THE BLACK-HEADED DUCK *HETERONETTA ATRICAPILLA* LAYS ORDINARY EGGS

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The Black-headed Duck Heteronetta atricapilla *is the only known obligate parasite among the waterfowl. As such, it is predicted that the eggs of this species would exhibit some of the specialized characteristics observed in the eggs of obligately parasitic passerines. Contrary to expectations, the eggs of this duck were neither rounder nor with a thicker shell than expected for eggs of this size. It is speculated that the lack of destructive responses by host species to eggs of this duck in their nest may not have favoured evolution of stronger eggs in this parasite.*

Key Words: Black-headed Duck, obligate parasite, shell thickness, egg shape

Avian brood parasitism is a reproductive strategy that has received considerable attention (Friedmann 1963, Eadie *et al.* 1988; Rohwer & Freeman 1989; Soler & Moller 1996; Sealy & Lorenzana 1997). In particular, obligate brood parasites (species that rely totally on the nests of other host species as sites for laying their eggs, and on these hosts to rear their young) have received special attention because their nesting behaviour often reduces the reproductive success of their host (e.g. Rothstein 1990), and hence many hosts try to remove parasitic eggs from their nests. To minimize the chance that their eggs are recognized or removed by hosts, obligate brood parasites have evolved adaptations in their eggs. For example, among the cuckoos (Family Cuculicidae), egg mimicry has evolved such that regional variation occurs in the appearance of eggs, and this corresponds to the predominant host in the region (Davies & Brooke 1988; Soler & Moller 1996). In addition, eggshells of parasitic cuckoos are stronger than those of non-parasitic cuckoos, presumably to increase the chance that hosts cannot puncture and remove their eggs. In the cowbirds (*Molothrus* spp.), this is even more pronounced, in that selection has favoured the evolution of strong eggshells in which eggs are quite round (yielding greater strength than oval eggs) and in which eggshells are proportionally thick for the size of the eggs (Spaw & Rohwer 1987;

Rahn *et al.* 1988). Strong eggs have probably evolved because they are more likely to minimize damage when quickly deposited in a host nest, and they are more likely to withstand attempts at puncture ejection by hosts (Picman 1989).

Among waterfowl, intra- and interspecific brood parasitism are quite common compared to other bird groups (Eadie *et al.* 1988). However, only one species, the Black-headed Duck *Heteronetta atricapilla*, a member of the waterfowl Tribe *Oxyurini*, is known to be an obligate brood parasite (Rees & Hillgarth 1984). The Black-headed Duck nests in South America, lays immaculate, cream-coloured eggs, and parasitises nests of over a dozen bird species (Weller 1968a; Höhn 1975), with the most common hosts being coots (Family *Fulicidae*). Based on what we know about the eggs of obligate brood parasites in other birds, it was hypothesized that eggs of the Black-headed Duck would be rounder and have thicker shells than expected for the size of the egg.

Methods

Data on egg length and breadth, shell thickness and egg mass were obtained from Schönwetter (1960), Cramp (1977), Johnsgard (1978), Poole & Gill (1998), and from unpublished data. For Black-headed Ducks, measurements were obtained for length and breadth (n=18) and shell thickness (n=10) from the egg collections at the Western Foundation for Vertebrate Zoology (eggs collected in the 1930s in Chile), and Two eggs were collected and measured from captive ducks at The Wildfowl and Wetlands Trust, Slimbridge. Length and breadth of these eggs were measured to the nearest 0.1mm with calipers, and shell thickness was measured at three locations around the equator of the egg with microcalipers (to the nearest 0.01mm). The mean of the three values from each egg was used in analyses. Data on fresh egg mass for Black-headed Duck eggs were not available, but Johnsgard (1978) indicates that their eggs weigh approximately 60 g.

Linear regression (PROC REG; SAS Institute Inc. 1990) was used to examine relationships between egg mass and shell thickness, or egg shape and egg mass. Data for these parameters from all waterfowl species except the Black-headed Duck were used to generate predictive equations for egg shape and shell thickness based on egg mass, and then the values for the Black-headed Duck were compared to the expected values for an egg of that mass using confidence intervals. This procedure was repeated for data restricted to the waterfowl Tribe *Oxyurini*, to help control for potential egg characteristics specific to that phylogenetic group. To compare shell thickness of Black-headed Ducks in relation to egg shape, data were used only for species with eggs between 50 and 70 g (to minimize the effect of egg mass on shape and shell thickness). Because egg strength can be affected by both shell thickness and egg shape, data were further restricted to species with egg shape within one standard deviation of the egg shape for Black-headed Ducks. Relationships between raw data were non-linear (**Figure 1**), so all data were $\log_e$ transformed to better meet assumptions of linear regression analyses. All means reported +/- one standard deviation.

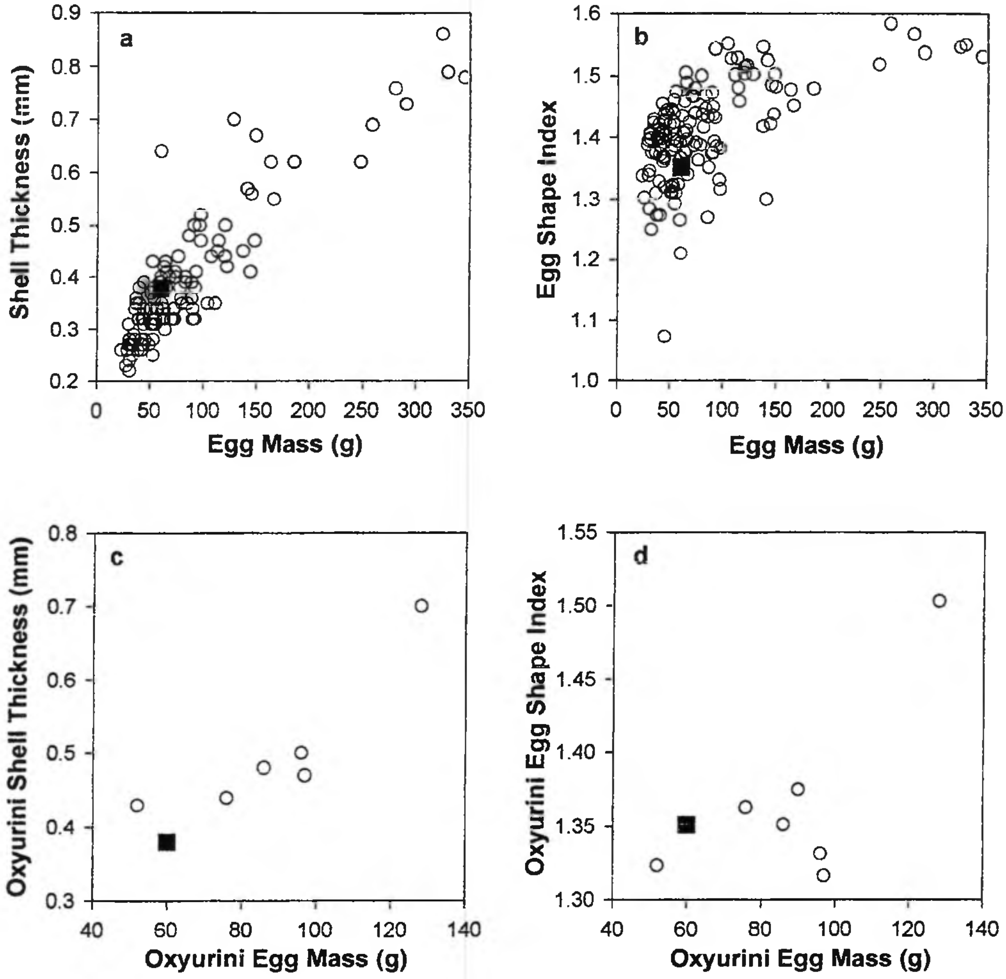

Figure 1. Relationships between egg mass, shell thickness and egg shape for all waterfowl (plots a and b) and restricted to the waterfowl Tribe *Oxyurini* (plots c and d), as well as the relationship between shell thickness and egg shape for all waterfowl (plot e). The values for the Black-headed Duck are noted by squares. Note that in the text, these values have been $\log_e$ transformed for statistical analyses.

Results

Black-headed Duck egg measurements

For 20 Black-headed Duck eggs, mean egg length was 59.4 ± 2.4mm and egg breadth was 43.8 ± 1.1mm (**Table 1**). These values provide an mean egg shape index (length/breadth) of 1.36 ± 0.05. For 12 of these eggs, mean shell thickness was 0.38 ± 0.03mm.

Predicted eggshell thickness

To determine whether Black-headed Duck eggs had abnormally thick shells,Their shell thickness was compared to that predicted from a relationship between egg mass and shell thickness for all waterfowl (**Figure 1a**), and for that within the waterfowl Tribe *Oxyurini* (**Figure 1c**). Across 122 waterfowl species, shell thickness can be predicted from egg mass by the equation:

Log_e thickness = -2.818 + 0.434 (Log_e mass);

R^2=0.76, $F_{1,120}$=386.5, P<0.001

From this equation, a 60g egg is predicted to have a shell thickness of 0.35mm, with a 95% CI on the prediction of 0.26 – 0.47 mm (note that even if egg mass varied by ± 10g, the predicted shell thickness would be 0.33 - 0.38mm, well within the 95% CI). As all of the empirical measurements for shell thickness (**Table 1**) fell well within this predicted 95% CI, by definition the measured values are not statistically different from the predicted values (P>0.05).

Within the waterfowl tribe *Oxyurini,* shell thickness can be predicted from egg mass by the equation:

Log_e thickness = -2.844 + 0.481 (Log_e mass);

Table 1. Sizes of Black-headed Duck eggs collected in Chile (n=18, except shell thickness taken on 10 eggs) and United Kingdom (n=2).

Characteristic	Chile	United Kingdom
Length (mm)		
Mean	59.23±2.41	
Range	55.20 - 63.49	59.4, 63.1
Breadth (mm)		
Mean	43.85 ± 1.14	
Range	41.64 - 45.83	44.0, 43.2
Shell Shape Index		
Mean	1.36 ± 0.01	
Range	1.24 - 1.46	
Shell Thickness (mm)		
Mean	0.379 ± 0.029	0.38
Range	0.322 - 0.419	0.36 - 0.39

R^2=0.66, $F_{1,4}$=8.0, P=0.048

From this equation, a 60g egg is predicted to have a shell thickness of 0.42mm, with a 95% CI on the prediction of 0.28 – 0.61 mm. All measured values were within the 95% CI for predicted shell thickness, therefore shell thickness did not differ significantly from predicted thickness for this tribe (P>0.05).

Predicted egg shape

As with shell thickness, the egg shape of Black-headed Ducks were compared to that predicted for all waterfowl (**Figure 1b**), and to that for the waterfowl tribe *Oxyurini* (**Figure 1d**). Across 122 waterfowl species, egg shape can be predicted from egg mass by the equation (see **Figure1b**):

$$\text{Log}_e \text{ shape} = 1.067 + 0.083 (\text{Log}_e \text{ mass});$$
$$R^2=0.45, F_{1,120}=97.9, P<0.001$$

From this equation, a 60g egg was predicted to have a shape index of 1.41, with a 95% CI on the prediction of 1.30 – 1.52mm. Mean measured shape index, and all but one of the measured shape values, were within this 95% CI, and thus measured egg shapes were not statistically different from that predicted for eggs of this species (P>0.05).

Restricting the analysis to the tribe *Oxyurini*, egg shape was predicted from egg mass by the equation:

$$\text{Log}_e \text{ shape} = 0.709 + 0.147 (\text{Log}_e \text{ mass});$$
$$R^2=0.40, F_{1,4}=2.65, P=0.17$$

Although this equation was not significant (presumably due to the small sample size as the R value was relatively high), a 60g egg was predicted to have a shape index of 1.31 mm, with a 95% CI on the prediction of 1.11 – 1.52. All measured values were within the range of the 95% CI, and hence measured egg shape does not differ from that predicted for eggs of this mass in the Tribe *Oxyurini* (P>0.05).

Eggs of Black-headed Ducks did not have thicker shells than expected for their egg shape when analyses were restricted to eggs of similar mass (**Figure 1e**). Mean shell thickness for other waterfowl species (0.37 ± 0.04 mm, n=19) did not differ from the mean for Black-headed Ducks (0.38 ± 0.03mm, n=12; *t*-test, P>0.10). Hence, Black-headed Duck eggs did not have thicker shells than expected for eggs of this shape.

Discussion

Eggs of the Black-headed Duck display none of the adaptations observed in other obligate parasite birds. In fact, other waterfowl species with eggs weighing approximately 60 g have similar eggshell thicknesses, such as *Aythya australis* (0.39 mm), *A. merila* (0.35 mm), and *Bucephala clangula* (0.39 mm). Typically, obligate brood parasites lay eggs that mimic the colouration and pattern of hosts to reduce the risk of detection, and/or they lay eggs with relatively stronger shells to withstand ejection attempts by hosts. Increased shell strength has been achieved by making eggs rounder or with thicker shells than expected for eggs of similar mass (Mallory & Weatherhead 1990; Picman 1989). For Black-headed Ducks, their eggs are neither rounder nor with thicker shells than expected for eggs of that mass, and eggs are off-white and immaculate, and clearly do not match the maculated appearance of their various hosts (Weller 1968a,b; Höhn 1975). The obvious question that arises from this is why are Black-headed Duck eggs apparently unspecialized?

For at least one of these discrepancies, an explanation is probably simple. Unlike other parasites, Black-headed Ducks may simply lack the genetic variability in egg appearance to provide sufficient variation on which selection may act. Their off-white eggs are clearly different from those of their typical hosts, and they may simply lack capacity to produce maculated eggs.

For the other discrepancies, however, an explanation is not as obvious. For selection to favour the evolution of stronger eggshells in Black-headed Ducks, there must be a reproductive cost to hosts in keeping Black-headed Duck eggs in their nests. If there is a cost, then selection would favour hosts that recognize and remove the parasitic eggs from their nests (compared to hosts which accept these eggs and suffer reduced reproductive success). To remove the parasitic eggs, hosts species have several options: they can abandon their nests and build a new one, they could grasp the entire egg and remove it, they could roll the parasitic egg out of the nest cup, or they can puncture the parasitic egg with their bill and eject the egg from the nest. Hosts that exhibit the first three behaviours do not create a selective pressure for stronger eggshells (as eggshell strength would not help keep the egg in the nest); only hosts that use the puncture behaviour create selection for stronger eggshells. Black-headed Ducks typically lay their eggs in open, ground nests of a variety of species, especially coots (Weller 1968a,b; Höhn 1975). With coots, the response to these parasitic eggs is often to bury them in the nest, or build a new nest on top of them (Weller 1968a) – this type of behaviour might not produce any selective advantage to those birds laying eggs with stronger shells, as all parasitic and host eggs from the clutch are destroyed. Hence, it is possible that the host species of the Black-headed Duck do not respond to parasitic eggs with behaviours that would favour the evolution of stronger eggshells.

Although the physical features of Black-headed Duck eggs appear to be unspecialised, other aspects of this species' breeding biology are peculiar. Clearly this duck must be adept at finding nests of potential hosts, and it has adapted to parasitize nests near the water to nests in tree cavities (Weller 1968a,b; Höhn 1975). The young appear to be very precocial (Rees & Hillgarth 1984) and can survive in the absence of parents (Weller 1968a,b), and the species breeds over a very long season (Weller 1968b), presumably to take advantage of the breeding seasons of its suite of hosts.

Despite the unique reproductive strategy of the Black-headed Duck among waterfowl species, its eggs do not appear to have physical adaptations similar to those in other obligate brood parasites. Clearly further study of the reproductive biology of this species, including investigations of the response of its hosts to parasitic eggs, would yield valuable insight to the needs of this species for long-term management.

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References

Cramp, S. (1977). *The birds of the western Palearctic, vol. I. Ostrich to Ducks.* Oxford University Press, Oxford, United Kingdom.

Davies, N. B. & Brooke, M. de L. (1988). Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour* **36**: 262-284.

Eadie, J. M., Kehoe, F. P., & Nudds, T. D. (1988). Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Canadian Journal of Zoology* **66**: 1709-1721.

Friedmann, H. (1963). Host relations of the parasitic cowbirds. *U. S. National Museum Bulletin.* **233**. 276 pp.

Höhn, O. (1975). Notes on Black-headed Ducks, Painted Snipe and Spotted Tinamous. *Auk* **92**: 566-575.

Johnsgard, P.A. (1978). Ducks, geese and swans of the world. University of Nebraska Press, Lincoln, Nebraska.

Mallory, M. L. & Weatherhead, P. J. (1990). Effects of nest parasitism and nest location on eggshell strength in waterfowl. *Condor* **92**: 1031-1039.

Picman, J. (1989). Mechanisms of increased puncture resistance of eggs of Brown-headed Cowbirds. *Auk* **106**: 577-583.

Poole, A. & Gill, F. (1998). *The Birds of North America.* The Birds of North America Inc.. Philadelphia, PA, USA.

Rahn, H., Curran-Everett, L., & Booth, D. T. (1988). Eggshell differences between parasitic and nonparasitic Icteridae. *Condor* **90**: 962-964.

Rees, E. C. & Hillgarth, N. (1984). The breeding biology of captive Black-headed Ducks and the behavior of their young. *Condor* **86**: 242-250.

Rohwer, F. C. & Freeman, S. (1989). The distribution of conspecific nest parasitism in birds. *Canadian Journal of Zoology* **67**: 239-253.

Rothstein, S. I. (1990). A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics* **21**: 481-508.

Schönwetter, M. (1960). In: W. Meise (ed.), Handbuch der Oologie. Lieferung 1. Akademie Verlag, Berlin.

Sealy, S. G. &Lorenzana, J. C. (1997). Feeding of nestling and fledgling brood parasites by individuals other than the foster parents: a review. *Canadian Journal of Zoology* **75**: 1739-1752.

Soler, J. J. & Moller, A. P. (1996). A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism. *Behavioural Ecology* **7**: 89-94.

Spaw, C. D. & Rohwer, S. (1987). A comparative study of eggshell thickness in cowbirds and other passerines. *Condor* **89**: 307-318.

Weller, M.W. (1968a). The breeding biology of the parasitic Black-headed Duck. *Living Bird* **7**: 169-207.

Weller, M. W. (1968b). Notes on some Argentine *anatids*. *Wilson Bulletin* **80**: 189-212.