Musk Duck brood parasitism on Black Swans

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This paper describes incidences of brood parasitism of nests of Black Swans *Cygnus atratus* by Musk Ducks *Biziura lobata*. Black Swans have a long incubation period, and as they are unlikely to exhibit egg rejection behaviour, they are potentially suitable as hosts for Musk Duck parasitism. Model eggs were used to test whether the success of brood parasitism in this system is constrained by host responses (egg recognition or nest abandonment), or egg shell strength. The results showed that Black Swans readily accept foreign eggs, even when they are very different from their own. However, there was a substantial loss of weak-shelled model eggs, thought to be accidentally crushed by the swans. The relation of this to the unusually thick shell of Musk Duck eggs is discussed.

Key Words: interspecific brood parasitism, egg recognition, egg rejection, model experiments, shell thickness

Interspecific brood parasitism, or females purposely laying eggs in the nests of other species, is relatively widespread among wildfowl (Anatidae). The behaviour has been recorded in at least 36 out of 146 species (25%), and is particularly common among the Oxyurini (stiff-tailed ducks; Sayler 1992). The hosts of parasitic wildfowl mostly involve other wildfowl, but also gulls (Laridae), Coots *Fulica sp.* and ibises (Threskiornithidae). The success of interspecific brood parasitism may be constrained by the timing of the parasitism, and by host responses, such as nest site defence, displacement of parasitic eggs, egg rejection and nest abandonment (Sayler 1992). Furthermore, parasitic eggs may be damaged when quickly deposited in the nest or when the host attempts to puncture it (Mallory 2000). In response to these constraints, some avian brood parasites have evolved adaptations such as egg mimicry and strong egg shells (Davies 2000). Studies on wildfowl have so far found little evidence for egg discrimination among host species (Sorenson 1997, Dugger *et al.* 1999a, Dugger *et al.* 1999b). A study of Hooded Mergansers *Lophodytes cucullatus* reported that Common Goldeneye *Bucephala clangula* eggs were more likely to be at the periphery of the host clutch (Mallory & Weatherhead 1993). Furthermore, parasitic species do not seem to have evolved 'stronger' egg shells than non-parasitic species (Mallory & Weatherhead 1990). The lack of adaptations in relation to brood parasitism in both hosts and parasites among wildfowl is often taken as evidence that the costs of parasitism to hosts and the benefits to the parasites are relatively small in species with precocial young, compared to those with altricial young (Rohwer & Freeman 1989, Lyon & Eadie 1991).

In this paper, a rather unexpected host-parasite combination among Australian wildfowl is reported: Musk Ducks *Biziura lobata* laying eggs in the nests of Black Swans *Cygnus atratus*. Although Musk Ducks are known to be brood parasites (Attiwil *et al.* 1981), they have not previously been recorded parasitising Black Swans. Musk Ducks are a poorly-studied species, and it is not clear at present how important interspecific brood parasitism is as a reproductive strategy. Attiwil *et al.* (1981) is the only other study to report interspecific brood parasitism in the Musk Duck. Although further studies are needed, it is possible that interspecific brood parasitism by Musk Ducks may be relatively common, at least under certain circumstances. Musk Ducks are unusual among wildfowl in that females directly feed their offspring for a considerable amount of time after leaving the nest (Frith 1967). The incubation period of Black Swans takes on average about 41 days (Braithwaite 1977), considerably longer than that of Musk Ducks (about 24 days, Marchant & Higgins 1990). Black Swans thus offer a relatively large window of opportunity during which the parasitic egg can hatch before the host finishes incubation, compared to host species with shorter incubation. The main incubation periods of Black Swans and Musk Ducks overlap at our study site (see Methods). Furthermore, incubation of an additional small egg should not pose a large extra cost to the host and it would thus seem unlikely that Black Swans have evolved egg recognition abilities. Lastly, predation rates of Black Swan nests are low compared to those of smaller hosts. To assess whether Black Swans make suitable hosts for brood parasitism by Musk Ducks, a field experiment using model eggs of different mimetic qualities and shell strength was undertaken.

Study Area and Methods

The study was conducted between July and October 2000 at two sites in central Victoria, Australia: Lake Wendouree in Ballarat (S37°33' E143°49') and Reedy Lake, near Geelong (S38°11' E144°26'). The main incubation period for Black Swans in Victoria takes place between early July and mid-November and clutch size varies between two and seven (Kraaijeveld 2003). Lake Wendouree is a permanent lake of 238ha, with a population of around 170 Black Swans who are present at the site throughout the year. The swans breed mainly in beds of Tall Spike-rush *Eleocharis sphacelata*, and nests were found by searching vegetation by canoe. The lake also has a permanent population of about 20-60 Musk Ducks, which are known to breed regularly (Thomas & Wheeler 1983). Most egg-laying by Musk Ducks at the site occurs between September and November (Frith 1967; K. Kraaijeveld, pers. obs.). Reedy Lake is a system of shallow lakes containing numerous reed beds. The study site was an area of about 90ha around the perimeter of the reed beds, which only floods during spring. The vegetation consisted of low rushes and narrow strips of Reed *Phragmites australis* water of less than 50cm depth. During the study period about 130 swans inhabited the area, while at other times of the year the study area was dry and no swans were present. Nests were mostly located among strips of reeds and were easily found by wading through the study area. The contents of all nests at both study sites were monitored weekly. No Musk Ducks were ever recorded at Reedy Lake.

Egg recognition experiments were conducted at Reedy Lake during September 2000. No experiments were conducted at Lake Wendouree, because the swans refused to leave their nest, making it impossible to add experimental eggs unnoticed. Seven types of model eggs, differing in size, colour and shell strength, were added to Black Swan clutches of varying age. White and brown eggs came from domestic chickens, whitish eggs came from domestic ducks, and infertile swan eggs from the same population were also used. To investigate the effect of shell strength, we filled some of the brown and white chicken eggs with plaster of paris. Shells of swan eggs (filled or unfilled) were used as a control. The dimensions of the experimental study eggs are listed in **Table 1**. Each nest only received one model egg. Nests were checked two days after addition of a model egg. It was assumed that during this time both partners would have had an opportunity to reject the model eggs. All experiments described in this paper were approved by the Animal Experimentation Ethics Committee at the University of Melbourne.

To assess whether the egg shell of Musk Ducks is stronger than would be expected from its size, we followed the approach of Mallory (2000), using data from Mallory *et al.* (1990). Linear regression was used to examine the relationships between egg mass and shell thickness, or egg mass and egg shape. All waterfowl were initially included, and the residuals plotted as a histogram. A second regression was then performed on all waterfowl, except the Musk Duck, to generate predictive equations for egg shape and shell thickness based on egg mass. The values for the Musk Duck egg were then compared to the 95% confidence intervals of the predicted value. Data on egg characteristics were $\log_e$ transformed and tested for normality.

Results

At Lake Wendouree 66 Black Swan nests were located, constituting 95% of all nests on the lake, and three nests (5%) contained a Musk Duck egg. These eggs were greenish white in colour and unmarked, slightly lighter in colour than Black Swan eggs, and considerably smaller (**Table 1**). One was found in a clutch of five swan eggs, 21 days after the clutch had been completed. The egg was still present in the nest 17 days later, after the swan eggs had hatched and the cygnets had left the nest. The egg was cold and contained a fully developed Musk Duck embryo. The second Musk Duck egg was found in a clutch of four swan eggs, 20 days after clutch completion. This egg was still

Table 1. Dimensions (mm± SD) of different types of eggs found in nests of Black Swans and of those used in egg recognition experiments (the latter are marked with *). All eggs are plain in colour.

Egg Type	Length	Width	Colour
Black Swan (n=33)	106±3	67±2	Pale Green
Musk Duck (n=2)	58±1	47±7	Pale Greenish-white
White Ibis (n=1)	68	47	White
*Chicken (n=16)	57±2	43±1	Brown or White
*Duck (n=12)	62±3	47±1	White

present in the nest 14 days later. The swan eggs hatched a further seven days later, so the Musk Duck egg could have been incubated for over 21 days. The eventual fate of this egg was unknown, but a Musk Duck chick unaccompanied by a parent was observed about 600m from the nest on the first day the swan pair were seen with cygnets away from the nest. The third Musk Duck egg was found with a clutch of two swan eggs. This nest was found after the clutch was completed, but judging from the hatching date it was seven days old when found. A week later the egg had disappeared. Thus the Musk Duck cannot have been in the nest for longer than 15 days. The clutches of swan eggs in all the nests remained intact and none of the nests were deserted after being parasitised. At Reedy Lake, 31 nests were found and monitored. As all of the study area at this site is easily accessible, it is likely that all nests were located. None of the nests at Reedy Lake contained Musk Duck eggs.

The results of the egg recognition experiments are summarised in **Figure 1**. None of the experimental nests were deserted after addition of the model egg. All model eggs that remained in the nests after two days were warm, indicating that they had been incubated. None of the model eggs had been pushed outside the nest cup or buried into the nest material. The percentage of normal chicken eggs remaining in the nest after two days was low, but increased significantly when eggshells filled with plaster were used (Fisher Exact test, $P<0.0001$). Plaster-filled chicken eggs did not differ significantly from control swan eggs in their likeli-

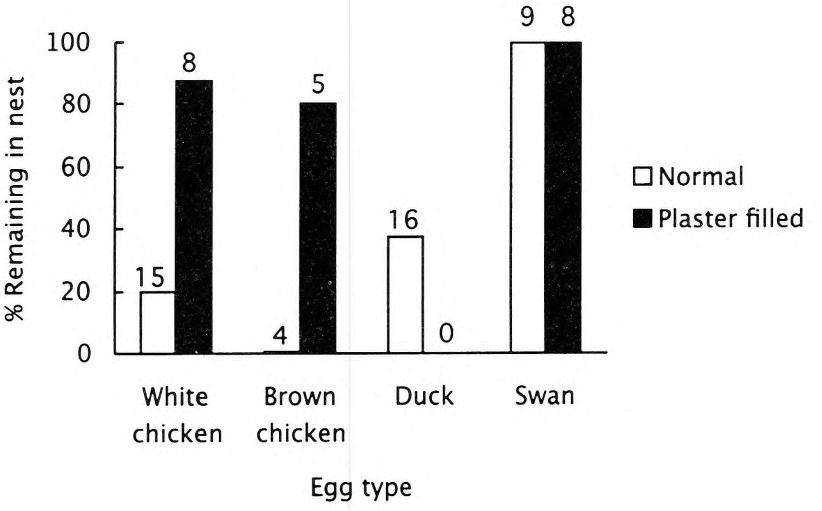

Figure 1. Percentage of experimental eggs remaining in the nests of Black Swans two days after addition. Sample sizes are indicated above the bars. No plaster-filled duck eggs were used.

hood of remaining in the nest. The slightly higher percentage of unfilled duck eggs remaining in the swan nests compared to unfilled chicken eggs was not significant and probably due to their stronger shell. There was no significant difference between unfilled chicken eggs of different colour in their likelihood of remaining in the nest.

Figure 2 shows the residuals of the regression of egg shell thickness on egg mass for all waterfowl. The egg of the Musk Duck has a large positive residual, second only to that of the Hooded Merganser. When Musk Duck is removed from the regression, shell thickness can be predicted from the egg mass by the equation:

Log_e thickness = -2.847 + 0.440 (Log_e mass); R^2=0.77, $F_{1,120}$=408.9, P<0.001

From this equation, a 128g egg (the weight of an average Musk Duck egg) is predicted to have a shell thickness of 0.49mm, with a 95% confidence interval on the prediction of 0.37 - 0.65mm. The average shell thickness of a Musk Duck egg is 0.70mm (Mallory *et al.* 1990), which falls outside this confidence interval, indicating that it is significantly thicker than expected for its mass. A similar analysis on egg shape showed that the shape index for the Musk Duck egg is not different from the expected value. Egg shape can be predicted from egg mass by the equation:

Log_e shape = 0.096+ 0.059 (Log_e mass); R^2=0.44, F1,120=93.90, P<0.001

From this equation, a 128g egg is predicted to have a shape index of 1.462, with a 95% confidence interval

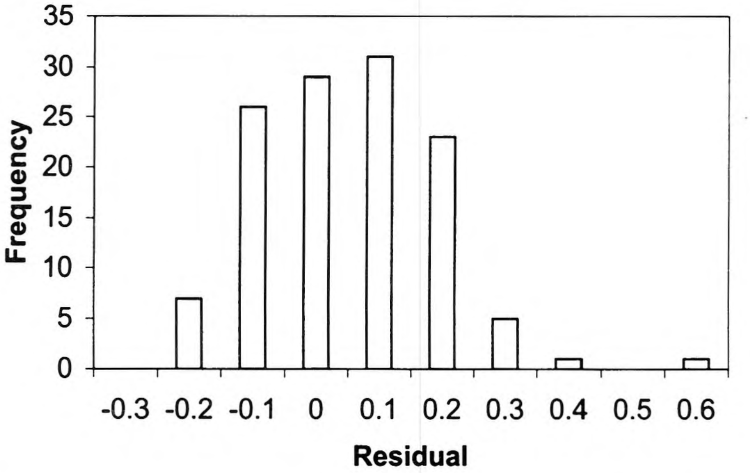

Figure 2. Histogram of residual values from the regression of egg shell thickness on egg mass for 122 species of waterfowl (data from Mallory *et al.* 1990). The Musk Duck is indicated with an asterix.

on the prediction of 1.35 - 1.58. The shape index of a Musk Duck egg is 1.503 (Mallory *et al.* 1990), which falls inside this confidence interval, indicating that the shape of a Musk Duck egg is not significantly different from that predicted.

Discussion

At first sight, the disappearance of experimental eggs from Black Swan nests seems consistent with anti-parasitic behaviour. However, many of our model eggs had thin shells (the shells of chicken eggs are generally about 0.33- 0.36mm thick, Verna *et al.* 1998; Nwosu *et al.* 1987) and probably disappeared because they were accidentally crushed by the incubating swans. This suggestion was supported by the fact that when similar model eggs filled with plaster were added, these were accepted by the swans. This highlights the caution required when interpreting evidence of egg-recognition or anti-parasitic behaviour. The study suggests that Black Swans did not display egg recognition behaviour, even when presented with model eggs that were very different from their own. In order to have any chance of hatching, the parasitic egg needs: (i) to be deposited in the host nest within the first 17 days of the start of incubation of the host clutch, and (ii) to have a shell that is strong enough to withstand the weight of a Black Swan. Even though the window of opportunity for parasitism of a swan nest is long compared to that of smaller potential hosts, the observed incidences of parasitism in this study appear not to have occurred within the requisite time window. It has also been demonstrated that the shell of Musk Duck eggs are strong enough to avoid being crushed by an incubating swan, and is substantially thicker than expected for its mass when compared to other waterfowl. Without further study of the basic biology of the Musk Duck, it remains unclear whether thick shells produced by the species are an evolutionary adaptation to parasitism of Black Swans, or are a by-product of some other function.

It is possible that incidences of parasitism of Black Swans at the study site are due to a lack of nests of other hosts. Previously, Musk Ducks have been recorded parasitising Pacific Black Duck *Anas superciliosa*, Grey Teal *Anas gibberifrons*, Hardhead *Aythya australis*, Pink-eared Duck *Malacorhynchus membranaceus*, Blue-billed Duck and Dusky Moorhen *Gallinula tenebrosa* (Attiwil *et al.* 1981). Of these, the Pacific Black Duck and the Dusky Moorhen breed commonly at Lake Wendouree, while the Blue-billed Duck breeds in small numbers (Thomas & Wheeler 1983). As many of these were observed breeding concurrently with Black Swans, it is unlikely that no other host nests were 'available'.

The Black Swan, Musk Duck, and experimental eggs that were added to nests were plain in colour. The lack of markings might constrain recognition of parasitic eggs by the host. However, this seems unlikely, as the eggs used in our experiment also differed from Black Swan eggs in colour and size. Diederik Cuckoo *Chrysococcyx caprius* parasitise several species of Weavers (Davies 2000), and in this host-parasite system both have unmarked eggs and the host is able to recognise parasitic eggs.

The success of brood parasitism of Black Swans by Muck Ducks as a reproductive strategy appears to be facilitated by host egg acceptance, and may also depend on egg strength and the timing of parasitism. However, unlike the precocial young of most other waterbirds, Musk Duck young appear to be far more dependent on parental care once they leave the nest (Frith 1967), and females are known to feed the young for several weeks. As the majority of their potential hosts, including Black Swans, do not exhibit such behaviour, it would seem that the survival chances of the parasitic duckling would be low unless females collect the ducklings once the host has finished incubation. Such retrieval of young from parasitised nests would be unique among brood parasites (Davies 2000) and has not been observed.

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