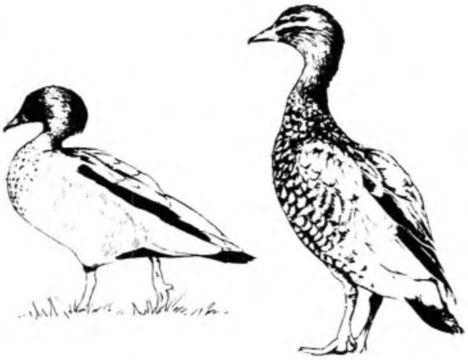
Effects of egg manipulations on clutch size of Australian Wood Ducks *Chenonetta jubata*



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Egg manipulation experiments can be used to test the hypothesis that clutch size in indeterminately laying birds is limited by the level of nutrients stored by females prior to egg production. The number of eggs laid by Australian Wood Ducks was not affected by experimental removal or addition of eggs during laying. This is consistent with the hypothesis that the level of a female's nutrient store proximately controls clutch size in this species.

The aim of this study was to determine whether clutch size of wild Australian Wood Ducks (synonymous with Maned Ducks) *Chenonetta jubata* could be altered by experimentally manipulating the number of eggs in their nests during laying, and thus to test the hypothesis that the size of the female's nutrient store proximately limits the number of eggs in her clutch. This hypothesis states that the number of eggs produced by a female bird is proximately determined by the amount of stored material (fat and/or protein) available to her for yolk and albumen deposition (Klomp 1970: 102, Ankney & MacInnes 1978, Drent & Daan 1980, Ankney & Afton 1988). The nutrient reserve hypothesis can be tested in indeterminate layers by egg manipulation experiments (Table 1) (Klomp 1970: 102). The hypothesis is refuted if removal or addition of eggs during laying causes birds to produce a larger or smaller clutch (Table 1). This study deals specifically with proximate determination of clutch size in Maned Ducks; ultimate determination is investigated in Briggs (1990) and will be the subject of a future paper.

Traditionally, determinate and indeterminate layers have been distinguished by their response to egg manipulation (Cole 1917, Winkler & Walters 1983). Birds that react to removal or addition of eggs by continuing or ceasing to lay have been regarded as indeterminate. Birds that do not reduce or increase their clutch size when eggs are added or removed have been regarded as determinate. However, response to egg manipulation is an inadequate test of determinateness *vs.* indeterminateness. This is because indeterminate layers, with the inherent capacity to vary their clutch size during laying (i.e. they can increase or decrease the number of enlarging follicles in their ovaries while laying), cannot do so if their level of stored nutrients proximately determines their egg production (see Klomp 1970: 102, Briggs 1985). Therefore, lack of effect of egg removal or addition on clutch size is consistent **either** with determinate follicle development, **or** with indeterminate follicle development combined with proximate limitation of clutch size by the female's level of stored nutrients (Table 2).

Table 1. Laying patterns inferred from effects of egg manipulations on clutch size (adapted from Klomp 1970: 102).

Effect of egg removal/addition	Implications of effect of egg removal/addition
Laying extended/curtailed	Indeterminate layer: clutch size not proximately controlled by stored nutrients (indirect effect of food).
Laying not extended/curtailed	Either: Indeterminate layer: clutch size proximately controlled by stored nutrients (direct effect of food); or: Determinate layer: clutch size proximately controlled or not controlled by stored nutrients (cannot determine whether effect of food is direct or indirect).

Table 2. Mean (± SE) clutch sizes of Australian Wood Ducks.

Year	Control	Treatment Removal	Addition
1987	10.7±0.4	12.0±0.9	11.7±1.2
n	6	4	3
1988	10.8±0.4	10.0±0.4	9.9±0.4
n	9	5	8
1987+1988	10.7±0.3	10.9±0.6	10.4±0.5
n	15	9	11

Ideally, whether a bird is a determinate or an indeterminate layer should be ascertained by ovarian examination. The follicles of indeterminate layers develop asynchronously (Anderson 1989). They have a succession of enlarging follicles in the ovary, which together total more than the number of eggs in the final clutch (Houston *et al.* 1983). In contrast, the number of enlarging follicles in determinate layers is determined before laying begins, and corresponds to the number of eggs in the clutch (Houston *et al.* 1983, Anderson 1989). Determinate layers show a distinct size boundary between the developing follicles and those undeveloped (Houston *et al.* 1983, Anderson 1989). However, ovarian examination is also a limited test for distinguishing determinateness *vs.* indeterminateness because the number of rapidly growing follicles can be influenced greatly by how long each takes to mature relative to the total number of eggs laid (see Houston *et al.* 1983), and by how many follicles become atretic (Hamann *et al.* 1986) rather than ovulating. However, as the only currently available means of distinguishing determinate and indeterminate layers is from their ovarian characteristics, I used it in this study.

Australian Wood Ducks are common in semi-arid to humid temperate Australia (Blakers *et al.* 1984). They are grazers, and ecologically they resemble geese (Kingsford 1986). They were chosen for this study because they nest readily in artificial nest boxes, and their clutches are easy to find and manipulate. The experiment reported here formed part of a larger investigation into the ecology of Australian Wood Ducks in southeastern Australia (Briggs 1989, 1990, Lawler & Briggs 1991).

Methods

The experiment was conducted during the 1987 and 1988 breeding seasons near Canberra (35°15'S, 149°10'E) in southeastern Australia. The study area was modified woodland, and included university grounds, golf fairways, artificial ponds and pasture grazed by domestic stock. Australian Wood Ducks use such environments readily. All clutches in the experiment were found in nest boxes.

Nest boxes were checked for new clutches every four days. New clutches were randomly allocated between treatments as they were found. Active nests were visited daily for manipulation, usually in the afternoon. All eggs were removed, numbered, measured, and depending on treatment, replaced. Clutch size was measured at the beginning of incubation because additional eggs may be laid parasitically after incubation commences (Briggs 1991). Eggs deposited at a rate greater than one per day were considered parasitic and were excluded from the analyses. One clutch of 24 eggs was also excluded because at least three females had contributed eggs to it (three eggs were deposited in one day). Clutches larger than twice the mean size are usually the result of laying by more than one female (Yom-Tov 1980).

Only clutches that were subsequently incubated were included in the analyses. During the study, Australian Wood Ducks laid an average of one egg every 1.6 days, and went up to six days without laying an egg in subsequently incubated clutches (Briggs 1990, unpubl. data). Consequently, a nest was regarded as deserted during laying if an interval of greater than six days passed with no egg laid. Incubation was considered to commence with maintenance of egg warming. Some incubated clutches were deserted before hatching.

Treatment schedules were as follows: in control nests clutches were not manipulated; in removal nests all eggs above four were removed; and in addition nests one egg was added each day that an egg was laid, after four eggs were present. Clutches were manipulated after four eggs had been laid for the reasons given by Rohwer (1984, 1986). In 1988, parasitic eggs were also removed from control nests, and one was left as the added egg in addition nests. These slight differences in control and addition treatments between 1987 and 1988 were because of the previously unknown high levels of parasitic laying found in 1987 (Briggs 1991). Since the treatment differences were minor and had no measurable effects on clutch size, the 1987 and 1988 clutch data were combined where appropriate.

Four laying Australian Wood Ducks were shot away from the study site between 1986 and 1988, and their ovaries were removed. I recorded the number of follicles in the ovaries of these shot Australian Wood Ducks that were > 4 mm, the number that were > 7 mm, and the number of post-ovulatory follicles. I chose these size classes because no Maned Ducks were shot outside the breeding season with follicles > 4 mm (see Briggs 1989), and rapidly growing follicles in ducks are usually > 7 mm diameter (Donham *et al.* 1976, Drobney 1980, Tome 1984, Barzen & Serie 1990). I also measured the diameter of the three larger follicles in two breeding Australian Wood Duck females shot in 1985.

Results

Neither adding nor removing eggs affected clutch size at the beginning of incubation in 1987 (one-way ANOVA, $F_{2,10} = 0.99$, $P>0.25$), in 1988 (one-way ANOVA, $F_{2,19} = 1.41$, $P>0.25$) or in the two years combined (combined data, one-way ANOVA, $F_{2,32} = 0.37$, $P>0.25$) (Table 2). The mean clutch size at the beginning of incubation was 10.7 (SE = 0.2, n = 35). The ovaries from the four shot Australian Wood Ducks contained an average of 5.3 (SE = 1.1, n = 4) follicles > 7 mm, and an average of 8.3 (SE = 1.0, n = 4) follicles > 4 mm. The mean diameters (mm) of the six larger follicles (excluding oviducal eggs) were 19.7 (SE = 3.6, n = 6), 11.0 (SE = 1.7, n = 6), 7.6 (SE = 1.1, n = 5), 6.0 (SE = 0.7, n = 4), 5.0 (SE = 0.5, n = 4) and 4.8 (SE = 0.5, n = 4). The average number of post-ovulatory follicles was 2.8 (SE = 0.8, n = 4).

Discussion

My results are consistent with either proximate limitation of clutch size in Australian Wood Ducks by the female's nutrient store, or with Australian Wood Ducks being determinate layers. Australian Wood Ducks appear to be indeterminate layers because their follicles develop asynchronously, their average number of rapidly growing follicles (5.3) plus their average number of post-ovulatory follicles (2.8) was less than their mean clutch size (8.1 *cf.* 10.7), and there was no indication of a sharp size boundary between rapidly developing and undeveloped follicles. Therefore, the results are consistent with proximate control of clutch size in Australian Wood Ducks by the nutrient store of the female. The separate finding that female Australian Wood Ducks store fat prior to laying and lose it during egg production (Briggs 1990) is also consistent with proximate control of clutch size by the nutrient level of the pre-laying female.

The timing of egg removal or addition in egg manipulation experiments can affect the consequent response of laying females (Andersson & Eriksson 1982, Winkler & Walters 1983, Duncan 1986). At some point during laying, a female's clutch size is set and further follicular development is inhibited (Duncan 1986, Klomp 1970: 9-10). Developing follicles of Australian Wood Ducks, like those of Blue-winged Teal *Anas discors* (Rohwer 1984), showed an exponential progression in size from large to small with no sharp size boundary separating larger (rapidly growing) from smaller (not developing) follicles. Thus, manipulating clutches of Australian Wood Ducks (as of Blue-winged Teal (Rohwer 1986)) after four or five eggs had been laid should have been sufficiently early to induce a response in clutch size, if such a response was possible.

Egg manipulation studies by Rohwer (1984) with wild Mallards *Anas platyrhynchos* and Blue-winged Teal produced similar results to mine. However, removing eggs increased the clutch size of some captive Mallards which were fed *ad libitum* (Rohwer 1984). This difference between wild and captive Mallards may be caused by different food availability, and hence different sources of material for eggs in wild and captive birds. Krapu (1981) found that wild Mallards used stored fat to produce eggs, and he further showed that their seasonal reductions in average clutch size were correlated with seasonal reductions in average levels of stored body fat. Conversely, Batt & Prince (1978) found that clutch sizes in captive Mallards given *ad libitum* food were independent of body weights in pre-laying females. Other species of waterfowl also show a positive association between apparent control of clutch size by stored nutrients on the one hand, and no change in clutch size with egg manipulation on the other.

For example, clutch size in American Wood Ducks *Aix sponsa* appears to be limited by the fat level of the female, as depletion of lipid reserves caused laying to cease (Drobney & Fredrickson 1985). American Wood Ducks did not significantly reduce their clutch size when eggs were experimentally added to their nest (Heusmann *et al.* 1980). Arctic-nesting geese also have a low propensity to lay replacement eggs (Winkler & Walters 1983: 47), and their clutch size is strongly related to their level of body reserves just prior to laying (Ankney & MacInnes 1978, Raveling 1979, Hamann & Cooke 1989).

In contrast, Common Goldeneyes reduced their clutch size when eggs were added experimentally to their nests (prior to their clutch size being fixed (Andersson & Eriksson 1982)). Although they carry fat reserves, Common Goldeneyes depend on invertebrates consumed on their breeding grounds to form their clutch (H.G. Lumsden, unpubl. data, quoted in Thomas 1988). Their lower clutch size in response to egg addition is consistent with relying directly on ingested food for egg formation, rather than on stored reserves.

Determining the sources of nutrients used for egg production is essential for understanding regulation of clutch size in birds. Manipulating the number of eggs in clutches during laying provides a test of the hypothesis that clutch size in indeterminate layers is proximately limited by the level of female nutrient reserves. Egg manipulations should preferably be conducted in association with food manipulation (see Reid 1987), analysis of body condition of breeding females (see Ankney & Afton 1988, Briggs 1990), and ovarian examination. Further study of follicular development, and of ovarian hierarchies (Thomas 1988), would aid our understanding of the differences between determinate and indeterminate layers, and would thereby advance our knowledge of the factors that proximately control clutch size in birds.

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