Evidence of regular seasonal migration by Australian Painted Snipe to the Queensland tropics in autumn and winter.

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ABSTRACT

We report a series of sightings of Australian Painted Snipe in the marine plain wetlands of tropical Queensland, including two breeding records. Ten records from nine locations were all in the autumn and winter, the period when records of Australian Painted Snipe in south-eastern Australia are extremely rare. Examination of historical records of Australian Painted Snipe confirmed this pattern for coastal Central and North Queensland. We suggest that there may be a regular seasonal migration of a significant part of the Australian Painted Snipe population between south-eastern Australia and wetlands of central and north coastal Queensland, to exploit the favourable seasonal conditions.

INTRODUCTION

The Australian Painted Snipe *Rostratula australis* is a rare endemic shorebird which is mostly found in shallow, muddy wetlands with some dense low cover (Rogers *et al.* 2005). Optimum conditions for Australian Painted Snipe appear to occur as temporary wetlands are drying. The inundation of ephemeral wetlands triggers a surge of production of the benthic organisms on which they feed, and subsequent drying makes this accessible to feeding birds (Rogers *et al.* 2005).

The reporting rate of Australian Painted Snipe in Australia has declined greatly since the 1970s, beyond the decline of waterbirds in general with current rates at about 10% of those before 1970 (Lane and Rogers 2000). A current revision of their status recommends a change from *vulnerable* to *endangered*.

Most historical records are from south-eastern Australia, but there are also scattered records from northern Australia (Marchant & Higgins, 1993). In south-eastern Australia (including south-eastern Queensland), almost all sightings occur between September and March and little is known of the location of Australian Painted Snipe in the autumn and winter months (Threatened Bird Network 2008, Lane & Rogers 2000). Ninety percent of the Australian Painted Snipe records of Birds Australia's Threatened Bird Network in south-eastern Australia were between September and March (Threatened Bird Network 2008). In 2002 the Australian Painted Snipe group of the Threatened Bird Network called for volunteers to survey wetlands in winter to help solve the question of whether Australian Painted Snipe migrated away from south-eastern Australia in winter, or simply became much more cryptic. Despite a determined effort, these surveys failed to find any Australian Painted Snipe (Chris Tzaros pers. comm.).

We conducted a series of surveys of the marine plain wetlands of Central Queensland studying Capricorn Yellow Chats and other wetland birds between March 2003 and December 2008. An outcome of this was ten sightings of groups of Australian Painted Snipe, two of which included breeding records. All these sightings were between March and September, the period when records in south-eastern Australia are rarest. From these observations, it was hypothesized that the apparent rarity in south-eastern Australia could be explained by movement of Australian Painted Snipe to wetlands of coastal central Queensland during the autumn-winter period (March-August). To verify this pattern of seasonal presence, Queensland records from WildNet (EPA 2009) were examined along with other Queensland records for evidence of the location of Australian Painted Snipe in autumn and winter. The pattern of seasonal occurrence and its relationship to habitat availability in various regions was also examined.

METHODS

Surveys

Central Queensland University and Wetlands International conducted surveys of waterbirds in the Fitzroy Delta, Fitzroy Lagoons and Broad Sound wetlands of Central Queensland from March 2003 to December 2008, a period of nearly six years. These were carried out regularly throughout these years, and surveying effort was similar across the seasons. Surveys of wetlands north to Townsville occurred in May and June 2005, and late September 2008. Incidental sightings of Australian Painted Snipe in the region during this period were also recorded.

Wetlands were surveyed from the margins using binoculars and spotting scopes, and by systematic walking through flooded areas. Some wetlands were surveyed only once or twice while seeking new Capricorn Yellow Chat populations, while others were repeatedly searched during Yellow Chat or waterbird monitoring surveys (Jaensch *et al.* 2004b, Houston *et al.* 2004).

Database Records

Records from Wildnet (EPA Wildlife Database) of Australian Painted Snipe in Queensland were examined. In total 3,037 records were evaluated for evidence of seasonal use of regions of Queensland. Of these, 2,693 were found to be nil records of regular Australian Painted Snipe surveys in south-east Queensland between 1990 and September 1998. Of the remaining 344 records, 78 records dated January 1st (presumably a default date) or with no month were rejected as these provided no information on seasonal presence. Another 15 records dated 23/5/1770 were also rejected, as the date was considered unreliable. Another 29 duplicate entries, with the same date and coordinates as others, were deleted from the remaining 251 records, leaving 222 records. Although some Wildnet records were probably repeat sightings of the same group of birds at different dates or nearby locations, it was not possible to accurately assess this, so these records were all retained. However this applies to records from all areas of Queensland, so the comparison of regional data should not be distorted.

Additional records of Australian Painted Snipe in Queensland were obtained from *Painted Snippets* (Threatened Bird Network publication) between 2003 and 2008 (10 records), and *Birding-Aus* (a birdwatchers website) between 2001 and February 2009 (9 records) giving a total of 251 including the survey data.

These were sorted by location and month of sighting and categorised by geographic location and season. Six broad geographical regions were defined based on a north-south gradation and inland-coastal zones (SE for south-eastern Queensland; SW for south-western Queensland; CE for central eastern Queensland; CW for central western Queensland; NE for north-eastern Queensland; NW for north-western Queensland) and two broad seasons (Autumn-winter for March to August and Spring-summer for September to February).

The minimum number of actual birds recorded in Autumn-winter in Queensland since 1977 was plotted. Records of birds or groups of birds at the same site over a few months

were assumed to be repeats, and the highest count used. Records without a count (21 of 79) were given a count of one, giving a minimum Autumn-winter total of Australian Painted Snipe in Queensland per year.

RESULTS

Surveys

Ten groups of Australian Painted Snipe were observed during the survey period, ranging from three to seven birds. At least one group was recorded in every year of the surveys (2003-2008) except 2006. Two breeding events were recorded, both on the Torilla Plain in the eastern part of the Broad Sound wetlands, about 125 km north of Rockhampton, and it is possible that breeding also occurred at other sites where immature (sub-adult) birds were recorded.

Sightings occurred in two ways; on six occasions the birds were observed while scanning wetlands by eye or with binoculars; the other four groups were flushed while walking through the wetlands.

1- On 30 April 2003 three male and three female Australian Painted Snipe were seen by four observers in drying freshwater ponds on the Torilla Plain, an extensive marine plain system about 125 km NNW of Rockhampton (Jaensch *et al.* 2004a). A male was flushed from a nest with four eggs, sheltered by freshwater couch *Paspalum distichum*, on a low muddy islet. The ponds had shallow open water, and broad fringing areas of moderately dense couch grass, *Cyperus* and *Eleocharis* sedges and Beetle Grass *Leptochloa fusca*.

2- On 31 March 2004 an adult male Australian Painted Snipe was observed with three downy young at another, more saline location on the Torilla Plain. The young appeared to have recently left the nest, were yellowish with dark streaks, and had long legs and bill. They walked across a 3 m by 2 m open gap in a dense *Schoenoplectus litoralis* swamp, about 90 m long and 60 m wide. The brackish water was about 3 cm deep at this point. The dense *Schoenoplectus* area was surrounded by muddy ground with shorter grasses and Samphire including *Halosarcia pergranulata* and *Halosarcia indica* and this may have been the nesting habitat. Extensive reedbeds are avoided as nesting habitat (Rogers *et al.* 2005).

3- On 11 May 2005 at 16.30 six Australian Painted Snipe were seen in a drying freshwater *Cyperus alopecuroides* swamp about 150 m long and 40 m wide at Wunjunga, about 30 km south of Ayr, on the Burdekin delta. They were resting in water to 10 cm deep in the shelter of tall *Cyperus* clumps, and feeding in the open muddy areas between the clumps. The swamp was located in a grassy plain with some Samphire, and is part of the extensive Wunjunga marine plain wetlands.

4- On 12 May 2005 at 9.00 two Australian Painted Snipe were flushed from the edge of a small muddy pool with a rocky edge on the Goorganga Plain, an extensive marine plain about 10 km east of Proserpine. They were crouched between clods and rocks in very open habitat with short Green Couch grass *Cynodon dactylon*.

5- On 9 June 2005 at 16.15 four Australian Painted Snipe were flushed by three observers 20 m from the edge of a sparsely vegetated, seasonal freshwater lake at Balnagowan, about 30 km east of Rockhampton on the Fitzroy River delta. They were crouched in

cattle hoof depressions in very short Green Couch grass *Cynodon dactylon*, in a patch of very sparse *Cyperus scariosus* sedge only 30 cm tall. After being flushed they flew to the edge of the lake and started feeding on the open muddy shore. We concluded that the group comprised one sub-adult female and three males.

6- On 15 June 2005 at 15.00 seven Australian Painted Snipe were seen by two observers between a series of freshwater pools with dense *Cyperus alopecuroides* near Sheepstation Creek, 15 km north-west of Brandon, on the Burdekin delta. Four were flushed from cattle hoof depressions in dry open grassy ground with sparse short sedges, and flew about 30 m to the dense *Cyperus alopecuroides* fringing a nearby pool. Three more were flushed from the muddy edge of another pond, about twenty metres from where the first group were found, and flew to the same pool. We returned to the site in late afternoon, but could not see any Australian Painted Snipe feeding on the open pool edges.

7- On 29 June 2005 at 16.45 six Australian Painted Snipe were flushed by three observers 10 m from the edge of the lake at Balnagowan on the Fitzroy River delta, and about 200 m from where four were seen on June 9 (Wingspan, March 2006). They were crouched in cattle hoof depressions in very open habitat with short Green Couch grass *Cynodon dactylon*, and sparse short *Cyperus scariosus* sedge. After being flushed they flew about 80 m along the lake shore and crouched in hoof depressions in the shelter of some grass tussocks near a group of tall *Cyperus alopecuroides* clumps on the muddy edge. We concluded that the group comprised two sub adult females and four males. After being observed for 25 minutes they flew out into the shallow open water about 10 m from shore and began feeding.

8- On 11 May 2007 at about 16.30 three Australian Painted Snipe were seen by two observers in a shallow, sparsely vegetated, brackish swamp on the Waverley plain, 10 km south of St Lawrence, on the western marine plain of Broad Sound. There were two sub-adult males and one sub-adult female. They were in clay substrate that was subtly hummocky and were moving out to feed from taller *Schoenoplectus litoralis* cover into an area of low, flood killed samphire *Halosarcia pergranulata* and lush Nardoo *Marsilea mutica* with water to 10 cm.

9-On 19 April 2007 two immature Australian Painted Snipe were flushed from the edge of a freshwater wetland at St Lawrence, on the western marine plain of Broad Sound. They were in an area of sparse *Eleocharis* sedge, and flew 60 m along the wetland, from where they flew into the flooded *Melaleuca* swamp upstream.

10- On 3 March 2008 two Australian Painted Snipe, a male and a female, were observed on the edge of a shallow, recently inundated, flooded wetland at Gavial Swamp on the Fitzroy River delta. They were in an area of shallowly flooded, sparse tussocks of dry grass and some sprouting *Eleocharis* sedges; otherwise the site was extensively bare due to drought, then recent rapid inundation by floodwaters.

The series of bird surveys during which these records were obtained was the most comprehensive ever undertaken of the Central Queensland marine plain wetlands, for which few systematic surveys existed (Jaensch *et al.* 2003). The surveys resulted in nine separate records (the two records at Balnagowan were probably the same group) of the occurrence of groups of Australian Painted Snipe in the coastal Queensland dry tropics. The five records in 2005 occurred during the most systematic and widespread survey

period. All records were from early March (initiation of breeding in March 2004) to late September, the period when south-east Australian records are rarest.

Database Analysis

Of the 251 records of Australian Painted Snipe in Queensland, one hundred were in the Autumn-winter period (March to August) and one hundred and fifty one in the Springsummer period (September to February) (Figure 1). Thus, one hundred records were from the seasons when few Australian Painted Snipe sightings are made in south-eastern Australia. Most of these one hundred records (71) were from central and north Queensland, while only twenty nine Autumn-winter records were from south Queensland. In contrast, most Queensland Spring-summer records (96) were from south Queensland, with fifty four records from central and north Queensland. The ratio of Autumn-winter to Spring-summer records has remained consistent since 1970, before which few records are available (Figure 2).



Figure 1: Monthly Australian Painted Snipe records in South Queensland and Central and North Queensland.

Between October and January most records are from south Queensland, while from March to August there is a dominance of records from central and north Queensland. February and September are transitional months when the north-south dominance reverses (Figure 1). We can expect the number of records to be higher from Southeast Queensland due to the larger number of observers, greater effort and smaller total area, so it is likely that the central and northern records under-represent actual occurrence more than the south Queensland records do. Australian Painted Snipe are thought to be more easily detectable while breeding (Marchant & Higgins 1993) and the peaks in records correspond to the reported main breeding season in both regions (October to December in south Queensland, the same period as in south-eastern Australia, and February to April in central and northern Queensland).



Figure 2: Australian Painted Snipe in Queensland in winter and summer by decade.

Seasonal patterns of regional occurrence were examined for each of the six broadly defined regions; South-eastern and South-western Queensland, central Eastern and central Western Queensland and North-eastern and North-western Queensland (Figures 3, 4 & 5). These show that seasonal use of areas of Queensland varies by region with:

- a predominately Spring-summer pattern of occurrence in two regions; Southeastern Queensland with 73% (78) of 107 records and South-western Queensland with 100% (19) of 19 records (Figure 3). This resembles the pattern of occurrence from south-eastern Australia.
- a predominately Autumn-winter pattern in two coastal regions; Eastern central Queensland with 80% (40) of 50 records and North-eastern Queensland with 65% (11) of 17 records (Figure 4).

In contrast, Western central Queensland and North-western Queensland records do not conform to either pattern, with peak records in February-April and September-November. However 20 records from this region are from the March-August period (Figure 5).



Figure 3: Australian Painted Snipe records in south Queensland by month.



Figure 4: Australian Painted Snipe records in eastern central and north-eastern Queensland by month.



Figure 5: Australian Painted Snipe records in north-western and central western Queensland by month.

To provide an overview of these patterns of occurrence on a state-wide basis, all 251 Queensland_Australian Painted Snipe records with location and seasonal data are shown on a map (Figure 6). February and September records are shown separately as these months appear to be times of transition into and out of Central and North Queensland (Figure 1). Significant points to note are:

- Almost all records from coastal Central and North Queensland are from the March-August period, corresponding to the period in southern Australia when snipe are rarely seen.
- Most records from Southeast Queensland are from the October to January period, corresponding to the period when snipe are usually seen in southern Australia.
- Almost no records from western South Queensland are from the March-August period.
- Seasonal occurrence in western North Queensland is more opportunistic.



Figure 6: Queensland Australian Painted Snipe records showing areas of Springsummer dominance in southern Queensland and Autumn-winter dominance in coastal central and northern Queensland.

March-August = black circle, October-January = white circle, February and September = black triangle.



Figure 7: Minimum annual Autumn-winter totals of Australian Painted Snipe in Queensland since 1977. North Queensland includes central Queensland.

To quantify Australian Painted Snipe abundance (as opposed to records of seasonal occurrence examined in the previous sections), the minimum number recorded between March and August each year since 1977 was plotted. Records without a count (21 of 79) were given a count of one, giving a minimum Autumn-winter total in Queensland per year.

The rarity of this species is demonstrated by the highest winter count (in 2005) of 21 birds. This count resulted from hundreds of hours of surveys within suitable Australian Painted Snipe habitat between Bundaberg and Townsville.

No clear trends in numbers of birds were apparent and the higher counts in later years probably reflected increased search effort. Highest counts in the early 1990s and mid 2000s corresponded to times of greatest survey effort in South-eastern and Eastern central Queensland respectively. The high north Queensland counts in 2004 and 2005, with a peak count of 21 birds in 2005, corresponded to the period of most intensive survey effort in coastal wetlands of central and north Queensland.

The absence of Queensland winter records from 1995 to 1999, a period of regular systematic surveys in Southeast Queensland, demonstrates the unreliability of Australian Painted Snipe occurrence. Between 1991 and 1994 eighteen separate sightings of individuals or groups of birds occurred in south-eastern Queensland. Fourteen of these were in the Spring-summer period, and four in Autumn-winter. These sightings led to a series of regular systematic surveys in Southeast Queensland, which searched 24 sites monthly from 1992 to 1998, another 13 sites for most of those years, and a further 11 sites for at least two years of that period. Despite this intensive survey effort, no further sightings of Australian Painted Snipe occurred in the region until a group of birds recorded at Lake Samsonvale in early 1999.

DISCUSSION

Migration

Based on the strong seasonality in occurrence of Australian Painted Snipe in southern Australia, there has been previous speculation that they are seasonal migrants, and may leave the spring and summer breeding areas of south-east Australia in autumn and winter (Blakers *et al.* 1984). However, the scarcity of autumn and winter records anywhere provided scant evidence of where the 'missing' snipe are over-wintering. The present study provides the first compelling evidence of migration to coastal central and north Queensland based on a preponderance of records, including breeding, during the autumnwinter period in this region. This could only be proved by data from banding or tracking, which would be difficult due to the very low number of annual sightings of the species, difficulty in capturing and the low probability of re-capturing or even sighting banded birds.

One of the reasons why this evidence was overlooked is that previous studies of Australian Painted Snipe have not used the Wildnet EPA database. This is probably due to the nature of the database, where 222 records with useful seasonal information are obscured within 3,037 total records, most of which are nil results from regular Australian Painted Snipe surveys in the 1990s.

Also contributing to the few records from coastal central and north Queensland are the vast scale of wetlands, difficulty in access due to land tenure (many are on private land), and the paucity of birdwatchers and survey effort. The wetlands of tropical coastal Queensland comprise approximately 750,000 ha: Fitzroy River wetlands 265,000 ha, Broadsound-Shoalwater Bay wetlands 335,000 ha and the Burdekin-Townsville coastal wetlands 150,000 ha (Environment Australia 2001). Prior to 2003, waterbird populations in these wetlands had been studied only superficially.

The number of autumn-winter (100) and spring-summer (151) records of Australian Painted Snipe in Queensland may seem to indicate that the autumn-winter records in north Queensland are the same birds that are recorded in south Queensland in spring and summer, with seasonal migration occurring just within the state. It is likely that some birds remained in Queensland in summer during the extended drought period since the early 1990s, when many wetlands in south-east Australia have become unsuitable for Australian Painted Snipe. However, the survey effort is far greater in south-east Queensland, at least tenfold in the Birds Australia Atlas (Barrett *et al.* 2003), with many more birdwatchers and a thorough series of regular monthly surveys targeting all known Australian Painted Snipe sites between 1990 and September 1998, so it is probable that a much smaller percentage of birds in north Queensland is reported. Also, as noted in the previous paragraph, the extent of wetlands in central and north Queensland is far greater than that in southern Queensland, further increasing the lack of equivalence in search effort between these regions.

There are very few breeding records of Australian Painted Snipe from tropical Queensland (Lowe 1963, Jaensch *et al.* 2004a). This paper records two confirmed breeding events, in April 2003 and March 2005. These records support previous suggestions of an autumn breeding period in northern Australia (Rogers *et al.* 2005).

Many of the Australian Painted Snipe seen appeared to be sub-adult, so may have been raised in the south-east breeding season the previous summer, and thus would have been too young to breed. However, immature birds seen in April-June may also have been the result of local breeding in March-May.

There are few bird species that are known to regularly migrate between south-east and north-east Australia and breed in both regions. Most winter migrants to Queensland breed in southern Australia in spring and summer (Ref?). Recent records of breeding Whiskered Terns in the Northern Brigalow Belt (Jaensch *et al.* 2003) and subsequent records at the same site may be another example of a species breeding in both northern and southern Australia.

Habitat Attributes

The Australian Painted Snipe found in these surveys were mostly in sparse, open habitats with some cover in the form of grass or sedge tussocks, and in or near shallow muddy pools. Although the male with three very young juveniles found on March 31, 2004 was in a dense sedge bed, it is likely that this was a shelter they had moved to from a nearby nest. All sites were in marine plain wetlands. Where the habitat included open water bodies, the edges where Snipe were feeding included clods, rocks or plant tufts. This 'lumpy' shoreline may help to camouflage the shape of feeding birds.

Favourable habitat attributes of coastal central and north Queensland wetlands are thought to include: (i) suitable habitat is always available in the autumn and winter as a consequence of the extensive area of wetlands following the summer-autumn 'wet' season and the progressive drying of deeper wetlands; (ii) the high productive pulse of invertebrates as a consequence of seasonal drying and re-wetting; and (iii) the seasonal drying and residual salinity of many of these habitats that prevents dominance by dense emergent vegetation.

All the Australian Painted Snipe sightings from this survey were from coastal Queensland between Rockhampton and Townsville, an area of very seasonal (mostly summer and autumn) rainfall in the Brigalow Belt and Central Queensland Coast Bioregions. The level of wetland inundation varies greatly from year to year, but maximum inundation mostly occurs in February and March, and wetlands then shrink progressively, many drying completely by September in most years (Black *et al.* pers. obs.). This results in a succession of wetlands suited to Australian Painted Snipe, as some dry out and other deeper wetlands become muddy and shallower. Most sites would not retain good conditions for the entire March to September season. The six Australian Painted Snipe observed at Wunjunga Cyperus swamp, about 30 km south of Ayr on 11th May 2005 were not present on 13th June 2005, and by this time the wetland was almost completely dry. Seven Australian Painted Snipe found at Sheepstation Creek, about 25 km north-west of Ayr on 15th June 2005 may have been the same group. The extensive Sheepstation Creek wetlands are more permanent than the ephemeral Wunjunga wetlands, with deep Typha (bullrush) filled channels adjoining shallower sedge swamps.

Productivity of the seasonal wetlands used by Australian Painted Snipe in Central and North Queensland is mainly driven by the surge of invertebrate life after inundation of dried out wetlands. Food supply increases rapidly in the late summer wet season, and decreases as wetlands dry out in spring. Ephemeral wetlands have a great capacity for benthic productivity (Rogers *et al.* 2005, Crome *et al.* 1986) and their temporary nature prevents dominance by Typha rushes and sedges, resulting in open muddy areas ideal for feeding by Australian Painted Snipe (Rogers *et al.* 2005). In contrast, temperature may be a seasonally limiting factor for invertebrate production in southern Australia, so the food supply rises rapidly with warmer conditions in spring and decreases in autumn, even if wetlands are inundated through the winter.

Rainfall in north-east Queensland is also greatest in summer, but this region receives far more winter and spring rain than the dry tropics and many wetlands are active through the entire year. This may explain the greater number of summer records from this area.

In contrast to coastal Queensland, the rainfall of the arid western areas of Queensland is irregular, and occurs as infrequent inundation events without regular seasonality. Wetlands are also filled as a result of remote rainfall in northwestern Queensland in the summer and autumn, but this inundation only occurs in some years. Consequently, use of wetlands by birds tends to be opportunistic and this fits with the pattern observed for Australian Painted Snipe occurrence in these regions.

Implications for Population Assessment

These observations have implications for determining the conservation status of Australian Painted Snipe. If it regularly occurs in south-east Australia in spring and summer and moves to north-east Australia in autumn and winter then the same birds may be recorded twice, giving the impression that this threatened population is larger than it actually is. Current population estimates of 1500 are based on very few annual sightings and actual population size is unknown, but given that fewer than thirty birds are normally recorded annually for the whole of Australia, it could be considerably lower. This would suggest that endangered status rather than the current vulnerable may be appropriate.

Implications for Management

None of the localities of the nine sightings documented above are in formal protected areas, though current land use may not necessarily be a threat to the habitat or birds. However, some of these sites have been heavily grazed in the last two years, with very little cover remaining. As marine plains are prime grazing habitat, it is not surprising that no substantial tracts are in protected areas in Queensland.

There has been a substantial loss of habitat, much of it probably irreversible, for Australian Painted Snipe in south-eastern Australia, particularly in the Murray-Darling basin, formerly considered the core area of occurrence (Rogers *et al.* 2005). Recent extended drought has further diminished habitat availability in the region.

The evidence of regular migration in this paper suggests the need to conserve habitat for Australian Painted Snipe, particularly seasonal and ephemeral wetlands, in north-eastern Australia as well as in south-eastern Australia. Security of habitat is needed at <u>both</u> ends of the migration system. And whereas loss of habitat due to water harvesting may not be a present concern on much of the marine plain system of eastern Queensland, plans for agricultural and other development continue to be put forward.

The very specific ecological niche Australian Painted Snipe favour requires a series of highly productive wetlands throughout the year.

CONCLUSIONS

It is probable that a significant proportion of the eastern Australian population of Australian Painted Snipe migrates to coastal tropical Queensland in the period from February to August and also to inundated wetlands in western Queensland when these are available.

Some of these birds breed in the abundant wetlands available in early autumn. Australian Painted Snipe migration to the region apparently occurs when conditions are optimal for breeding, that is, flooded seasonal wetlands with falling water levels and abundant exposed mud (Marchant & Higgins 1993), and departure apparently occurs when little suitable habitat remains.

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