saylor 1992; (3) Marchant and Higgins 1990; (4) Johnsgard 1975; (5) Palmer 1976; (6) Cramp and Simmons 1977; (7) Livezey and Humphrey 1992; (8) Whitehead and Tschirner 1991; (9) Bergman 1994; (10) Briggs 1991; (11) Bellrose 1978; (12) Livezey 1995b; (13) Munro and Bédard 1977; (14) Robertson et al. 1992; (15) Bjorn and Erikstad 1994; (16) Bustnes and Erikstad 1991; (17) Gorman and Milne 1972; (18) Swennen 1989; (19) Kehoe 1989; (20) Savard 1987; (21) Zicus 1990; (22) Frith 1967; (23) Hori 1969; (24) McCamant and Bolen 1979; (25) Patterson et al. 1982; (26) Weigmann and Lamprecht 1991; (27) Williams 1994; (28) Lank et al. 1991; (29) Choudhury et al. 1993; (30) Forslund and Larsson 1995; (31) Sorenson 1993; (32) Sorenson 1991; (33) Henson and Cooper 1992; (34) Banko 1992; (35) Sorenson et al. 1992; (36) Perrins et al. 1994; (37) Green et al. 1994; (38) Bregnballe and Madsen 1990; (39) Veltman and Williams 1990; (40) Kingsford 1990; (41) Brewer 1989; (42) Buitron and Nuechterlein 1989; (43) Bartmann 1988; (44) Titman and Lowther 1975; (45) Alisauskas and Ankney 1992.