The dry season diurnal behaviour of the Madagascar Teal *Anas bernieri* at Lake Bemamba

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The behaviour of the globally threatened and little known Madagascar Teal was studied at Lake Bemamba, western Madagascar in July 1992. At least seven pairs and two single birds were observed. The pairs were tightly bonded and aggressively defended feeding space from conspecifics. Paired birds were dominant over and more aggressive than single birds. Paired males and females appeared to show similar levels of aggression. Copulation was observed but no other courtship behaviour, and there was no evidence of nesting activity. During daylight hours (0645 h to 1810 h), 80% of time was spent feeding. The amount of time spent resting increased notably between 1000 and 1300 h, but over 55% of time was spent feeding at all times. Madagascar Teal are active dabblers in shallow water, moving almost constantly. Of time spent feeding, 68% was conducted on foot and 32% swimming. Detailed descriptions of feeding and agonistic behaviour are made. The species has markedly different behaviour, habitat use and life cycle to the other six species of Anatidae present in the lake. There also appear to be important differences in behaviour in comparison with the other, closely related, Austral teal. However, it is likely that Madagascar Teal have the long term pair bonds typical of Austral teal.

Keywords: Madagascar Teal, Time Budget, Aggression, Feeding Behaviour, Threatened Species

The Madagascar Teal *Anas bernieri* is a globally threatened species with small known world population (Collar & Stuart 1985, Dee 1986, Green 1992, Safford 1993). In order to assess the status of the species in the Antsalova region of western Madagascar, its main known stronghold, a survey was conducted in the area in July and August 1992 by the Jersey Wildlife Preservation Trust and The Wildfowl & Wetlands Trust (Young et al. 1993). A small population was located in July at the southern end of Lake Bemamba, although the population had declined markedly since the previous survey of 1973 (Scott & Lubbock 1974), principally due to the conversion of all shallow, freshwater areas of the lake into rice-fields. Further surveys in 1993 identified other sites between Antsalova and Morondava that hold the species (Safford 1993).

Apart from basic descriptions of habitat in areas where Madagascar Teal have been collected or seen, and a general description of the behaviour of birds seen at Lake Bemamba in the first half of August 1973 by Scott & Lubbock (1974), the biology of the species is almost unknown. Shallow water in open, nutrient-rich mud seems to be the preferred habitat for foraging. The former abundance of the species at Lakes Bemamba and Masama (Green 1992) shows that freshwater habitats can be used, but rice agriculture has now become so extensive on the west coast that the species now appears to be confined to the few inland lakes that are too saline for rice culture and to saline, coastal areas such as mudflats (Safford 1993). In the last century, Madagascar Teal were reported as occurring in small flocks on estuaries, marshes or pools (Collar & Stuart 1985). No nests of the species have ever been observed in the wild, but Scott & Lubbock (1974) obtained contradictory local information that nesting at Lake Bemamba occurs in November or in April. Information collected in 1992 and 1993 suggested that almost all locals confuse Madagascar Teal with other wildfowl, and the only apparently reliable source reported that nesting of Madagascar Teal occurs in forest leaf litter some distance from the water’s edge in the wet season, which begins in December (Young et al. 1993).

Owing to this lack of basic information and the importance of understanding the biology of the Madagascar Teal as an aid to
its conservation, the opportunity was taken during the July 1992 survey to make an initial study of the dry season behaviour of the species at Lake Bemamba. The results of this study are presented here. The diurnal activity of Madagascar Teal is quantified, and the first ever detailed descriptions of the species’ feeding and agonistic behaviour are made. Basic comparisons of behaviour and ecology are made with the other Anatidae present at Lake Bemamba, and with the closest evolutionary relatives of the Madagascar Teal.

Methods

Behavioural observations of Madagascar Teal were made during the dry season between 20 July 1992 and 28 July 1992 in the southernmost section of Lake Bemamba, a brackish area that is too saline to grow rice and supports natural vegetation. The area of this southern marsh was roughly 200 ha at the time of study, but the lake was drying up and the wetland area was visibly shrinking from one day to the next. The marsh area was dominated by *Juncus* sp. rushes and was surrounded by rice-fields to the north and dried lake bed followed by degraded deciduous forest in other directions. Madagascar Teal were only present in more open areas of the marsh shoreline where shallow water less than 15 cm deep was combined with extensive areas free of emergent vegetation, thus enabling feeding along the water’s edge.

Madagascar Teal were seen in five distinct locations within the marsh, but the most important was a sandbar enclosed within the marsh that was relatively undisturbed. This area had particularly extensive areas of shallow, open muddy pools where the birds concentrated their feeding. It was surrounded by dense beds of *Juncus* sp. vegetation that were avoided by the birds. However feeding did also occur in very small surface pools amidst dense beds of a submerged macrophyte adjacent to the beds of *Juncus*. Dryland areas in the centre of the sandbar included beds of *Salicornia*-type glasswort. The sandbar was a major roost site for other waterbird species that fed in the ricefields (Young *et al.* 1993). The other locations where Madagascar Teal were observed were similar areas at the edge of the marsh that had smaller areas of open mud and were more disturbed by local people.

Behavioural observations were concentrated at the sandbar, with occasional short observations made in the other four locations during the course of more general surveys. Owing to the shortage of time, the importance of surveying additional areas to obtain a population estimate and the difficulty in collecting large quantities of data on a species that is so scarce, observation methods were selected that would provide as much data as possible on the bird’s behaviour at the expense of fine-tuned accuracy. The behaviour of all birds visible from the observation point was thus recorded continuously by a single observer for up to 275 minutes at a time. A dictaphone, telescope and stopwatch were used, scanning the birds continuously and recording the time and details whenever changes in behaviour were observed. The time was usually recorded to the nearest minute, with the precise duration of short behaviours such as social interactions being estimated later from memory in seconds, and thus being subject to a wide margin of error. However, during most of the observation periods, the birds conducted long bouts of continuous behaviours (either feeding, resting or preening) which makes the margin of error for these dominant behaviours insignificant.

When several pairs of birds were present in the study area, it was not always possible to identify distinct pairs throughout the observation period owing to the frequent changes in their position. Although different birds within a pair could sometimes be discriminated on the basis of size, the larger bird probably being the male, this was again not usually possible. It was also not considered a reliable method of sexing birds as measurements of birds captured in 1993 found that some of the smallest birds were males (Young *et al.* 1993). Hence observations of different birds within the same block could not satisfactorily be assigned to distinct individuals or sexes, and time-budgets were constructed by summing all data together in bird-minutes. Bird-minutes are the product of the time spent in a behaviour (in minutes) multiplied by the number of birds in that behaviour. They were chosen as the best unit for representative time budgets because they weight longer observation periods of more birds more strongly than shorter observation periods of fewer birds.
Observations were made during all daylight hours, spanning from first light to dusk (0645 h to 1810 h, local time), but were mostly concentrated in the early morning from 0700 h to 1200 h and late afternoon from 1500 h to 1800 h. However, on 27 and 28 July continuous observations were conducted at the sandbar throughout the daylight period by rotating two observers between observation periods of 150 to 180 minutes. No nocturnal observations were made.

Behavioural categories recorded were: Feeding; Resting (sleeping or loafing); Comfort (preening, bathing etc); Movement (walking, swimming or flying); Alert; Aggression (both intra- and interspecific interactions, included whether they were initiated by or targeted at the focal bird); Copulation. Movement during aggressive encounters was included within Aggression.

Results

Almost all Madagascar Teal seen were in firmly established pairs, each bird rarely separating from its partner by more than 2 m and each pair remaining well separated from other conspecifics except during aggressive encounters. Up to seven pairs were observed together at the sandbar site and one or two pairs were seen at four other sites. Two single birds were also seen at the sandbar, showing that the total population for the southern part of Lake Be-mamba was at least 16 birds. More than 16 birds are likely to have been present, although the majority of suitable habitat was thoroughly surveyed. Up to four sites were covered simultaneously by different members of the team, but as many as seven pairs were only seen on the one occasion.

Single birds were only seen on 24 July (two) and 29 July (one) and not in between. Thus some birds were either being frequently overlooked during observations or were moving to and from other sites.

Behavioural observations of Madagascar Teal were conducted for a total of 3158 minutes. Most data were collected at the sandbar, with only 1036 bird-minutes collected elsewhere. While a total of 14,954 bird-minutes of data were collected on paired birds, only 461 bird-minutes were collected on single birds. Hence the data collected provide mainly a picture of the behaviour of breeding pairs in the period prior to the nesting season. There was no behavioural evidence that nesting had begun and no prospecting of potential nest sites or temporary separation of pairs was observed. Apart from one copulation, no courtship behaviours were seen.

The number of pairs feeding in the sandbar was typically highest in the early morning before 0800 h and then reduced markedly during the middle of the day. This corresponded with the arrival of hundreds of other waterbirds (particularly Fulvous Whistling Duck *Dendrocygna bicolor*, White-faced Whistling Duck *D. viduata*, Comb Duck *Sarkidiornis melanotos* and Red-billed Pintail *Anas erythrorhyncha*) leaving the surrounding ricefields to roost in the sandbar, resulting in a reduction in the area of shallow water available to the Madagascar Teal for feeding. At this time, the teal dispersed more widely within the marsh making more use of apparently less preferred areas.

The overall diurnal time budget for paired birds is presented in Table 1. Feeding was the dominant activity accounting for 80% of time spent. Resting and comfort were the only other behaviours that ac-

Table 1. Diurnal time budget for paired Madagascar Teal in July.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Mean (%)</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding</td>
<td>79.60</td>
<td>16.92</td>
</tr>
<tr>
<td>Resting</td>
<td>10.32</td>
<td>11.03</td>
</tr>
<tr>
<td>Comfort</td>
<td>8.44</td>
<td>9.01</td>
</tr>
<tr>
<td>Alert</td>
<td>0.67</td>
<td>0.98</td>
</tr>
<tr>
<td>Movement</td>
<td>0.54</td>
<td>0.68</td>
</tr>
<tr>
<td>Aggression</td>
<td>0.42</td>
<td>0.59</td>
</tr>
<tr>
<td>Copulation</td>
<td>0.01</td>
<td>0.04</td>
</tr>
</tbody>
</table>

The percentage of total bird-minutes spent in each behaviour was first calculated for all hourly periods (0600-0659 h, 0700-0759 h etc) and the means and standard deviations of these figures (n = 13) are presented here. Resting includes sleeping (97.6%) and loafing (2.4%). Movement includes flying (44%), walking (34%) and swimming (21%). Aggression includes intraspecific (97%) and interspecific (3%) encounters.
counted for more than 1% of time. While birds tended to feed in exposed areas away from concentrations of roosting waterbirds, bouts of comfort and resting were conducted in close proximity to these groups of other species. Paired birds were strongly synchronised, switching between activities together. There was no evidence that birds may have been concentrating feeding at the sandbar from which most data were collected, and then moving to other sites to rest etc, as feeding was the dominant activity observed at all five observation sites.

In single birds, feeding was also dominant but only accounted for 60% of time, with resting accounting for 33%, comfort 6.1% and being the target of conspecific aggression 1.2%. The proportion of time spent feeding by single birds was not significantly lower than the proportion of time spent feeding by paired birds present in the study area at the same time (Mann Whitney U test, P>0.05).

**Figure 1.** Diurnal rhythms of paired Madagascar Teal in July. 0700h represents 0700h to 0759h, etc. Numbers alongside the plot for feeding indicate the number of bird-minutes of data for each hourly block. Data points for 0600h (32 bird-minutes) and 1800h (68 bird-minutes) are excluded owing to the much smaller amounts of data.
The diurnal rhythm of the three dominant behaviours of feeding, resting and comfort is shown for paired birds in Figure 1. This shows that feeding remains the dominant activity throughout daylight hours, always accounting for more than 55% of time. However, there is a marked reduction in time spent feeding and concurrent increase in time spent resting in the middle of the day from 1000 h to 1300 h.

**Feeding behaviour**

Madagascar Teal were observed dabbling both while on foot and while swimming, but 68% of the feeding (∑n=5231 bird-minutes) was conducted while on foot. Madagascar Teal are extremely active while feeding and move a considerable distance but regularly turn around so that they feed repeatedly over the same spots within a limited area. Thus from a single observation point a feeding pair could often be observed continuously for hours at a time.

When feeding while on foot, the Madagascar Teal feeds in a manner similar to the dabbling behaviour of Common Shelduck *Tadorna tadorna*. Although birds were occasionally seen feeding while standing stationary, during more than 95% of the time they were seen to move constantly forwards while feeding, with the neck outstretched. Occasional lateral movements of the head from side to side were made during foraging, covering an arc of about 20° in front of the body, but these were not made with a regular rhythm. Feeding birds appeared to be filtering water through their bill constantly while running their bill along the mud surface. They were often seen to dabble in water so shallow that from the observation point it appeared as if there was no water at all. Rapid, forward movements of the head were also sometimes observed as if birds were catching insects off the surface of the water. The feeding behaviour observed while swimming was similar to that while standing, with birds moving constantly and regularly dipping their heads under the water surface. Upending and diving were never observed.

**Social interactions**

Paired Madagascar Teal were found to defend aggressively feeding space from conspecifics and, to a lesser extent, from other waterbird species. Of time spent in aggression, 97% was against conspecifics. Aggressive encounters appeared to limit the number of teal present in the sandbar at any time, but were not observed at any other sites.

Pairs were observed to launch 27 attacks against conspecifics, 17 against other pairs and ten against single birds. They appeared to be initiated when one or both of the aggressive pair noticed the presence of conspecifics nearby and ended in increased spacing between the aggressors and their targets. Most encounters were initiated when both the aggressors and their target were feeding (Table 2). Single birds never initiated intraspecific aggression. On average, a pair was observed to attack another pair every 440 minutes and to be attacked by another pair every 440 minutes. In contrast, on average a single bird was attacked by a pair every 46 minutes.

The intraspecific encounters between two pairs varied considerably in their duration (up to c. 2 minutes) and level of aggression. The target pair were typically 10-50 metres away when the encounter began. Encounters which started when the aggressors were on foot (∑n=15) began with one or both of the attacking pair running towards the second pair with head and neck fully stretched in a manner similar to the Forward threat display of the True geese (Johnsgard 1965). In five encounters, one (∑n=1) or both (∑n=4) of the attacking

<table>
<thead>
<tr>
<th>Behaviour of target</th>
<th>Aggressive pair feeding on land</th>
<th>Aggressive pair feeding on water</th>
<th>Aggressive pair resting or comfort</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding on land</td>
<td>13/5</td>
<td>0/0</td>
<td>1/0</td>
</tr>
<tr>
<td>Feeding on water</td>
<td>0/0</td>
<td>1/2</td>
<td>0/0</td>
</tr>
<tr>
<td>Resting or comfort</td>
<td>1/0</td>
<td>0/0</td>
<td>0/3</td>
</tr>
<tr>
<td>Landing</td>
<td>1/0</td>
<td>0/0</td>
<td>0/0</td>
</tr>
</tbody>
</table>

Two numbers are given for the number of times each combination of aggressor and target behaviour was observed. The first number refers to encounters in which the targets were paired birds, and the second number to those in which the target was single birds.
pair took to the wing and flew at their targets. The target pair usually ran or flew rapidly away in the face of the aggressive approach bringing the encounter to an end, with the aggressors returning to their previous position and behaviour. However, physical contact was made between the pairs on several occasions. On two occasions, the encounter escalated when the pair that was initially attacked responded with a counter attack in which they ran or flew back at the aggressors. In both these cases, the aggression ended with the pairs spacing themselves apart much as before the encounter with no obvious winner.

Encounters between pairs and single birds were relatively less intense. The single bird always retreated rapidly in response to the aggression and the aggressors flew at their target on only one occasion. On three occasions, the encounter occurred when a single bird approached within 2 m of a pair that was in resting or comfort.

Head-pumping displays by one of the attacking pair were often observed during encounters with conspecifics, either during an aggressive approach \((n=6)\) or immediately after an encounter \((n=2)\). Sometimes the head-pumping was by the leading bird \((n=3)\), and sometimes it was the bird following behind \((n=4)\). On one occasion both members of a swimming pair were seen head-pumping together before attacking another pair.

A much lower rate of aggression was observed against other species feeding in the sandbar. Five short encounters (less than 10 seconds) were observed in which Madagascar Teal displaced another waterbird in its immediate path either by approaching it with head outstretched or by pecking at it. Paired birds thus displaced Hottentot Teal \(Anas hottentota\) \((n=3)\), Red-billed Pintail \((n=1)\) and Curlew Sandpiper \(Calidris ferruginea\) \((n=1)\). A single bird was once seen to displace a Hottentot Teal.

No encounters were observed with the large numbers of Fulvous Whistling Duck, White-faced Whistling Duck and Comb Duck that were roosting in the sandbar. On three occasions, paired birds (presumably female) conducted head movements in an apparent attempt to incite their partner to show aggression towards a Fulvous Whistling Duck \((n=1)\) and Red-billed Pintail \((n=2)\). The head movements observed in these displays were different to the simple up-and-down head-pumping seen in intraspecific encounters, and was much more similar to the typical incitement displays described for \(Anas\) species (Johnsgard 1965). The bird moved its head in sideways pointing movements so as to indicate the direction of the bird at which it was inciting aggression.

**Copulation**

At 0840 hours on 25 July, a pair of Madagascar Teal was seen to copulate. The pair were swimming in the water, the male head-pumping as he followed the female. He then mounted the female for about 20 seconds. After dismounting, the female bathed immediately while the male swam around her in almost a full circle in Bridling display. A further copulation was observed at 0807 h on 12 July 1993 (R. Safford in litt. 1994).

**Discussion**

The behaviour and ecology of Madagascar Teal was markedly different to that of the other six species of Anatidae present at Lake Bemamba. This was the only species which was confined to the remaining areas of natural habitat while all other species were observed to make regular use of the surrounding ricefields (Young et al. 1993). The difference in habitat use was most extreme in the African Pygmy Goose \(Nettapus auritus\), which was entirely confined to the ricefield area. Apart from Madagascar Teal, the only other duck species that showed obvious signs of pairing or breeding activity was the Hottentot Teal. Two broods of Hottentot Teal were seen at the end of July 1993. In the first half of August 1973, Scott & Lubbock (1974) found that “a large percentage (of Hottentot Teal) appeared to be paired”. Scott & Lubbock (1974) also observed courtship activity in Red-billed Pintail. Local information during the current study suggested that most duck species nest at some time after the arrival of the rains from December to February with Comb Ducks reported to undergo a flightless post-breeding moult in May. The behaviour of Madagascar Teal suggests that either they breed much earlier than the other ducks at Lake Bemamba or that they have longer pair bonds.

The timing of nesting and other aspects
of the breeding biology of the Madagascar Teal remain unknown. Approximately 90% of Madagascar Teal present at Lake Be-mamba were paired at a time when there was no evidence of breeding, suggesting that they separate into aggressive pairs many weeks or months prior to nesting or have permanent pair bonds. The lack of unpaired birds also suggests that, like all other Anatini (Johnsgard 1965), Madagascar Teal pair at one year of age. Scott & Lubbock (1974) observed birds in the first half of August, with most birds in pairs but no evidence of nesting. They observed three copulations followed by Bridling and Down-up displays. The observation of copulations is not strong evidence that the birds were close to breeding since copulations in the closely related Grey Teal *Anas gracilis* do not necessarily indicate immin-ent laying (Marchant & Higgins 1990). Local information suggests nesting of Madagascar Teal occurs in the wet season after December (see introduction). Detailed studies of the nesting and post-hatching breeding biology of Mada- gascar Teal are required urgently as an aid to the conservation of this globally threat-ened species, and Lake Antsamaka is prob-ably the most suitable study site (Safford 1993, R. Safford in litt. 1994).

During the season studied, Madagascar Teal were extremely active during daylight hours with 80% of time spent feeding. This level of activity is higher than all of the diurnal feeding rates for non-breeding dabbling ducks in the review of Paulus (1988). However, the activity pattern of Madagascar Teal is certain to vary from that ob-served in this study at different times of the year and at different sites. For example, it is possible that the timing of feeding activity on coastal mudflats is dictated by tidal rhythms. While many species of *Anas* have been observed to be mainly nocturnal feed-ers (Jorde & Owen 1988), it seems likely that in July and August Madagascar Teal are mainly diurnal feeders taking food chiefly from the substrate-water interface in very shallow water. The constant move-ment of feeding birds and the high propor-tion of time spent feeding suggests that the food is present at low density and intake rate or nutrient content is low.

The observed tendency to concentrate periods of resting in the middle of the day from 1000-1300 may be explained by a need to take breaks to allow thermoregulation in the hot middle of the day, or by an energy conservation benefit of concentrating ac-tivity during the coolest periods. The latter has often been suggested as a partial ex-plation for nocturnal feeding in ducks (Jorde & Owen 1988). Alternatively, the concentration of resting in the middle of the day may be a consequence of the high number of other waterbirds roosting at the sandbar at this time, reducing the area available to Madagascar Teal for feeding. It is possible that the activity pattern found at the sandbar is not representative of other areas where other species were not roosting and where Madagascar Teal con-tinued feeding throughout the middle of the day. However, feeding at the sandbar returned to high rates in the afternoon when the numbers of other waterbirds roosting at the sandbar were still high.

The activity of Madagascar Teal was in marked contrast to the other ducks pre-sent in the sandbar which spent a small proportion of daylight feeding and most of the time resting (with the possible exception of Hottentot Teal). The White-faced Whistling Duck, Fulvous Whistling Duck, Comb Duck and Red-billed Pintail fed mainly nocturnally in the ricefields and mainly rested during the day. The only other waterbirds in the sandbar that seemed to spend a similar proportion of daytime feeding to Madagascar Teal were various waders (see Young *et al.* 1993) and Crested Coot *Fulica cristata*.

During this study, single Madagascar Teal were much less aggressive than paired birds and were never seen to initiate an aggressive encounter or to win one. They were also the targets of aggression from conspecifics much more than paired Teal. This is probably because the low so-cial status of single birds makes them favoured targets for aggression (Lam-precht 1986, Black & Owen 1989). It is quite possible that these single birds are young birds from the previous breeding season that are not yet paired. Part of the high rate of aggression against single birds can be explained by their own behaviour, since they sometimes attempted to associate with nearby, paired conspecifics and thus invited attack. Dominance of paired birds over single birds has often been observed in wildfowl and may be an important force selecting for the evolution of long term pair bonds (Hepp & Hair 1984). This seems par-ticularly likely in a species such as Mada-
gascar Teal in which feeding space is aggressively defended. It seems likely that this aggression may have limited the number of Madagascar Teal present at Lake Bemamba, and may have forced single birds onto lower quality, marginal feeding areas, or to disperse to other sites (Alexander 1987, Choudhury & Black 1991).

The Madagascar Teal is considered to be a member of what have been called the Austral teal (Delacour 1956) recently classified as the Subgenus Nesoneetta (Livezey 1991). Opinions differ as to the number of full species in this group, with Marchant & Higgins (1990) recognising the largest number of species: Andaman Island Teal *Anas albogularis*, Indonesian Teal *A. gibberifrons*, Grey Teal *A. gracilis*, Chestnut Teal *A. castanae*, Brown Teal *A. chlorotis*, Auckland Islands Teal *A. aucklandica*, Campbell Island Teal *A. nesiotis* and Madagascar Teal. Grey Teal, Chestnut Teal and Brown Teal all sustain pair bonds throughout the year and often for life, although pairs associate to form flocks outside the breeding season (Marchant & Higgins 1990). The present study suggests that Madagascar Teal may also have sustained pair bonds, but it remains unclear whether or not flocks are formed at different times of the year.

The current study suggests that there are some important differences between Madagascar Teal and the other Austral Teal in feeding and agonistic behaviour. Grey Teal, Chestnut Teal, Brown Teal, Auckland Islands Teal and Andaman Island Teal have all been reported to have low levels of diurnal feeding and probably feed mainly at night (Phillips 1923, Marchant & Higgins 1990). Upending is a feeding method used by Grey Teal, Chestnut Teal and Brown Teal (Marchant & Higgins 1990) but has not been recorded in the field in Madagascar Teal. However, both upending and diving have been observed in captivity (HGY unpubl.). Of the other species, Chestnut Teal appears to have a similar preference to Madagascar Teal for dabbling at the edge of the water, often on saline wetlands (Marchant & Higgins 1990). However, the feeding behaviour of Brown Teal is said to be very similar to that described for Madagascar Teal in the present study (G.S. Dumbell in litt. 1994).

Outside the nesting period, Madagascar Teal appears to be more aggressive towards conspecifics than its relatives, although the levels of aggression in these other species have not been quantified in a directly comparable way (Marchant & Higgins 1990). The agonistic behaviour of Madagascar Teal during intraspecific disputes bears little resemblance to that described for the other Austral teal (Marchant & Higgins 1990). The vertical head-pumping frequently observed has not been described for the other species, and its function remains unclear. It may be an incitement movement of the female similar to the unusual incitement display described for female African Black Ducks *Anas sparsa*, which often provokes a similar response from their partner (Johnsgard 1965: 133). Likewise, the partner of a head-pumping Madagascar Teal was once seen to respond in a similar fashion. Alternatively, this head-pumping may have other functions such as signalling aggressive intent to the opponent or greeting the partner after an encounter. This display is unlike typical *Anas* incitement displays (Johnsgard 1965) in that it is conducted both before and after aggressive encounters and is conducted both by birds leading an attack and their partners. If it is indeed a female display, this shows that both male and female Madagascar Teal take an active part in aggressive encounters. In other Austral teal, females are less aggressive and only males engage in direct attacks (Marchant & Higgins 1990).

The display of Madagascar Teal seen in interspecific encounters is similar or identical to the incitement display described for other Austral teal (Marchant & Higgins 1990: 1272) which is itself typical for *Anas* species (Johnsgard 1965). Whilst this display is mainly used against conspecifics in other Austral teal, it is also used against other species, at least by the Grey Teal (Marchant & Higgins 1990).

These apparent differences in the use of displays by Madagascar Teal are probably associated with the evolution of displays suited to their apparently high levels of aggression in defending space while on foot. These differences in behaviour suggest that Madagascar Teal is more distinct from the other Austral teal than has been suggested previously (Johnsgard 1965) and is certainly worthy of full species status. This is compatible with the possibility that Madagascar Teal have reduced foot-webbing not found in any other *Anas* species (Young et al. 1993).
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