

EFFECTS OF NEST PARASITISM AND NEST LOCATION ON EGG SHELL STRENGTH IN WATERFOWL¹

MARK L. MALLORY AND PATRICK J. WEATHERHEAD²

Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada

Abstract. We examined the relationship between brood parasitism, nest location, egg shape, and eggshell thickness in waterfowl species. We found that within and across tribes, parasitic species did not have significantly rounder eggs or thicker shells than nonparasitic species. However, cavity-nesting species have both rounder eggs and thicker eggshells than open-nesting species. Cavity-nesting waterfowl may require stronger eggs because they often nest in sites that are too small or are irregularly shaped, thereby increasing the jostling of eggs against one another when the female enters or exits the nest. Using data for the Hooded Merganser (*Lophodytes cucullatus*), the species with the roundest egg and the proportionally thickest shell of all extant waterfowl, we found no evidence for a cost of increased eggshell strength, at least with regard to incubation period and egg hatchability. We also were unable to explain why Hooded Mergansers lay eggs like billiard balls.

Key words: Brood parasitism; cavity nesting; waterfowl; eggshell thickness; egg shape.

INTRODUCTION

The avian eggshell must serve numerous functions simultaneously, from preventing dehydration while allowing gas exchange (Ar et al. 1974), to protecting the contents while still allowing chicks to break out of the shell unaided. Thus, the observed characteristics of eggshells should reflect an evolutionary compromise between these conflicting functional demands, in addition to possible physical and physiological constraints that act on the females that produce the eggs. We should expect deviations from the norm in a specific eggshell trait to reflect unusual selection pressures on that trait. For example, the obligately brood-parasitic Brown-headed Cowbird (*Molothrus ater*) lays eggs that are relatively thicker shelled and rounder in shape than those of close relatives, which protects the cowbird eggs against puncture and cracking by hosts attempting to remove the eggs (Rothstein 1975, Blanckspoor et al. 1982, Spaw and Rohwer 1987, Picman 1989). In this paper we examine egg shape and shell thickness in waterfowl for evidence of similar patterns in relation to both brood parasitism and nest-site characteristics.

Many species of waterfowl exhibit inter- or intraspecific brood parasitism (or both) (Weller 1959, Lack 1968, Eadie et al. 1988). Note that in this paper we refer exclusively to prehatching

brood parasitism ("pre-HBA" in Eadie et al. 1988). Unlike the highly evolved host-parasite interactions in passerines (e.g., Rothstein 1975, Davies and Brooke 1988), however, there is little evidence from waterfowl of hosts intentionally damaging or ejecting parasitic eggs from their nests. Weller (1959) did show that the most conspicuously different eggs (marked chicken eggs) were ejected from the nests of several ground-nesting waterfowl species if these eggs were added during the laying period of the host. However, the less conspicuous eggs of normal hosts or parasites were accepted. Weller (1959, p. 352) concluded that "discrimination is not perfect in all cases for often the eggs of the host are buried as well." Nonetheless, if aggression by host females toward parasites forces the parasite to lay eggs quickly or causes eggs to get jostled (e.g., McLaren 1969), or if eggs in parasitized nests get jostled more simply due to the increased clutch size (Weller 1959), the evolution of thicker eggshells may have been favored in parasitic species.

Another aspect of waterfowl nesting that might influence the strength of their eggshells is where they nest. Although most waterfowl nest in the open, many species nest in cavities (Lack 1968, Bellrose 1976, Johnsgard 1978). Since waterfowl lack the necessary attributes to fashion cavities to their needs, they may often be forced to nest in cavities that are less than ideal (e.g., too deep, too narrow, irregularly shaped). Females climbing in and out of these cavities or incubating eggs may jostle the eggs much more than would an

¹ Received 2 April 1990. Final acceptance 31 July 1990.

² Author to whom correspondence should be sent.

open-nesting female. Thus, we would predict that cavity-nesting waterfowl lay stronger-shelled eggs than open-nesting waterfowl. Because nest sites for cavity-nesting species are often limited, brood parasitism is common in cavity-nesting waterfowl (e.g., Jones and Leopold 1967, Peterson and Gauthier 1985, Savard 1988). Therefore, an additional aim of this study is to assess the independent effects of both nesting habit (e.g., brood parasitism) and nesting location (e.g., cavity) on eggshell characteristics.

METHODS

We obtained data on egg mass, length, breadth, and shell thickness of waterfowl species from Schönwetter (1960). Because eggshell thickness increases logarithmically with egg mass (Spaw and Rohwer 1987), we used log values for both variables. The shape of eggs affects the strength of the shell (rounder eggs are stronger than more elongate eggs). We used the ratio of length to breadth (Picman 1989) as our index of egg shape.

We used Livezey's (1986) classification of waterfowl tribes. We relied on information in Johnsgard (1978) and Eadie et al. (1988) to designate species as parasitic. While many waterfowl species occasionally parasitize nests of other species (Rohwer and Freeman 1989), we considered a species as parasitic if it was documented to engage regularly in either intra- or interspecific parasitism (i.e., noted as parasitic in Johnsgard [1978], or classified as "occurs" in Eadie et al. 1988). Eadie et al. (1988) classified waterfowl in which parasitism "occurs" as those species for which parasitism was documented in several studies covering a broad geographic area. Johnsgard (1978) was less precise in his designation, but where both references dealt with the same species, they were in agreement in almost every case. We designated species as cavity-nesting if they obligately or predominantly nested in cavities according to Bellrose (1976), Johnsgard (1978), and Eadie et al. (1988). A summary of the egg characteristics for each species that we used is found in the Appendix. Data were analyzed using the Statistical Package for the Social Sciences (Nie 1988).

RESULTS

Our aim in this study was to determine whether brood-parasitic or cavity-nesting waterfowl produce stronger eggs. This first required removing

any effect of egg size on shell thickness or egg shape. For the family Anatidae, eggshell thickness increases with egg mass ($r = 0.89$, $P < 0.001$, $n = 121$, Fig. 1) and our egg shape index increases (i.e., eggs become more elongate) with egg mass ($r = 0.70$, $P < 0.001$, $n = 121$, Fig. 2). Note that in both analyses the Hooded Merganser (*Lophodytes cucullatus*) falls well outside the distribution of the other species. We have excluded Hooded Mergansers from the subsequent analyses to avoid this single species having an undue influence on our analyses, but consider reasons why Hooded Mergansers are anomalous in the Discussion. To remove the egg-size effects on shell thickness and egg shape, we use residual values from Figures 1 and 2 in the subsequent analysis.

EGG TRAITS AND BROOD PARASITISM

We predicted that brood parasitism should have favored the evolution of stronger eggs, and thus we expected that those tribes where parasitism predominates as a nesting strategy (e.g., Oxyurini and Aythyini) should have the strongest eggs. To assess the effect of brood parasitism independent of where species nested, we restricted our analyses to open-nesting species of the eight major waterfowl tribes (Dendrocygnini, Anserini, Cygnini, Tadornini, Anatini, Aythyini, Mergini, and Oxyurini). For open-nesting waterfowl, residual eggshell thickness differed significantly between tribes (ANOVA, $F = 11.24$, $df = 7$, 92 , $P < 0.001$, Table 1). Similarly, residual egg shape also differed between tribes (ANOVA, $F = 8.20$, $df = 7$, 92 , $P < 0.001$, Table 1). The Oxyurini and Aythyini, tribes typified by frequent nest parasitism, had rounder eggs and thicker eggshells than most other tribes. However, the Dendrocygnini also had relatively thick-shelled, round eggs and only one of the six open-nesting species is documented to be commonly parasitic. A problem with comparing egg traits between tribes is that some duck species may share egg characteristics for reasons of common ancestry rather than because of similar reproductive biology. Therefore, in all subsequent analyses we base our assessment of egg traits relative to parasitism on within-tribe comparisons.

Only the Anserini, Tadornini, Aythyini, and Mergini had two or more open-nesting species in both the parasitic and nonparasitic categories. In all cases, parasitic members of each tribe did not have significantly thicker eggshells or round-

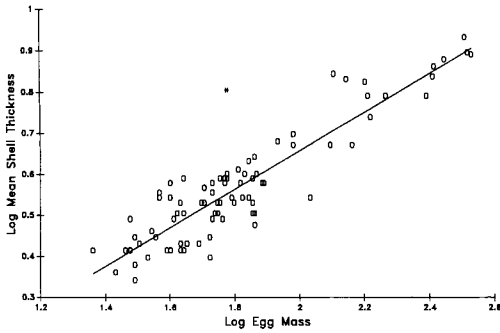


FIGURE 1. The relationship between waterfowl eggshell thickness and egg mass. The Hooded Merganser is represented by *.

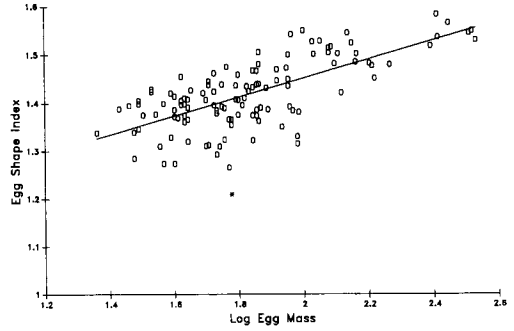


FIGURE 2. The relationship between waterfowl egg shape and egg mass. The Hooded Merganser is represented by *.

er eggs than nonparasitic members of the tribe (Table 2).

To compare parasitic and nonparasitic species across tribes, we cannot use residuals from the overall waterfowl regressions (Figs. 1, 2) because of the potential confounding effect of phylogenetic differences between tribes (Table 1). Effects of phylogenetic differences within tribes were considered small because open-nesting, parasitic species were not concentrated in any particular genus within each tribe (see Appendix). To combine samples for open-nesting species across these tribes, we repeated the regressions of egg shape and log eggshell thickness relative to log egg mass separately for each tribe. We restricted the regression analysis to open-nesting species to avoid possible effects due to cavity-nesting. For each open-nesting species we calculated the residual values from its within-tribe regressions. Therefore, the values for each species are based on how the species differs from other members of its own tribe. We then compared the residuals for all parasitic species with those of nonparasitic

species (see Pagel and Harvey [1988] for a review of this approach). Parasitic species did not have thicker eggshells or rounder eggs than nonparasitic species (Table 3). Thus, when we control for taxonomic effects, the relationship between eggshell strength and parasitism disappears.

EGG TRAITS AND NEST LOCATION

Four waterfowl tribes contain some species that nest in cavities: the Dendrocygnini, Tadornini, Anatini, and Mergini. We tested for differences in egg traits between cavity- and open-nesting species within each tribe. In all four cases, the mean residual eggshell thickness was greater in cavity-nesting species, but only significantly so in the Anatini and Mergini (Table 4). In three of four tribes, the mean residual egg shape indicated that cavity-nesting species had rounder eggs, with the difference being significant only in the Anatini (Table 4). Note that the result for the Mergini would have shown an even greater difference in both analyses had we included the Hooded Merganser.

TABLE 1. Mean and standard error of residual eggshell thickness (mm) and residual egg shape for open-nesting species of the eight major waterfowl tribes.

Tribe (n)	Eggshell thickness		Egg shape index	
	\bar{x}	SE	\bar{x}	SE
Oxyurini (6)	0.0794	0.0159	-0.0821	0.0239
Dendrocygnini (6)	0.0780	0.0170	-0.0793	0.0160
Aythya (15)	0.0316	0.0083	-0.0124	0.0125
Cygnini (8)	0.0148	0.0090	0.0010	0.0092
Tadornini (11)	-0.0045	0.0188	0.0094	0.0145
Anatini (30)	-0.0204	0.0055	0.0123	0.0077
Anserini (14)	-0.0212	0.0169	0.0266	0.0115
Mergini (10)	-0.0577	0.0128	0.0303	0.0089

TABLE 2. Comparisons of residual eggshell thickness (mm) and residual egg shape (based on within-tribe regressions) for parasitic and nonparasitic open-nesting members of waterfowl tribes in which these two strategies exist (Wald-Wolfowitz Runs tests).

Trait Tribe	Parasitic			Nonparasitic			z	P
	\bar{x}	SE	n	\bar{x}	SE	n		
Eggshell thickness								
Anserini	0.0134	0.017	3	-0.0037	0.013	11	0.00	0.67
Tadornini	-0.0053	0.005	2	0.0012	0.022	9	-0.90	0.20
Aythiini	0.0055	0.008	12	-0.0218	0.022	3	0.00	0.64
Mergini	-0.0071	0.028	2	0.0018	0.015	8	0.34	0.53
Egg shape index								
Anserini	-0.0004	0.004	3	0.0001	0.012	11	-0.18	0.42
Tadornini	0.0173	0.001	2	-0.0038	0.017	9	0.26	0.49
Aythiini	-0.0080	0.014	12	0.0320	0.024	3	-1.14	0.13
Mergini	-0.0140	0.008	2	0.0035	0.010	8	0.34	0.53

To combine data across these tribes, we repeated the procedure used in determining the effects of parasitism on egg traits across tribes (above), except that we included cavity-nesting members for calculating within-tribe regressions. We used residual eggshell thickness and residual egg shape calculated from these within-tribe regressions, and compared the residuals of cavity-nesting and open-nesting species. Collectively, cavity-nesting species had significantly thicker shells and rounder eggs than open-nesting species (Table 3).

DISCUSSION

Contrary to our first prediction, we found no evidence for waterfowl species that are regularly brood-parasitic to produce eggs with stronger shells. Our prediction was based on the observation from passerines, that the brood-parasitic Brown-headed Cowbird produces eggs that are thicker shelled and rounder than predicted for their size (Blankespoor et al. 1982, Spaw and Rohwer 1987, Picman 1989). Those features of

the cowbird egg are probably adaptations to specific host responses to the cowbird egg (e.g., puncturing) rather than to increased jostling of eggs associated with the parasitic egg being laid. The absence of well-developed egg ejection behavior by waterfowl in response to parasitic eggs may explain why brood-parasitic waterfowl have not evolved eggs with stronger shells.

Our prediction that cavity-nesting waterfowl should lay stronger shelled eggs was supported. This prediction was based on the reasoning that the irregularities of tree cavities might cause eggs to be bumped against each other and the cavity wall by the incubating females. This problem might be particularly pronounced when a female enters or exits the cavity. Because waterfowl lack a bill suitable for excavating cavities, nest sites are likely to be limited (e.g., Peterson and Gauthier 1985), forcing many birds to nest in sub-optimal sites where eggs would be more prone to damage. If this reasoning is correct, we predict that, among other avian families, cavity-nesting species that rely on either natural cavities or those

TABLE 3. Comparisons of mean residual eggshell thickness (mm) and residual egg shape (based on within-tribe regressions) for parasitic and nonparasitic species, and for cavity-nesting and open-nesting species (*t*-tests).

Trait	Comparison						t	P
	\bar{x}	SE	n	\bar{x}	SE	n		
Parasitic								
Eggshell thickness	0.004	0.006	19	-0.003	0.009	31	0.65	0.52
Egg shape index	-0.005	0.009	19	0.003	0.007	31	-0.66	0.51
Cavity-nesting								
Open-nesting								
Eggshell thickness	0.040	0.010	21	-0.020	0.010	57	-5.62	<0.001
Egg shape index	-0.030	0.010	21	0.010	0.010	57	3.77	<0.001

TABLE 4. Comparison of residual eggshell thickness (mm) and residual egg shape (based on within-tribe regressions) of cavity- and open-nesting members of waterfowl tribes in which these two strategies exist (Mann-Whitney *U*-tests).

Trait Tribe	Cavity-nesting			Open-nesting			<i>z</i>	<i>P</i>
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>		
Eggshell thickness								
Dendrocygnini	0.0069	0.038	2	-0.0023	0.017	6	0.54 ^a	0.64
Tadornini	0.0087	0.013	5	-0.0040	0.018	11	-0.62	0.53
Anatini	0.0573	0.007	9	-0.0172	0.005	30	-4.33	<0.001
Mergini ^b	0.0551	0.018	5	-0.0276	0.015	10	-2.57	0.01
Egg shape index								
Dendrocygnini	0.0238	0.028	2	-0.0079	0.015	6	0.54 ^a	0.64
Tadornini	-0.0293	0.013	5	0.0133	0.014	11	-1.75	0.08
Anatini	-0.0390	0.011	9	0.0177	0.007	30	-3.20	<0.001
Mergini ^b	-0.0203	0.016	5	0.0101	0.009	10	-1.47	0.14

^a Due to small sample size in each group, a Wald-Wolfowitz Runs test was used.

^b The value for the cavity-nesting Mergini excludes the Hooded Merganser, an outlier for both eggshell thickness and egg shape.

made by other birds, should have stronger shelled eggs than those species that excavate their own cavities.

If the shape and thickness of the "average" avian egg reflect some optimal compromise between all the functions an eggshell must serve, then we should expect some trade-off in egg performance (e.g., hatchability) in those species that produce atypical eggs (e.g., thicker shells). The Hooded Merganser would seem a prime candidate to examine for evidence of such a trade-off. First, we should point out that the values we presented in Figures 1 and 2 for Hooded Mergansers are not due to error. We confirmed those values from two sources (Soulliere 1987, Zicus et al. 1988) and found other allusions to this oddity. For example, J. H. Bowles (in Bent 1923, p. 24) noted that the eggs of the Hooded Merganser "... are just about the same size, shape and color of white billiard balls, and every bit as hard in their composition." Although Hooded Mergansers are both cavity-nesters and brood parasites (Eadie et al. 1988), we have no explanation for why they produce eggs that are so much stronger than other cavity-nesting brood parasites.

We can, however, examine the consequences of producing eggs like billiard balls. On the positive side, several studies have noted the rarity of cracked Hooded Merganser eggs (Lumsden and Wenting 1976, Zicus et al. 1988), even when the eggs have been seriously traumatized (M. L. Mallory, pers. observ.). However, we can find no evidence of impaired egg performance. The hatching success of Hooded Merganser eggs

(90.7%) is similar to the mean for the rest of the tribe ($88.0 \pm 6.3\%$), and for most other North American species ($86.6 \pm 12.5\%$, all values from Bellrose 1976). In addition, the incubation period for Hooded Mergansers is approximately 30 days, similar to that of related species (Bellrose 1976). The incubation period is presumably unaffected by the increased shell thickness because shell porosity and water conductance of Hooded Merganser eggs do not differ significantly from eggs of other ducks (Hoyt et al. 1979). Other possibilities that we cannot address are costs to the female from mobilizing sufficient calcium to produce the shells, or effects on posthatching survival of ducklings due to the cost of breaking out of such hard shells. The Hooded Merganser would appear to be a fertile subject for future studies, both to unravel the mystery of why they produce such unusual eggs, and as a model system for waterfowl in general to investigate the consequences of producing strong-shelled eggs.

ACKNOWLEDGMENTS

We thank members of the Weatherhead lab for helpful discussions on egg characteristics in relation to nesting habit, and Dave Shutler and Karen Metz for helpful comments on the manuscript. This work was supported by a grant from the Natural Sciences and Engineering Research Council of Canada to PJW, and a NSERC scholarship to MLM.

LITERATURE CITED

- AR, A., C. V. PAGANELLI, R. B. REEVES, D. G. GREENE, AND H. RAHN. 1974. The avian egg: water vapor conductance, shell thickness, and functional pore area. *Condor* 76:153-158.

- BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA.
- BENT, A. C. 1923. Life histories of North American wild fowl. U.S. Natl. Mus. Bull. 130:22-30.
- BLANKESPOOR, G. W., J. OOLMAN, AND C. UTHE. 1982. Eggshell strength and cowbird parasitism of Red-winged Blackbirds. *Auk* 99:363-365.
- DAVIES, N. B., AND M. DE L. BROOKE. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim. Behav.* 36:262-284.
- EADIE, J. McA., F. P. KEHOE, AND T. D. NUDDS. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Can. J. Zool.* 66:1709-1721.
- HOYT, D. F., R. G. BOARD, H. RAHN, AND C. V. PAGANELLI. 1979. The eggs of the Anatidae: conductance, pore structure, and metabolism. *Physiol. Zool.* 52:438-450.
- JOHNSGARD, P. A. 1978. Ducks, geese, and swans of the world. Univ. of Nebraska Press, Lincoln.
- JONES, R. E., AND A. S. LEOPOLD. 1967. Nesting interference in a dense population of wood ducks. *J. Wildl. Manage.* 31:221-228.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen and Company, London.
- LIVEZEY, B. C. 1986. A phylogenetic analysis of recent anseriform genera using morphological characters. *Auk* 103:737-754.
- LUMSDEN, H. G., AND R. WENTING. 1976. Common Goldeneyes hatching from cracked eggs. *Auk* 93:833-835.
- McLAREN, W. D. 1969. Further data on interspecific competition at a joint bufflehead-goldeneye nest site. *Can. Field-Nat.* 83:59-60.
- NIE, N. H. 1988. SPSS statistical package for the social sciences. McGraw-Hill, New York.
- PAGEL, M. D., AND P. H. HARVEY. 1988. Recent developments in the analysis of comparative data. *Q. Rev. Biol.* 63:413-440.
- PETERSON, B., AND G. GAUTHIER. 1985. Nest site use by cavity-nesting birds of the Cariboo Parkland, British Columbia. *Wilson Bull.* 97:319-331.
- PICMAN, J. 1989. Mechanism of increased puncture resistance of eggs of Brown-headed Cowbirds. *Auk* 106:577-583.
- ROHWER, F. C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. *Auk* 105:161-176.
- ROHWER, F. C., AND S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. *Can. J. Zool.* 67:239-253.
- ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250-271.
- SAVARD, J.-P. L. 1988. Use of nest boxes by Barrow's Goldeneyes: nesting success and effect on the breeding population. *Wildl. Soc. Bull.* 16:125-132.
- SCHÖNWETTER, M. 1960. In W. Meise [ed.], *Handbuch der Oologie*. Lieferung 1. Akademie Verlag, Berlin.
- SOULLIERE, G. J. 1987. Distinguishing hooded merganser and wood duck nests by eggshell thickness. *J. Wildl. Manage.* 51:534.
- SPAW, C. D., AND S. ROHWER. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. *Condor* 89:307-318.
- WELLER, M. W. 1959. Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. *Ecol. Monogr.* 29:333-365.
- ZICUS, M. C., M. A. BRIGGS, AND R. M. PACE III. 1988. DDE, PCB, and mercury residues in Minnesota Common Goldeneye and Hooded Merganser eggs, 1981. *Can. J. Zool.* 66:1871-1876.

APPENDIX. Mean egg mass (g), egg shape, mean eggshell thickness (mm), and nesting habits of the eight major waterfowl tribes. Nomenclature follows Rohwer (1988). Mean values of egg mass, eggshell thickness, egg length, and egg breadth (for shape calculations) are all from Schönwetter (1960). Data on nest location and parasitism are from Bellrose (1976), Johnsgard (1978), and Eadie et al. (1988).

Tribe Species	Egg		Eggshell thickness	Nest	
	Mass	Shape		Location ^a	Strategy ^b
Dendrocygnini					
<i>Dendrocygna guttata</i>	50	1.311	0.34	2	U
<i>D. eytoni</i>	40	1.274	0.35	1	U
<i>D. bicolor</i>	51	1.313	0.37	1	P
<i>D. arcuata</i>	40	1.372	0.38	1	U
<i>D. javanica</i>	37	1.274	0.35	1	U
<i>D. viduata</i>	36	1.310	0.28	1	U
<i>D. arborea</i>	54	1.293	0.36	1	U
<i>D. autumnalis</i>	44	1.366	0.39	2	P
Anserini					
<i>Anser cygnoides</i>	145	1.486	0.56	1	NP
<i>A. anser</i>	160	1.483	0.67	1	P
<i>A. albifrons</i>	125	1.482	0.47	1	NP
<i>A. erythropus</i>	100	1.551	0.35	1	NP
<i>A. fabalis</i>	146	1.503	0.47	1	NP
<i>A. indicus</i>	141	1.525	0.57	1	NP
<i>Chen canagica</i>	120	1.515	0.50	1	NP
<i>C. rossi</i>	92	1.543	0.32	1	NP
<i>C. c. caerulescens</i>	120	1.505	0.44	1	P
<i>Branta sandvicensis</i>	131	1.422	0.41	1	NP
<i>B. c. canadensis</i>	163	1.478	0.62	1	P
<i>B. leucopsis</i>	107	1.528	0.44	1	NP
<i>B. ruficollis</i>	90	1.450	0.34	1	NP
<i>B. bernicla</i>	90	1.501	0.36	1	NP
Cygnini					
<i>Coscoroba coscoroba</i>	185	1.480	0.62	1	NP
<i>Cygnus atratus</i>	258	1.584	0.69	1	NP
<i>C. olor</i>	340	1.531	0.78	1	NP
<i>C. melancoryphus</i>	247	1.519	0.62	1	NP
<i>C. cygnus</i>	331	1.550	0.79	1	NP
<i>C. buccinator</i>	324	1.546	0.86	1	NP
<i>C. columbianus</i>	280	1.567	0.76	1	NP
<i>C. bewickii</i>	260	1.537	0.73	1	NP
Tadornini					
<i>Tadorna tadornoides</i>	93	1.385	0.41	2	U
<i>T. variegata</i>	91	1.393	0.50	1	NP
<i>T. cana</i>	83	1.470	0.39	1	P
<i>T. ferruginea</i>	83	1.447	0.40	2	NP
<i>T. radjah</i>	59	1.366	0.38	2	U
<i>T. tadorna</i>	78	1.387	0.38	2	P
<i>Malacorhynchus membranaceus</i>	31	1.405	0.28	1	P
<i>Neochen jubata</i>	63	1.407	0.42	2	NP
<i>Alopochen aegyptiacus</i>	97	1.382	0.52	1	NP
<i>Chloephaga melanoptera</i>	113	1.529	0.45	1	NP
<i>C. poliocephala</i>	89	1.473	0.36	1	NP
<i>C. rubidiceps</i>	90	1.436	0.32	1	NP
<i>C. picta</i>	122	1.517	0.42	1	NP
<i>C. hybrida</i>	137	1.546	0.45	1	NP
<i>Hymenolaimus malacorhynchus</i>	73	1.440	0.41	1	NP
<i>Tachyeres pterenes</i>	166	1.452	0.55	1	NP

APPENDIX continued.

Tribe Species	Egg		Eggshell thickness	Nest	
	Mass	Shape		Location*	Strategy*
Anatini					
<i>Cairina moschata</i>	74	1.391	0.40	2	P
<i>C. scutulata</i>	72	1.374	0.39	2	NP
<i>Aix sponsa</i>	44	1.320	0.32	2	P
<i>A. galericulata</i>	41	1.369	0.31	2	NP
<i>Nettapus pulchellus</i>	30	1.285	0.31	2	NP
<i>N. coromandelianus</i>	30	1.285	0.31	2	U
<i>N. auritus</i>	23	1.338	0.26	2	NP
<i>Anas sparsa</i>	72	1.386	0.34	1	NP
<i>A. penelope</i>	44	1.408	0.26	1	NP
<i>A. americana</i>	43	1.410	0.27	1	NP
<i>A. sibilatrix</i>	53	1.424	0.28	1	NP
<i>A. falcata</i>	49	1.421	0.27	1	NP
<i>A. strepera</i>	44	1.391	0.27	1	P
<i>A. formosa</i>	31	1.405	0.22	1	NP
<i>A. crecca</i>	30	1.339	0.26	1	NP
<i>A. flavirostris</i>	39	1.421	0.26	1	NP
<i>A. capensis</i>	50	1.407	0.27	1	NP
<i>A. gibberifrons</i>	35	1.377	0.29	2	NP
<i>A. castanea</i>	40	1.386	0.32	1	NP
<i>A. aucklandica chlorotis</i>	62	1.408	0.34	1	NP
<i>A. platyrhynchos</i>	54	1.379	0.31	1	NP
<i>A. rubripes</i>	63	1.376	0.34	1	NP
<i>A. undulata</i>	55	1.310	0.32	1	NP
<i>A. poecilorhyncha</i>	57	1.324	0.34	1	NP
<i>A. specularis</i>	53	1.462	0.31	1	NP
<i>A. specularioides</i>	70	1.468	0.32	1	NP
<i>A. acuta</i>	45	1.427	0.27	1	NP
<i>A. georgica</i>	42	1.397	0.28	1	NP
<i>A. bahamensis</i>	34	1.429	0.25	1	NP
<i>A. erythrorhyncha</i>	39	1.329	0.26	1	NP
<i>A. versicolor</i>	34	1.424	0.27	1	NP
<i>A. querquedula</i>	27	1.388	0.23	1	NP
<i>A. discors</i>	29	1.395	0.26	1	NP
<i>A. cyanoptera</i>	32	1.375	0.27	1	NP
<i>A. smithii</i>	45	1.427	0.28	1	NP
<i>A. rhynchotis</i>	42	1.455	0.27	1	NP
<i>A. clypeata</i>	40	1.414	0.26	1	NP
<i>Cheonetta jubata</i>	54	1.385	0.38	2	U
<i>Amazonetta brasiliensis</i>	31	1.398	0.24	1	U
Aythini					
<i>Marmaronetta angustirostris</i>	31	1.346	0.27	1	P
<i>Netta rufina</i>	56	1.393	0.34	1	P
<i>N. erythroptalma</i>	59	1.266	0.39	1	P
<i>N. peposaca</i>	60	1.355	0.40	1	P
<i>Aythya valisineria</i>	68	1.425	0.40	1	P
<i>A. ferina</i>	66	1.411	0.38	1	P
<i>A. americana</i>	65	1.396	0.41	1	P
<i>A. collaris</i>	51	1.445	0.34	1	NP
<i>A. australis</i>	60	1.366	0.39	1	P
<i>A. baeri</i>	43	1.361	0.32	1	NP
<i>A. nyroca</i>	43	1.374	0.34	1	P
<i>A. fuligula</i>	56	1.439	0.32	1	P
<i>A. novaeseelandiae</i>	63	1.459	0.32	1	NP
<i>A. marila</i>	67	1.435	0.35	1	P
<i>A. affinis</i>	51	1.438	0.34	1	P

APPENDIX continued.

Tribe Species	Egg		Eggshell thickness	Nest	
	Mass	Shape		Location ^a	Strategy ^b
Mergini					
<i>Polysticta stelleri</i>	58	1.475	0.31	1	NP
<i>Somateria mollissima</i>	108	1.502	0.35	1	P
<i>S. spectabilis</i>	73	1.506	0.30	1	NP
<i>S. fischeri</i>	73	1.481	0.32	1	NP
<i>Histrionicus histrionicus</i>	53	1.396	0.25	1	NP
<i>Clangula hyemalis</i>	43	1.398	0.26	1	NP
<i>Melanitta nigra</i>	72	1.467	0.32	1	NP
<i>M. perspicillata</i>	62	1.437	0.35	1	NP
<i>M. fusca</i>	77	1.432	0.38	1	NP
<i>Bucephala albeola</i>	37	1.399	0.36	2	P
<i>B. islandica</i>	70	1.375	0.43	2	P
<i>B. clangula</i>	57	1.390	0.39	2	P
<i>Lophodytes cucullatus</i>	60	1.210	0.64	2	P
<i>Mergellus albellus</i>	42	1.405	0.32	2	P
<i>Mergus serrator</i>	72	1.439	0.34	1	P
<i>M. merganser</i>	70	1.433	0.35	2	P
Oxyurini					
<i>Oxyura dominica</i>	70	1.323	0.43	1	P
<i>O. jamaicensis</i>	73	1.363	0.44	1	P
<i>O. leucocephala</i>	96	1.316	0.47	1	P
<i>O. maccoa</i>	96	1.331	0.50	1	NP
<i>O. vittata</i>	86	1.351	0.48	1	P
<i>Biziura lobata</i>	128	1.503	0.70	1	P

^a 1 = open- (ground-)nesting, 2 = cavity-nesting.

^b U = unknown, P = parasitic, NP = nonparasitic.