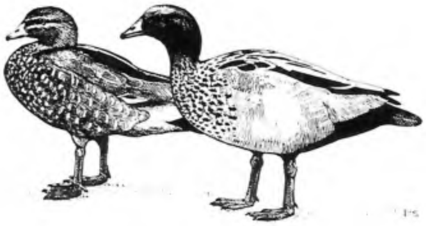
Biparental care of the Australian Wood *Chenonetta jubata*



R.T. KINGSFORD

Australian Wood Ducks are unusual among ducks in having extended biparental care. Males and females were equally likely to lead ducklings away from danger or to attack conspecifics or potential avian predators. Pairs that were laying, incubating or attending young, performed more Extreme head up behaviour than other paired birds. In family groups, differences in vigilant behaviour existed between the sexes. Males performed more Extreme head up and stood on higher ground more than females, who stayed closer to the brood. Male Extreme head up was highest when females were laying or incubating and declined with age of the ducklings. In contrast, female vigilance was lowest during laying and incubation, and increased with duckling age. During laying, incubation and early brood care, much of female activity away from the nest site was grazing. Females probably grazed intensely during brood care to recover energy lost during incubation and laying. As small grazing birds, the risks of predation are probably high. To overcome this, males attend the brood, which probably increases duckling survival.

Parental investment theory predicts that birds with precocial offspring will be polygynous because little parental care is needed (Emlen & Oring 1977). Males can pursue alternative strategies of looking for other mates or moulting and avoid the risks of parental care.

Waterfowl are mostly monogamous but there are variations within this family. Anserini (geese and swans) and some shelducks (Tadornini) have long pair bonds and extended biparental care (Raveling 1969, Scott 1980, Summers 1983) while Northern Hemisphere dabbling ducks are usually monogamous for one breeding season and the female alone cares for the offspring (McKinney 1986). However, in Southern Hemisphere species and the perching ducks (Cairinini), parental care patterns are variable (Norman & McKinney 1987, McKinney & Brewer 1989).

Kear (1970) considered that biparental care and long pair bonds were a primitive condition in waterfowl but Maynard Smith (1977) suggested that differences between the mating systems of the Anserini and Anatinii could be because young of the latter have less risk of predation because of concealed nest sites and injury-feigning behaviour of the parents. Male parental care in dabbling ducks probably does not increase duckling survival and possibly reduces it (Rohwer & Anderson 1987). Geese occupy open habitats and their offspring are likely to be more vulnerable to predation. Two parents are probably better than one in the detection and avoidance of predators. Lamprecht (1987) found that reproductive success was lowest in lone Bar-headed Geese *Anser indicus* and highest in paired Bar-headed Geese.

In this study, I investigated parental care in a Southern Hemisphere perching duck, the Australian Wood Duck *Chenonetta jubata*. This species is related to the Anatinii (Delacour 1964, Delacour & Mayr 1945) but has many behavioural characteristics of a goose, hence its other common name, the Maned Goose. It spends much of its time grazing on land (Kingsford 1989a) with only about 7% of diurnal time on the water and it sometimes grazes at night but usually rests on the edge of the dam (Kingsford 1986a). It also has long-term pair bonds (Kingsford 1990) and is an obligate hole nester often nesting up to 1 km from water (Frith 1982). Although there is little direct evidence ducklings are then usually led to the nearest water. Over three years, the average brood size, when families first appeared on water, was 6.2 with over 80% of ducklings surviving to fledging in two years of normal rainfall and only about 20% of ducklings surviving to fledging in a drought year (Kingsford 1989b). The fledging period is about 57 days (Kingsford 1986b).

In this study, I documented the extent of parental care in *C. jubata*, compared male and female roles and related parental care to brood age and size. I also explore the hypothesis that biparental care is an anti-predator adaptation associated with the hazards of grazing.

Methods

This study was done near Goulburn on the Southern Tablelands (34~S0o~T 18’S, 149~S0o~T 42’E) of New South Wales, Australia. The 1500 ha study site was grazed by cattle and sheep and had 64 farm dams or ponds that served as watering points for livestock. These were simple habitats with virtually no emergent cover.

I observed parental care of Australian Wood Ducks 1981-83 (August-December each year) which included the entire brood period. Male and female roles during parental care were examined in 1983, using 10 minute focal samples (Altmann 1974). Focal samples were only collected when there was no disturbance to the brood (i.e. no predators present). Since many family groups did not move from specific dams, it was possible to age most broods, based on their age at first sighting, compared to broods of known age (Kingsford 1986b). I also collected data on the behaviour of paired Australian Wood Ducks without broods during this period.

Six activities or postures were recorded: Extreme head up (EHU), Head up (HU) (these after Lazarus & Inglis (1978)), Grazing (GR), Loafing (birds resting or sleeping), Comfort (preening) and an agonistic Rush display. In the Rush, the head was held parallel to the ground with neck outstretched, usually while pursuing a conspecific. In EHU, Australian Wood Ducks stretched their necks upwards to the fullest extent. This had the effect of slightly raising the axis of the body anteriorly. In contrast, during HU, the axis of the body remained parallel to the ground and the neck was not fully stretched. An event recorder made it possible to record the activities of both male and female birds simultaneously.

The relationship between parental behaviour and size and age of broods was explored using analyses of variance that tested the effects of duckling age, number of ducklings in the brood and the sex of parent on the three most frequent behaviours - Extreme head up, Head up and Grazing. I used a four factor design with repeated measures on two of the factors, sex of parent and the behaviour (Winer 1971), analysed with SPSS MANOVA (Hull & Nie 1981). Separate analyses were used to examine variation in the total amount of time spent in behaviours and, the mean bout length of behaviours. As postures and displays changed rapidly in any 10 minute focal sample, the bout length was the mean duration of all occurrences of a particular posture or display within a 10 minute focal sample. Degrees of freedom for the latter analysis were reduced because not all three behaviours occurred in all samples.

These repeated factor analyses assume homogeneity of variances for groups (Winer 1971). For total amount of time spent, Cochran’s tests for homogeneity of variances for factor combinations, showed that variances differed. However, plots of means against variances and standard deviations did not exhibit any consistent abnormalities. The second assumption, that the covariance matrix be positive definite (Hull & Nie 1981), was satisfied in both analyses.

I recorded the position of both parents relative to the brood and which parent was on higher ground. Parents were scanned (Altmann 1974) every 30 seconds for a period of 5 minutes. These data were separated into two groups: foraging birds and resting birds, and were analysed using the binomial test (Zar 1974).

Data on peck rates of paired birds with or without broods were recorded as the time it took birds to peck 20 times while grazing. Data were analysed using an unbalanced one factor analysis of variance after a log transformation to improve normality (Zar 1974).

Results

Both parents performed the Rush display when the following bird species approached the brood: White-faced Heron *Ardea novaehollandiae*, Kookaburra *Dacelo novaeguineae*, Australian Magpie *Gymnorhina tibicen*, Sulphur-crested Cockatoo *Cacatua galerita*, Galah *Cactua roseicapilla* and Australian Raven *Corvus coronoides*. In all encounters, the intruding species was driven off. Parents also Rushed conspecifics which approached the brood. Twice, Australian Wood Ducks that were not part of any family group pecked at ducklings, before being driven off by the parent using the Rush display. Males and females performed similar lengths of this agonistic display ($t_{14} = 0.7$, $P>0.5$, mean = 3.0 ± 0.46 S.E. secs, $n = 118$). As family groups tended to feed away from other Australian Wood Ducks, this behaviour was not often performed. Rush was not recorded in any

Table 1. Three factor analysis of variance of amount of time spent by paired Australian Wood Ducks performing the three behaviours; Extreme head up, Head up and Grazing over 10 minute focal samples. Factors were; sex of the paired Australian Wood Duck (SEX), behaviour (BEHAV) and age of the ducklings (AGE). Age categories were; adults with no ducklings (0), "incubating" adults, and adults with ducklings aged (2-5); (6-15); (16-22); (23-28); (29-34); (35-42); (43-68) days old. (* $P<0.05$, ** $P<0.01$, *** $P<0.001$).

BETWEEN BROODS	DF	MS	F	SIGNIF
AGE	8	246682.68	1.86	***
BROODS WITHIN GROUPS	109	132538.18		
WITHIN BROODS				
SEX	1	8181.90	0.86	ns
AGE by SEX	8	158645.11	0.86	ns
SEX by BROODS WITHIN GROUPS	109	95035.24		
	DF	Error DF	F	SIGNIF
BEHAV	2	108	6.15	**
AGE by BEHAV	16	216	3.14	***
SEX by BEHAV	2	108	32.23	***
AGE by SEX by BEHAV	16	216	3.73	***

of the focal samples of birds without broods ($n = 20$) although it was seen at other times in this group.

Family groups grazed up to about 30-40 m from the dam although most time was spent within 20 m of a dam. Families tended to preen and sleep within about 10 m of the dam, usually not on the edge of the dam.

Parents responded to my presence by: (1) leading ducklings away from the dam into surrounding vegetation, during which males and females continually vocalised; (2) crouching motionless with the ducklings in a group, with their heads stretched out on the ground; or (3) feigning wing injury. Which one was performed depended on my proximity - the first (100 m - 1 km), the second (10 m - 100 m) and the third within 10 m. If families in the third category were disturbed, ducklings ran in all directions. I saw two successful attacks by predators: a Wedge-tailed Eagle *Aquila audax* and two Australian Ravens. The eagle took an almost fully grown duckling. The ravens took two smaller ducklings. Both family groups which were attacked were grazing and immediately scattered. Often when an alarm call from another bird species was heard, parents led families to water. Parents were leaders to broods with similar frequency (males - 4 times, females - 3 times), in response to my presence. Parents continued to attempt to lead offspring after they fledged, but the young did not always follow.

One family group increased its brood size by adopting three ducklings which were about ten days younger than its ducklings. There was no obvious difference in parental care before and after adoption and the family group remained together until all young were fledged. From the 98 focal samples collected for family groups, brood size did not influence time spent performing parental behaviours, but both duckling age and parental sex did influence behaviours (Appendix - Table 1a). To further investigate the importance of AGE and SEX on the three main behaviours, brood size was ignored and broods subdivided by age into seven categories (Table 1). Two additional groups were also included: paired Australian Wood Ducks without young and laying or incubating birds.

Duckling age significantly influenced the time parents spent in the three major activities of EHU, HU and GR (Between Broods - Table 1). Parents of older ducklings spent more time in these activities than did parents with younger broods (Fig. 1). Parents with broods aged 35-42 days spent more time performing the three behaviours compared to parents with broods aged 2-5 days (Fig. 1). Comfort and loafing activities occupied more of the behaviour of parents in the

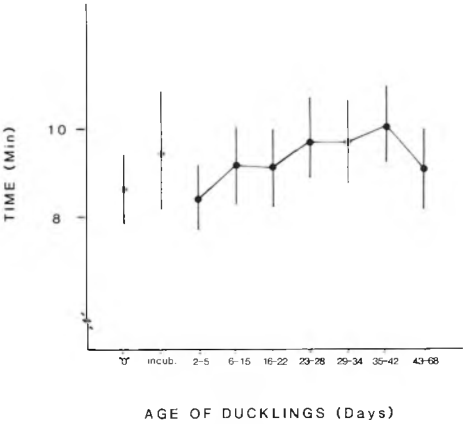


Figure 1. Summary of the significant age effect between broods summed over the three behaviours Extreme head up, Head up and grazing performed by Australian Wood Ducks. Means (±95% C.L.) calculated from the residual.

2-5 day age group than in any other age group (Fig. 2a and 2b). Females spent more time loafing and performing comfort activity during early brood care than later, while males spent less time overall in both these behaviours and this did not vary with age of the brood.

Interest lay principally in "within broods" variation. There was a significant second order interaction, AGE by SEX by BEHAV ($F_{16,216}$ = 3.73, P<0.001) which subsumed other effects (Table 1). Males and females changed their behaviour as ducklings aged but they changed in different ways. Figure 3 summarises results of this interaction. The greatest difference in the behaviour of the sexes existed between EHU (Fig. 3a) and GR (Fig. 3c). Performance of EHU was highest for males with "incubating" females. This appears to decrease with age of ducklings. Males with broods aged up to 34 days old and those with "incubating" females had higher EHU compared to males without young (in group O). However, with ducklings aged 34 days and over, EHU in males with broods and those in group "O" was similar. It was not until broods were at least 16 days old that the EHU of female parents matched that of the male. This was due to both an increase in EHU of females and a decrease in male EHU. Female EHU was lower than that of most males throughout the brood care period. In broods that were 42 days and older, there was a reduction in EHU for both males and females. Laying or incubating females seldom performed EHU and spent much more of their time grazing than their partners. This continued into early brood care. It was not until ducklings reached 6-15 days old that female parents reduced grazing time (Fig. 3c) so that it was no longer different from male's grazing time.

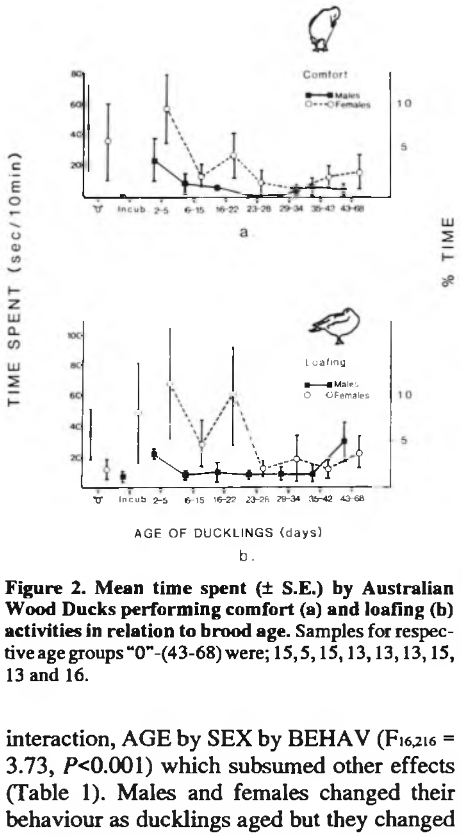


Figure 2. Mean time spent (± S.E.) by Australian Wood Ducks performing comfort (a) and loafing (b) activities in relation to brood age. Samples for respective age groups "0"-(43-68) were; 15, 5, 15, 13, 13, 13, 15, 13 and 16.

Nearly all 95% confidence intervals overlapped for Head up behaviour (Fig. 3b), although parents with broods over 29 days performed more of this behaviour than "incubating" females. There was a linear increase in HU with the age of ducklings. EHU may be replaced by HU late in the brood care period.

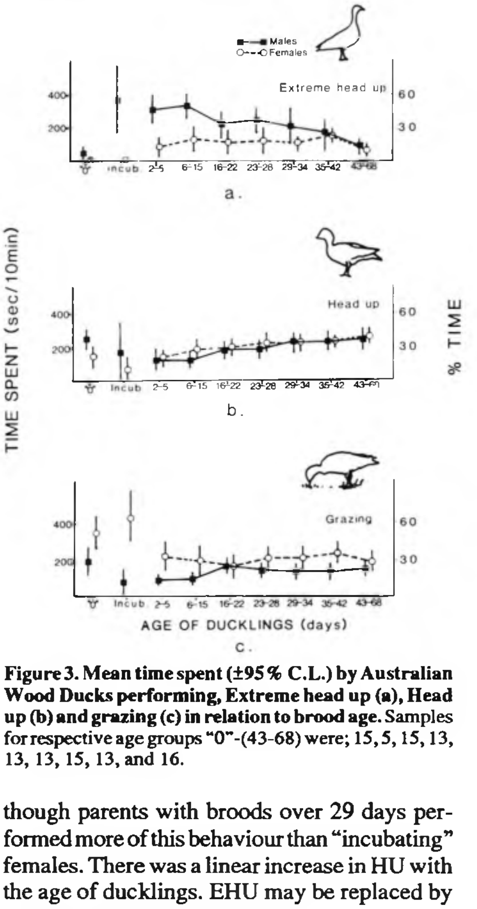


Figure 3. Mean time spent (±95% C.L.) by Australian Wood Ducks performing, Extreme head up (a), Head up (b) and grazing (c) in relation to brood age. Samples for respective age groups "0"-(43-68) were; 15, 5, 15, 13, 13, 13, 15, 13, and 16.

Following a similar sequence of analysis, neither number in brood nor age of brood were important factors determining mean bout duration (Appendix - Table 2a). However, mean bout duration of the behaviours was different and varied according to the sex of the paired bird ($F_{12,80}$ = 11.98, P<0.001, Table 2). Mean durations of female EHU, HU and GR did not differ (Fig. 4), but males spent significantly longer periods in EHU than either males or

Table 2. Three factor analysis of variance of the mean bout length of behaviours, Extreme head up, Head up and Grazing within 10 minute focal samples. Categories for age of ducklings (AGE) were; (0 - no ducklings), (2-10), (11-20), (21-28), (29-37), (38-63) days old. Data transformed by log (x+1) to overcome heterogeneity of variances (* $P<0.05$, ** $P<0.01$, *** $P<0.001$).

BETWEEN BROODS	DF	MS	F	SIGNIF
AGE	5	0.05	1.21	ns
BROODS WITHIN GROUPS	81	0.41		
WITHIN BROODS SEX	1	0.11	1.52	ns
AGE and SEX	5	0.03	0.49	ns
SEX by BROODS WITHIN GROUPS	81	0.07		
	DF	Error DF	F	SIGNIF
BEHAV	2	80	12.21	***
AGE by BEHAV	10	160	1.61	ns
SEX by BEHAV	2	80	11.98	***
AGE by SEX by BEHAV	10	160	0.76	ns

Factors are as described in Table 1.

females performing HU and GR. HU in males was also significantly longer than grazing bouts in males. Males also spent less time grazing than females but this was offset by a faster pecking rate than either females with and without broods or males without broods ($F_{3,93} = 14.91$, $P<0.001$, Fig. 5).

Out of 69 broods over the three years, there were three single parent broods (1 female, 2 male) with respective brood sizes of 11, 4 and 4. The remains of one of the female parents were found close to one of the single parent broods. These brood sizes were not significantly different to two parent brood sizes (seasonal and annual averages 4-7, Kingsford 1989b). However, it appeared that single parents spent more time being vigilant than their counterparts in two parent broods.

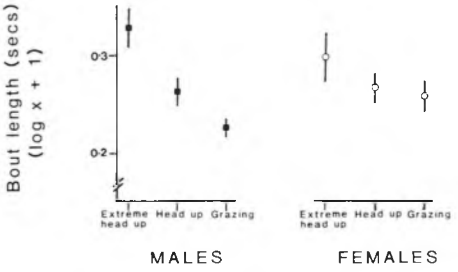


Figure 4. Mean bout duration (±95% C.L.) of the three behaviours; Extreme head up, Head up and grazing, according to the sex of paired Australian Wood Ducks (n = 87 broods).

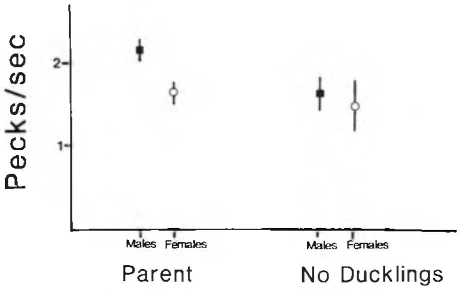


Figure 5. Mean peck rates (±95% C.L.) for Australian Wood Ducks with broods and paired birds without ducklings.

Parents adopted different positions in relation to their brood. Data were analysed separately for family groups that were actively foraging and those that were resting, usually loafing. It was not always possible for one of the birds to be on a higher piece of ground. Where height differences existed for resting groups, males were higher for all five minute samples collected ($n = 21$). This pattern exists for foraging groups as well, with the male usually higher than the female parent ($z = 3.00$, $n = 109$, $P<0.01$). One male Australian Wood Duck with a brood perched in a tree and adopted the Extreme head up posture. In contrast, females were always nearer to the brood while loafing ($n = 26$); they also grazed closer to the ducklings than did males ($z = 56.0$, $n = 227$, $P<0.001$).

Discussion

Male and female Australian Wood Duck parents provided extended parental care. Both initiated anti-predator strategies and attacked duckling predators. Such behaviour seemed dependent on which parent first detected a predator. Of the behaviours common to all Australian Wood Ducks, parents did more agonistic Rush displays than non-parent adults. Although this agonistic display may reduce competition for food

(Lazarus & Inglis 1978), the protection of offspring from conspecifics may be equally important.

There were also differences in the amount of time spent in EHU, HU and GR behaviours. As these comprised much of the behaviour of Australian Wood Ducks, a reduction in one would allow an increase in either one or both the other two. A number of workers have equated the EHU and HU behaviours with vigilance or alert behaviour in other Anatidae, either for predators or conspecifics (Dwyer 1975, Bruggers & Jackson 1977, Inglis 1977, Asplund 1981). Lazarus & Inglis (1978) addressed the possibility that this type of behaviour may be important in obtaining food information in Pink-footed Geese.

Three observations indicate that EHU primarily functions to detect predators. First, males spent considerable time in EHU when they accompanied their mates during incubation. If this was to obtain food information, then it might be expected that the male would direct the female to good food patches. There was no evidence of this. The male often remained behind his mate and followed while she fed, possibly even out of her sight. Second, when there was little natural food, as in 1982 (Kingsford 1989a), one might expect an increase in EHU, to search more for food, but I detected no such trend. Finally, the frequent performance of such behaviour in the presence of predators is an indication that EHU functions primarily in predator detection.

HU may serve a dual purpose. It incorporates two postures; one during grazing where the head is not fully lifted above the body and that illustrated in Figure 3b. Of the postures described as HU, the former may be important for finding food as well as detecting predators.

Most variation in the three most common behaviours was in EHU and GR (Fig. 3a and 3b), an increase in one reflecting a decrease in the other. Changes were dependent on the sex of the duck and the age of the brood (Fig. 3). This variation reflects the differences in energy demands. Females lay a clutch that may exceed her total weight (Lack 1968) and increase her daily energy expenditure by as much as 50-70% (King 1973). Incubation also places a considerable energetic burden on the female. Female Anatinae spend considerable time on the nest (McKinney 1965, Miller 1976, Bruggers 1979, Afton 1980) and may lose, on average, 25% of their weight during incubation (Krapu 1981). Incubating female Australian Wood Ducks confine their feeding to a few bouts during the day. To compensate for decreased foraging time, laying or incubating females need to feed more intensively. One female on an incubating recess, fed for the full ten minute sample without raising her head once.

Female Australian Wood Ducks continued to spend much of their time feeding during early brood care, presumably to recover energy lost during laying and incubation (Fig. 3c). They also spent more time in comfort and loafing, in early brood care, than either males or paired females without young in group "O" (Fig. 2a and 2b). Females may loaf and perform more comfort activity in this period to reduce energy costs.

Constrastingly, EHU in male Australian Wood Ducks was highest in the "incubating" group, significantly higher than EHU of females in this group (Fig. 3a). Similar results have been found for a number of other Anatinae during the breeding season (Dwyer 1975, Bruggers & Jackson 1977, Asplund 1981). In some Anatidae, vigilant behaviour during breeding has been correlated with increased territoriality, allowing the female access to vital food resources (Dwyer 1975, Inglis 1977, Asplund 1981). Despite accounts of males defending localities (Rowley 1975, Frith 1982), I found little evidence for such territoriality. Male Australian Wood Ducks defended neither feeding areas nor dams. This is not an unexpected result since feeding areas are not defensible and it is questionable whether dams would be considered a resource. However, pairs did defend a moving territory around them. During laying and incubating, when male EHU was highest, males may have been mate-guarding (McKinney *et al.* 1983) to avoid any chance of mates being inseminated. I saw only one forced extrapair copulation.

Brood size did not affect the total time spent by either parent in the three main behaviours EHU, HU and GR. The absence of a brood size effect has been found in other waterfowl (Lazarus & Inglis 1978, Guinn & Batt 1985), and provides further evidence that EHU and HU behaviours functioned as vigilant behaviours to detect predators. If these behaviours functioned either to monitor the young or obtain food information, then they would be expected to increase with brood size since these are shared parental behaviours in geese (Lazarus & Inglis 1986).

Male parents also had shorter GR and longer EHU bouts than females (Fig. 4). Therefore, males would be more likely to detect predators since the length of interscan intervals was shorter (Hart & Lendrem 1984). The posture of vigilant behaviour suggests an attempt to achieve maximum height. The use of high ground by males may be an important part of their vigilant behaviour. The extension in height likely increases the area that can be surveyed and hence the effectiveness of predator detection.

Female Australian Wood Ducks spent more time in EHU later in brood care, which may be related to an improvement in their condition, resulting from the additional time spent feeding. Towards the end of brood care, parental care in the form of EHU begins to decline in both parents (Fig. 3a), as predicted by parent-offspring conflict (Trivers 1974). Older ducklings probably are less vulnerable to predation; duckling mortality decreased with age of the duckling (Kingsford 1989b). It was noticeable that duckling EHU and HU increased with age which may decrease the need for parental EHU.

Male parental care in Australian Wood Ducks is important during incubation and early brood care, since it allows the female to regain some of the costs of reproduction by feeding intensively, while the male is vigilant for predators. Without compensatory vigilance from the male during early brood care, predation of the female and ducklings might be high. In later parental care, the male may increase his individual fitness by further contributing to parental care until the young are fledged. This may result in the long-term pair bonds observed in this species (Kingsford 1990).

Australian Wood Ducks, like geese, have a highly terrestrial lifestyle and are probably more vulnerable to predation than more aquatic anatids. In addition, Australian Wood Ducks are relatively small anatids and may be more vulnerable to predation than geese, especially at the duckling stage.

The absence of biparental care in predominantly grazing species like the Wigeon *Anas penelope* is interesting. Perhaps these anatids are relatively new to the grazing lifestyle. Wigeons frequently feed by upending during high water levels (Owen & Thomas 1979) and so may not be as adapted to grazing as the geese and the Australian Wood Duck (Kingsford 1989a).

High predation intensity may be more important than nest site concealment and injury-feigning behaviour in causing biparental care and long-term pair bonds. Similar selection pressures may have shaped not only the ecology but also the mating systems of grazing anatids.

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R.T. Kingsford School of Biological Sciences, University of Sydney, Sydney, N.S.W. 2006, Australia.
Present address: New South Wales National Parks and Wildlife Service, P.O. Box 1967, Hurstville, N.S.W. 2220, Australia.

Appendix

Table 1a. Four factor analysis of variance of the amount of time spent by paired Australian Wood Ducks in the behaviours, Extreme head up, Head up and Grazing. The number of ducklings in each brood, factor (NO), had three levels; (1-5), (6-8), (9-16) ducklings. Groups for age of ducklings (AGE) were; (2-10), (11-22), (23-37), (36-68) days old. (* *P*<0.05, ** *P*<0.01, *** *P*<0.001).

BETWEEN BROODS	DF	MS	F	SIGNIF
AGE	3	489015.70	3.90	*
NO	2	96357.34	0.77	ns
AGE by NO	6	152162.13	1.21	ns
SUBJ WITHIN GROUPS	86	12538.10		
WITHIN BROODS				
SEX	1	108604.21	0.99	ns
AGE by SEX	3	230927.36	2.11	ns
NO by SEX	3	111871.29	1.02	ns
AGE by NO by SEX	6	8846.73	0.81	ns
SEX by SUBJ WITHIN GROUPS	86	109594.10		
	DF	Error DF	F	SIGNIF
BEHAV	2	85	2.16	ns
AGE by BEHAV	6	170	3.12	**
NO by BEHAV	4	170	1.87	ns
AGE by NO by BEHAV	12	170	0.90	ns
SEX by BEHAV	2	85	21.43	***
AGE by SEX by BEHAV	6	170	3.59	**
NO by SEX by BEHAV	4	170	0.82	ns
AGE by NO by SEX by BEHAV	12	170	0.70	ns

Other factors as described in Table 1.

Table 2a. Analysis of variance of mean bout length of behaviours, Extreme head up, Head up and Grazing. Age of the ducklings (AGE) groups were; (2-16), (17-35); (36-63) days. The three groups, (1-5), (6-8), (9-16) ducklings represent the three levels of the factor NO, number of ducklings in broods. Data transformed by log (x+1) to overcome heterogeneity of variances. (* *P*<0.05, ** *P*<0.01, *** *P*<0.001).

BETWEEN BROODS	DF	MS	F	SIGNIF
AGE	2	0.47	0.25	ns
NO	2	2.48	1.29	ns
AGE by NO	4	0.69	0.36	ns
SUBJ WITHIN GROUPS	67	1.92		
WITHIN BROODS				
SEX	1	0.93	4.98	*
AGE by SEX	2	0.05	0.28	ns
NO by SEX	2	0.18	0.94	ns
AGE by NO by SEX	4	0.05	0.25	ns
SEX by SUBJ WITHIN GROUPS	67	0.19		
	DF	Error DF	F	SIGNIF
BEHAV	2	66	28.69	***
AGE by BEHAV	4	132	1.57	ns
NO by BEHAV	4	132	0.53	ns
AGE by NO by BEHAV	8	132	0.84	ns
SEX by BEHAV	2	66	8.96	***
AGE by SEX by BEHAV	4	132	1.42	ns
NO by SEX by BEHAV	4	132	2.03	ns
AGE by NO by SEX by BEHAV	8	132	0.06	ns