Flock structure and pair bonds of the Australian Wood Duck *Chenonetta jubata*

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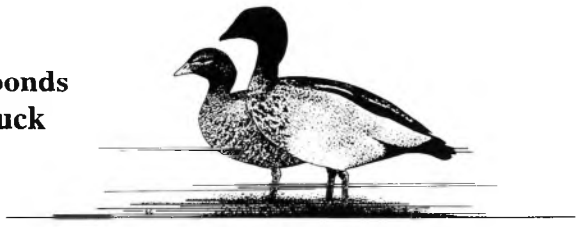

Flocks of Australian Wood Ducks were composed of pairs of birds which moved independently between flocks over periods of more than 24 hours. Sixteen groups formed with a similarity greater than 0.75, following Single Linkage Clustering analysis using the Jaccard similarity coefficient. All were groups of two ducks, invariably male and female. Records confirmed that most of these were paired birds. Only about 40% of a flock remained the same after a period of 24 hours. This declined to 20% over a two day period. After breeding when the young have fledged, family groups joined other individuals in flocks but it was not known how long these family groups remained together. Pair bonds were long-term with six pairs recorded together for more than one year: two pairs were paired for a minimum of 16 months. Pairs remained together throughout the year but pairs did not usually behave independently of other individuals within a flock. Flocks usually behaved as a unit when grazing or loafing. Individuals remained close together while they grazed, with over 50% of the flock grazing at any instant.

Grazing waterfowl, like geese and shelducks, typically form flocks composed of family groups (Raveling 1969, Patterson 1982, Craven & Rusch 1983, Summers 1983). Dabbling ducks (Anatini) tend not to exhibit such complex structure. Pairs do not tolerate conspecifics (Dwyer 1975) and families disperse (Martinson & Hawkins 1968). Like some shelducks and geese, the Australian Wood Duck *Chenonetta jubata* is a grazer (Frith 1982, Kingsford 1989a), spending about 30% of the day grazing in frequent bouts of 10-15 minutes (Kingsford 1986a).

Australian Wood Ducks are nearly always seen in flocks usually numbering less than 100 birds but sometimes reaching 2000 (Frith 1982: 264). I found mean flock sizes between September and December to be 8.4 (n = 330) in 1981, 25.0 (n = 396) in 1982 and 7.5 (n = 324) in 1983 with a maximum of 153 (Kingsford 1986a). Little is known about the composition or the behaviour of individuals within the flock. Flock size seems to be related to seasonal factors with birds dispersing during breeding and congregating after breeding (Frith 1982: 264, Kingsford 1986a). These groups of Australian Wood Ducks may simply be aggregations around a resource. One would expect that if this were true, individuals would behave independently. Evidence of groups of Australian Wood Ducks banded together and found together some years later (Frith 1982: 265) suggest some coexistence of individuals. This is intriguing and I aimed to find out whether there were units of Australian Wood Ducks within flocks which remained together over periods of up to four months. I also investigated the behaviour of these flocks over the period of a day to see if individuals behaved independently once collected as a flock.

The duration of the pair bond is also critical to understanding the social behaviour of any bird species. While most anatids are monogamous, there is considerable variability among waterfowl species. Geese, swans and shelducks (Delacour & Mayr 1945, Akesson & Raveling 1982, Summers 1983, Rohwer & Anderson 1988) tend to have pair bonds that last longer than a season, while dabbling ducks usually remain paired for only one breeding season (McKinney 1986). Little is known of the duration of pair bonds in wild Australian Wood Ducks although captive birds are reported to have long-term pair bonds (Kear 1970). This paper also reports on durations of male-female associations in wild birds to assess the mating system of the species.

Study site

The study was done near Taralga on the Southern

Tablelands (34° 18'S, 149° 42'E) of New South Wales, Australia during 1981-83. Climatically, 1982 was unusual with little rainfall compared to the other two years (Kingsford 1989b). The 1500 ha study site included three farms and was grazed by cattle and sheep. It had 64 farm dams, or small reservoirs, which served as watering points for livestock. The dams were surrounded by pasture on which Australian Wood Ducks graze. Australian Wood Ducks could be found on most of these. The study site was surrounded by similar farms with dams suitable for Australian Wood Ducks.

Methods

Data collection

I trapped 873 Australian Wood Ducks between April 1981 and December 1983 with funnel traps (McNally & Falconer 1953) baited with wheat grain. Birds were colour-banded using a combination of anodised aluminium bands (supplied by the Australian Bird Banding Scheme) and coloured celluloid bands. Most trapping was done before August each year to avoid interference with breeding activity in the spring. After trapping, I released all captured ducks together so that any social structure which may have existed was maintained. Birds usually flew off as a small flock to the next dam.

About every four days between September and December (1981-83), I identified all banded individuals in flocks on any dams where they were present. A flock was defined as any group of birds seen on a dam on a particular day. Data on flock size were also collected during these surveys. An average of 10.8± 0.49 (S.E.) flocks were found on each survey day of the study (Kingsford 1986a). Within flocks, I also noted any paired Australian Wood Ducks. These were male and female ducks which maintained close proximity and engaged in pair maintenance displays (Kingsford 1986a). Trappings or sightings of ducks together provided data for pair bond tenure.

I investigated whether the whole flock behaved as a unit when they were on a dam, by examining the behaviour of all individuals in the flock instantaneously. Data were collected on flock behaviour in 1982 over 170 hours, as part of another study on activity patterns (Kingsford 1986a). Observations were also made on the proximity of birds to each other. To examine the behaviour of all individuals in a flock, I separated activities into land and water based behaviours. Activities on water accounted for 7% of diurnal time (Kingsford 1986a) and so they were grouped. Terrestrial activities were further separated into grazing, loafing, walking, comfort, social and vigilance. I scanned flocks instantaneously (Altmann 1974) every two minutes and recorded the number of individuals within the flock that were performing each activity. Most flocks that were observed had more than 10 birds ($x = 14.9 \pm 7.00$, S.D., $n = 41$). Data were collected in half hour bouts throughout the diurnal cycle, followed by half an hour to rest and observe displays (Kingsford 1986a). The proportion of individuals in the flock performing any one activity, during a particular instantaneous scan, was a measure of the behavioural dependence of the members in the flock. A high proportion meant that most individuals in the flock were performing an activity.

Data analysis

For the analysis of behavioural synchrony, I reduced dependence due to other behaviours and the preceding two minute scan, by randomly selecting only one two minute instantaneous scan per activity, for each half hour observation period. One-way analysis of variance was then used to test among behaviours to see which behaviours had a higher proportion of individuals in the flock performing that same behaviour at any one time. Data were transformed by arcsine to improve normality (Zar 1974).

I used cluster analysis to investigate flock structure (see example in Morgan *et al.* 1976). Cluster analysis is a statistical technique which groups those attributes or objects which are most similar (Romesburg 1984). I used flock data collected in 1982 (June-December) which covered breeding and non-breeding periods (Kingsford 1989b). Forty-six percent of the population was banded that year compared to other years when banding effort was less. Banded ducks seen only once were omitted from the analysis.

I calculated a similarity measure for every pair of banded ducks in the data set which reflected how often they were found together. The Jaccard similarity coefficient (Sokal & Sneath 1963) seemed the most simple and applicable. It is based on a two-way table of the presences and absences of two Australian Wood Ducks in a flock (Table 1). If two ducks are always found together in all flocks, then they will have a similarity of one: they have no mismatches ("b", "c"). I did not include those

times when neither bird was seen in a particular flock ("d") in this measure. Where flock structure is stable over time, individuals have a high similarity measure and birds are clustered together.

Table 1. Jaccard similarity measure used to analyse flock structure of Australian Wood Ducks. "a" is the number of times duck i and duck j were in the same flock.

		Duck i	
		Presence	Absence
Duck j	Presence	a	b
	Absence	c	d

$$\text{Similarity coefficient } Cij = \frac{a}{a+b+c} \quad 0 \leq Cij \leq 1$$

I used the hierarchical single linkage method (Romesburg 1984) to cluster similarities for each duck, using GENSTAT (Alvey *et al.* 1982). This method sometimes results in chaining (Sneath & Sokal 1973) which may hide detail about clusters but it is simple to apply and understand (Morgan *et al.* 1976). First, clusters are formed between those ducks with the highest similarity. If a cluster already has more than one duck, the method takes the highest similarity to the duck to be included from any one of the ducks already in the cluster. This continues until all ducks have been clustered into one group, as it is heirarchical.

I also examined the stability of 118 flocks over periods up to 14 days, on four dams. Any two flocks were considered to be the same over time, if they had at least one marked individual in common and were on the same dam. A percentage difference between the two flocks was then calculated. This was the number of banded ducks common to both flocks divided by the total number of banded birds in both flocks, converted to a percentage. A flock with the same banded individuals a day later would have a similarity of 100%; any addition or loss of individuals would reduce this similarity.

Results

Cluster analysis on data from 135 banded individuals (median observations per duck = 5) and 138 observations of flocks revealed that distinct clusters of two Australian Wood Ducks were predominant (Fig. 1). At high similarities, clusters consisted of only two ducks which showed the two birds' close association. There were six clusters of two ducks with a similarity of one. These pairs of ducks were always found together. At similarities greater than 0.75, there were 16 clusters; all were two-duck clusters. Clusters of two birds did not result from infrequent observations. The mean number of observations per duck for the 16 clusters was 9.7 ± 6.98 S.D. (n = 32) compared to a mean for other ducks of 5.4 ± 4.39 S.D. (n = 103). This was a significant clustering pattern, above or equal to a similarity of 0.75 (Binomial test, two bird clusters against larger clusters, z = 7.22, P<0.001). Not until the similarity declined to

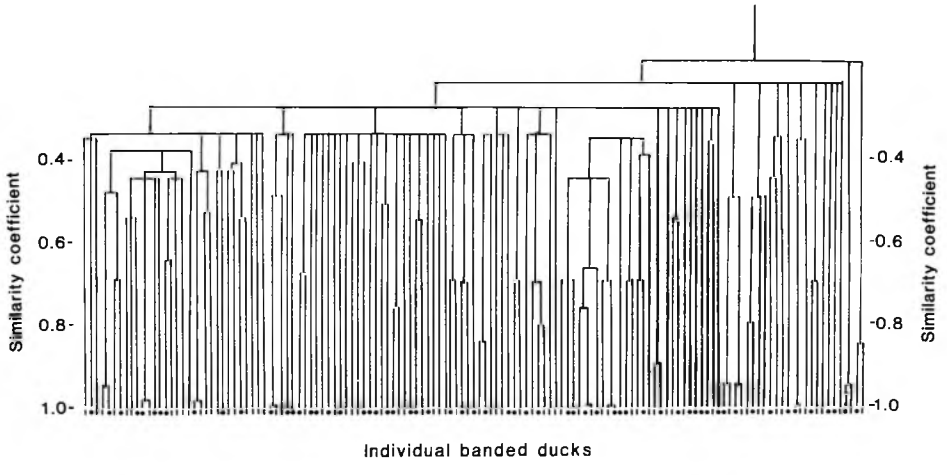

Figure 1. Dendrogram illustrating flock structure, formed after Single Linkage clustering on flock associations of 135 colour banded Australian Wood Ducks in 1982. Similarity levels are calculated from the Jaccard similarity measure ($0 \leq \leq 1$). Filled in circles represent males and vertical dashes females.

0.75 was there a cluster of three ducks. Similarity measures for these three ducks were based on only three, three and four observations respectively. Above a similarity of 0.55, over 48% of all Australian Wood Ducks included in this analysis formed clusters of two. More significantly, individuals in these two bird clusters were, without exception, male and female birds. In many (17 out of 25), my observation records confirmed that these clusters were paired birds (i.e. were seen to perform pair maintenance displays). This pattern was also noticeable when I observed foraging flocks. Pairs moved as a unit within flocks as they fed. Flocks were also often unstable even over a period of 24 hours as either new individuals joined a flock or individuals left, which were there the day before (Fig. 2). Most of these compositional changes happened in the first two days. After this, the flock retained about 20% similarity to the original flock. While there were fewer data from other years, observations suggested a similar pattern in flock structure although there was one major difference. Towards the end of 1981 and 1983, flocks contained family groups.

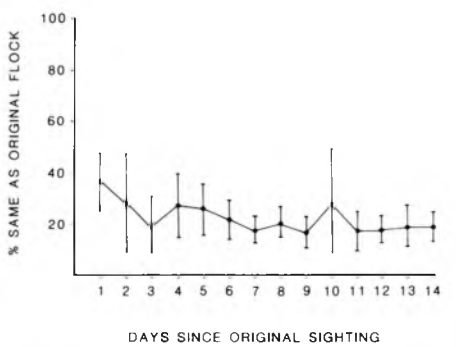

Figure 2. Changes in the composition of particular flocks of Australian Wood Ducks over time (periods of more than one day). Flocks were defined as the same over time if they had one Australian Wood Duck in common and were on the same dam. Percentage of the flock which remained the same (mean ± S.E.), was the number of colour banded ducks which were the same in two flocks divided by the total number of banded individuals.

Data on pair bond duration were collected throughout the study but only data on pairs seen together for more than one month or individuals that were paired and subsequently seen separately are considered. This was because, of the 873 Australian Wood Ducks that were colour-banded, many were never seen again (59%). Others only remained for a short period within the study site. Twelve pairs fell into this category: the period between the first and last records of these as a pair was less than one month. Of these pairs, neither banded bird in the pair was seen again within the study site without the other bird in the pair. Such data contributed little to an understanding of pair bond duration, being more a reflection of movement. Data on pair bond duration (the time-gap between the first and last observations of a pair together), showed that six pairs remained together for more than a year (Table 2). Two pairs were together for more than 16 months. These data represent minimum estimates as pairs were likely to move out of the study area and data were only collected over a period of three years. Table 2 indicates that some of the pairs were probably paired before observations began as they had band numbers in sequence or close together, an indication that they were trapped together. One pair, 54467-58398, produced broods in consecutive years. Pair 11619-11620 was the only pair seen in separate flocks (Table 2); the female subsequently formed a pair with a male that was not banded and produced a brood. I saw the pair 11619-11620 perform pair maintenance displays for almost two months. Both birds were hatched the previous breeding season. In other break-ups (marked * in Table 2), only one of the birds in the pair was seen subsequently, so the

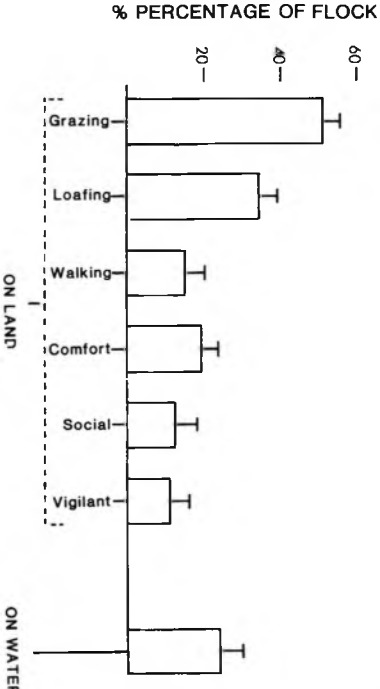

Figure 3. Percentage of Australian Wood Ducks (mean ± 95% confidence limits) in the flock performing particular activities during an instantaneous scan.

Table 2. Pair bond tenure in Australian Wood Ducks. Only data where the difference between first and last sighting of a pair together exceeds one month are presented, except if the members of a bonded pair were subsequently seen in separate flocks. Durations were the differences between initial and final sightings of pairs together. They are open-ended. Ducks whose bands could not be identified are signified by their coloured band combinations. * identifies pairs where one of the pair was subsequently sighted alone.

Band No.	Initial sighting	Final sighting	Duration (months)
54448-54450*	10/08/81	6/09/82	13.1
54440-54442	14/08/81	6/12/81	3.8
54419-54422*	23/08/81	12/10/81	1.7
03430-03465	16/09/81	27/12/81	3.4
54475-54474	25/09/81	26/11/81	2.1
13198-54457	29/10/81	21/06/82	7.8
30088-O/R/G	2/03/82	25/06/83	16.0
11682-11699	9/06/82	4/12/82	5.9
11686-11689*	10/06/82	11/12/82	6.1
11619-11620*	16/06/82	4/08/82	1.7
11698-11695	19/06/82	18/08/82	2.0
58335-58363	21/06/82	3/11/82	4.5
58272-58273	6/07/82	19/12/82	5.5
33619-B/R	7/07/82	5/11/83	16.2
58395-58396	16/07/82	27/11/82	4.5
54467-58398	17/07/82	12/10/83	15.1
54409-58270	19/07/82	14/09/82	1.9
13157-13158	24/07/82	18/05/83	9.9
58276-58277	24/07/82	30/09/83	14.4
13160-58328	25/07/82	4/06/83	10.5
03572-11615	29/07/82	19/12/82	4.8
33605-33606	12/08/82	3/11/82	2.8
33640-33641	23/08/82	3/06/83	9.5
03518-03575	20/09/82	14/10/83	12.8
11628-R/O	23/09/82	5/06/83	8.6
33824-33828	18/05/83	13/10/83	4.9
33849-33850	25/08/83	4/10/83	1.3
38856-38857	14/08/83	7/10/83	1.8
11660-11661*	20/09/83	6/12/83	2.6

reason for the separation could not be determined.

The number of individuals actually grazing in a flock at any one time was reasonably high, over 50% (Fig. 3). Loafing activity also exhibited a reasonably high degree of synchrony within flocks. More individuals were likely to be grazing or loafing at any one time in a flock compared to the other activities ($F_{7,554} = 27.9$, $P<0.001$). The proportion of the flock simultaneously performing other activities, other than grazing and loafing, tended to be low (Fig. 3).

Discussion

In 1982, flocks were made up of pairs of Australian Wood Ducks which moved independently among flocks: most marked birds clustered as male-female pairs (Fig. 1). This may be consistent with Frith's (1982: 265) observations of groups of Australian Wood Ducks found together year after year; unfortunately there was no information of the size of these groups. The cluster of three birds at a similarity of 0.75 was probably the result of few observations rather than an indication of a more complex organisation. It may also have reflected the process of mate choice but there were too few observations to be sure. Other clusters of more than two birds, at a lower similarity, were due to the heirarchical nature of the analysis. Flock composition was usually unstable over a period of as little as 24 hours, retaining only about 40% similarity to the original flock (Fig. 2). The stability in this similarity measure after about two days at about 20% was probably due to a pair of birds which remained on the dam. These birds might be involved in nest searching or occasionally incubation.

These data on flock composition were only collected in 1982, a drought year, when there was little breeding (Kingsford 1989b) and flock size was much larger than in other years (Kingsford 1986a). This may have resulted in more movement of pairs between flocks as they searched for food. However, opportunistic observations of flock composition in the other two years indicated a similar pattern to that found in 1982. In addition, data on pair bond duration

collected over the full study (1981-83), showed no more complex pattern in composition beyond that of the pair, except towards the end of the years, 1981 and 1983.

In 1981 and 1983, when there was extensive breeding, flocks of Australian Wood Ducks which collected after breeding (Nov-Dec) contained fledged juveniles. Since parental care continued after ducklings had fledged (Kingsford 1986a), these flocks probably contained family groups. How long the family group remains together is not known. However, there must be an upper limit of seven months as there was no evidence of family cohesion from 1981, carried through to 1982.

The importance of the pair as a unit in the flock is underlined by the data on pair bond duration. There were 17 pairs which were monogamous for more than four months (Table 2). The longest period over which broods hatched was just over three months recorded in 1983 (Kingsford 1989b). More importantly, some pairs remained together for up to 12 months. Two were paired for 16 months. The fact that some pairs were banded together provides further evidence that they were paired for longer. These records represent minimum durations which were totally dependent on the birds being observed on the site. The shorter duration in Table 2 were most likely due to the pair moving off the site given their mobility (Norman 1971), the smallness of the study site and the availability of similar habitat surrounding the site. Unfortunately, the data do not provide a measure of variability in pair bond duration. Of the two pairs where only one member was subsequently sighted (Table 2), mortality may have been the cause for the break-up since neither remaining bird was subsequently seen paired.

Rohwer & Anderson (1988) suggest that body size and latitude are the main determinants of male parental strategy. Large waterfowl, geese and swans, can actively defend their broods against predators while ducks have other antipredator strategies of avoidance and escape behaviour. The latitude hypothesis accounts for the presence of male parental care and long-term pair bonds in some Southern Hemisphere species (McKinney 1986, Norman & McKinney 1987, McKinney & Brewer 1989). Long-term pair bonds in such waterfowl may result from irregular breeding seasons (McKinney 1985).

Long-term pair bonds in Australian Wood Ducks probably result from the necessity for biparental care although living in an unpredictable environment may contribute to the patterns observed. Male parents perform the same parental duties as females and are particularly important in early brood care when the female is recovering energy lost during laying and incubation (Kingsford 1990). At this time, male parents spend much of their time in vigilance behaviour which decreases but continues throughout the brood care period. After brood care (fledging period about 57 days: Kingsford 1986b), it may be advantageous for the male to remain with the female until they breed again. In the arid parts of the continent where rainfall is unpredictable, Australian Wood Ducks can also breed throughout the year (Frith 1982: 267). Already paired birds could quickly take advantage of any suitable breeding conditions which in the inland probably occur following rainfall.

If flocks are made up of pairs, what evidence is there that a flock of Australian Wood Ducks is not simply an aggregation of individuals around a resource, all behaving independently? Observations of high behavioural synchrony and the proximity of individuals in a feeding flock show that this is not true. Two factors preclude results of behavioural synchrony being a chance occurrence, resulting from birds being simultaneously hungry. First, the pasture can be grazed at any time so birds feeding independently would not be expected to show any synchrony in behaviour, particularly as they graze in frequent bouts throughout the day. Second, they graze close together separated by no more than 4-5 duck lengths. The pasture surrounds the dam so if they fed independently, they would be expected to feed in different areas around the dam. Individuals will graze different areas around a dam but only in a flock.

Most of the flock would move off to feed as a unit. This was not obvious from the analysis of behavioural synchrony (Fig. 3). There were three reasons why the mean number of individuals grazing at any one time was not a lot higher than about 50% (Fig. 3). First, in larger flocks of 20-30 birds, a subunit of 10-15 birds sometimes moved off to graze but the others did not join them. Second, early in the breeding season pairs sometimes behaved independently. This was when they were nest searching, laying or incubating. At other times, paired birds moved and fed with the feeding flock. Finally, in any feeding flock, there were always a few individuals walking to new patches of pasture, being vigilant or scratching themselves. Australian Wood Ducks associate with others when feeding but, like some geese (Boyd 1953), there were few social interactions amongst individuals within flocks. Those that did occur tended to be

agonistic, further emphasizing the loose structure of flocks.

These observations of composition and behaviour of flocks suggest that Australian Wood Ducks must benefit in some way by forming flocks. It is interesting that the most dependent behaviours were feeding and loafing. Flocking behaviour in this species may have similar advantages to the individual that have been found in other species of birds. They may be able to detect predators sooner (Powell 1974, Siegfried & Underhill 1975) or increase their food intake by decreasing the amount of time spent in vigilant behaviour (Siegfried & Underhill 1975, Lazarus 1978, Caraco *et al.* 1980). As a small grazer, they are vulnerable to many avian predators (Kingsford 1986a). Grazing bouts were often cut short by the individuals in the flock running or flying to the safety of the water in response to the alarm calls of other birds which usually heralded an avian predator (Kingsford 1986a). Twice, I saw Australian Wood Ducks avoid attacks by avian predators by swimming to the middle of the dam. Australian Wood Ducks apparently use the water as a refuge from aerial predators.

The social system of this species contrasts that of Northern Hemisphere dabbling duck species (McKinney 1986, Rohwer & Anderson 1988) and the closely related *Aix* species (the Mandarin Duck and the North American Wood Duck) (Kear 1970, Armbruster 1982, Gilmer *et al.* 1978) in which the male deserts the female each breeding season. Instead, Australian Wood Ducks have similar social behaviour to other grazing anatids which flock, have long-term pair bonds, biparental care and family groups. How long family ties persist, remains unresolved. As Australian Wood Ducks probably mature faster than geese and shelducks, family groups may not remain together as long as in the larger anatids.

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