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Moult timing and morphometrics of Mangrove Gerygones: a comparison of monsoon-tropical and subtropical populations

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Mangrove Gerygones *Gerygone levigaster* were banded at six sites in the Greater Brisbane region, Queensland over 5.5 years, and at three sites in Darwin, Northern Territory, over 8-9 years. The species was highly sedentary in both regions, and no movements were recorded among sites at either location. In Darwin, males were larger than females in three out of five morphometrics, whilst in Brisbane they were larger in the remaining two, suggesting that different selection pressures may be operating on morphometrics in the two areas. Juvenile birds were present year-round in Brisbane, the highest numbers occurring from April to July and November to January, indicating that the breeding season, like that in Darwin, is biannual, but with a lag of 1-2 months. Months in which breeding activity occurred, indicated by the presence of cloacal protuberances or brood patches, and the occurrence of fledglings, also suggested that there were two egg-laying peaks. In Darwin, primary wing moult occurred mostly from October to December, after the second annual egg-laying pulse, whilst very few individuals (possibly in their first year) moulted after the first egg-laying pulse (March-April). In Brisbane, however, primary moult occurred from November to April, peaking in February and March, about four months after the peak in Darwin. Sites that were inundated only on king tides had a higher proportion of juveniles than those in riparian or intertidal areas, suggesting that the former may offer better breeding or foraging habitat for non-breeding birds. Body mass adjusted for structural size varied significantly among months in Brisbane, being highest in March and April, and lowest during May.

INTRODUCTION

Of the 14 or 15 species of mangrove-specialised birds in Australia (Noske 1996), the Mangrove Gerygone *Gerygone levigaster* has one of the broadest geographical ranges, stretching from the southwest Kimberley region of Western Australia to Port Hacking, New South Wales, and including the southern coast of New Guinea (Higgins and Peter 2002; Cooper *et al*. 2016). However, this range is discontinuous, and a gap on the east coast of Cape York Peninsula separates two recognised Australian subspecies, the nominate *levigaster*, which is confined to the tropics, and *cantator*, which occurs in eastern Australia from around Townsville southwards (Higgins and Peter 2002). Plumage differences between these two races are slight, but *cantator* is heavier and larger in most dimensions (Ford 1981; Higgins and Peter 2002). Throughout its range, the species is largely restricted to mangroves in estuaries and along tidal rivers, but in parts of the Kimberley it also occurs in adjacent paperbark thickets (Ford 1982; Johnstone 1990).

Although the reproductive ecology and morphometrics of the Mangrove Gerygone have been studied in detail in Darwin, Northern Territory (Noske 2001; Mulyani 2004), there has been no comparable published study covering southern Australia. In Darwin, the species was found to breed biannually, with egg-laying peaking in both March-April and September-October (Noske 2001; Mulyani 2004). In contrast, in New South Wales and south-eastern Queensland, egg-laying reputedly occurs from late August to late January, with a single peak in late October–early November (Ford 1981; see also Higgins and Peter 2002). If the apparent disparity in breeding seasons between north-western and south-eastern populations of the species is real, we might also expect differences in the timing of moult, as adult Australian passerines normally moult after breeding. A preliminary analysis of moult based on museum skins suggested that the moult of nominate (tropical) individuals often started just before the wet season, but sometimes not until after the wet season (Higgins and Peter 2002).

Since 2007, Mangrove Gerygones have been banded as part of a long-term study of the demography of mangrove-dwelling birds in the Brisbane region. This study provided an opportunity to compare the annual cycle of the population in this region with that of Darwin. In this paper, we compare the timing of moult and breeding, as well as the morphometrics of these two populations.

METHODS

Climate of study areas

Darwin's (12.4634° S, 130.8456° E) climate is monsoon-tropical, with year-round warm to hot temperatures, and a mean annual rainfall (MAR) of c.1,500 mm, of which roughly 90% falls in the wet season (November through April) and the remainder in an equally long dry season (May to October, Fig. 1a). In contrast, Brisbane (27.4698° S, 153.0251° E) is sub-tropical, with warm summers and drier, cooler winters, and a MAR of c.1,050 mm, with a short dry season (c.10% of MAR) from July through September (Fig 1b). About two-thirds of Brisbane's MAR falls during Darwin's wet season (Australian Bureau of Meteorology 2017).

Capture and measurement of gerygones

In Darwin, Mangrove Gerygones were captured and banded at three mangrove sites, the majority at Ludmilla Creek, between January 1986 and April 2009 (Table 1). At each of these sites, banding was conducted over 8-9 years; 149 sessions were conducted in total, but sampling was not systematic. Nevertheless, at each site sampling occurred in each calendar month in at least one of the study years. In Brisbane, Mangrove Gerygones were captured and banded at six sites between June 2007 and December 2012 (Table 1) as part of a constant-effort bird banding program. The majority were caught at Nudgee Road cycle track, Kedron Wetlands and Nudgee Beach Mangrove Boardwalk. Smaller numbers were captured infrequently at a further three sites (Osprey House, Eagleby Wetlands and Wynnum Mangrove Boardwalk). Each site was sampled each month for the duration of its use, giving a total of 261sampling sessions. The dominant mangrove species at all sites was the Grey Mangrove *Avicennia marina*.

In both Darwin and Brisbane, birds were captured in mist-nets (2.6 m high × 6-18 m long, mesh size 12 or 14 mm). In Brisbane, each net location at each site was marked using a GPS device, so that the same number of nets could be set in the same locations on every banding visit. The sites, number of visits and dates of visits are shown in Table 1. Mist-netting commenced at dawn and continued for 4– 6 h. After processing, captured birds were released at the capture site. All birds were banded with Australian Bird and Bat Banding Scheme (ABBBS) aluminium bands, but in Darwin they were also colour-banded for individual recognition during regular monitoring (Mulyani 2004). However, the smallest available coloured, celluloid bands could slip over the toes of gerygones, so aluminium bands were placed on each tarsus and a single coloured, celluloid band was placed above them. Anodized (coloured, metal) bands were used for nine birds, but because of the limited range of available colours and the difficulty of distinguishing them in the field, these bands were not used after 2000.

Each captured bird was scored for wing moult, using the methods described in Lowe (1989). Morphometrics obtained comprised flattened wing chord length and tail length (both ± 1 mm), total head length, tarsus length and bill length (all ± 0.1 mm) and body mass (± 0.1 g). In Brisbane, the sex of the bird was determined by examining the underparts for evidence of a well vascularised brood patch (females) or distinct cloacal protuberances (males); in Darwin, birds were sexed on whether a brood patch was present during the breeding season and this sexing was later checked by observation of colour-banded birds at the nest. Following Rebeira (2006), birds were aged according to the colour of the eyebrow. Those with yellow eyebrows were recorded as Age "1" (juveniles), those with buff tones to the eyebrow as Age "2-" (sub-adult) and those with pure white eyebrows as Age "2+" (adults). The yellowish tone to the eye brow in age code "1" birds is lost during the first post-juvenile moult when the bird attains adult plumage and small numbers of retained and worn juvenile feathers are the only means of distinguishing older juveniles (age code "2-") from adults. Unfortunately, post-juvenile moult in this species is not well documented and the time between fledging and the first post-juvenile moult is not known (Higgins and Peter 2002), although in most bird species this normally occurs within the first few weeks after fledging (Ginn and Melville 1983).

Morphometric data were analysed with StatsDirect v3.1.18. Samples were compared using independent t-tests and Analyses of Variance (ANOVA). Variation in the percentage of sub-adults over the six calendar years of the study in Brisbane was examined with simple linear regression analysis. Principal Components Analysis (PCA) was used to further analyse and describe size variation between male and female Mangrove Gerygones in the two study areas. To remove the influence of body size on the body mass measurement, an adjusted body mass index was calculated by dividing body mass by tarsus length (Coleman *et al*. 2002; Coleman *et al*. 2009).

RESULTS

Geographical and sexual variation in morphometrics

Table 2 compares the morphometrics of 112 adult or subadult Mangrove Gerygones banded at Darwin sites and 257 banded at Brisbane sites. Darwin birds were significantly smaller than Brisbane birds in wing, head-bill and tail lengths, and lower in body mass (Table 2). Sixty of the Mangrove Gerygones banded in Darwin were reliably sexed, 39 (65%) being male, whilst 33 (63%) of the 52 birds sexed in Brisbane were male. In Darwin, male Mangrove Gerygones were significantly larger than females in wing and tail length, and were also heavier (Table 3). However, tarsus and head-bill lengths did not differ significantly between the sexes. In Brisbane, males were significantly larger than females in tarsus and head-bill length, but not in wing or tail length or mass (Table 4).

Further analysis of size variation between males and females using PCA showed that the first PCA component only accounted for 45.8% and 44.2% of the variance in the Brisbane and Darwin data, respectively, with subsequent components being even weaker in their power to describe the variance observed. Scatter plots of PCA components 1 and 2 showed no separation of the data into discrete clusters, confirming that although some morphometric variation occurs between the sexes, there is significant overlap in size.

Moult and adjusted body mass

In Darwin, primary moult was evident in most birds captured from October through December, and in a minority of birds captured in February, April and May (Fig. 2a). The highest proportion of moulting birds caught was in October, when 84.6% were in active wing moult, followed by November with 72.7%. In Brisbane, primary moult was evident in captured birds from November through April, but the highest proportions showing active wing moult were in February (63.6%) and March (57.1%) (Fig. 2b). Of the 44 Brisbane birds caught while in active primary moult, 32 (72.7%) were aged as being adult (Age 2+), nine (20.5%) as immature (Age 2-) and three (6.8%) as juvenile (Age 1) (Fig. 1b).

Table 1

Study sites where Mangrove Gerygones were captured.

Site Name	Lat, long	Month of first visit	Month of final visit	Habitat	No. birds caught
Nudgee Road Cycle Track, Qld	27.36S, 153.1E	June 2007	December 2012	Rarely inundated mangroves	120
Kedron Wetlands, Qld	27.4S, 153.1E	November 2010	November 2012	Rarely inundated mangroves	104
Nudgee Beach, Qld	27.36S, 153.1E	October 2007	June 2012	Frequently inundated mangroves	66
Ludmilla Creek, NT	12.41S, 130.85E	April 2000	March 2009	Rarely inundated mangroves	66
Rapid Creek, NT	12.38S, 130.86E	April 2000	January 2008	Rarely inundated mangroves	33
Osprey House, Qld	27.28S, 153.0E	July 2011	November 2011	Riparian mangroves	12
Palmerston Sewage Ponds, NT	12.50S, 130.95E	January 1986	November 1994	Rarely inundated mangroves	11
Eagleby Wetlands, Qld	27.71S, 153.2E	November 2006	December 2012	Riparian mangroves	4
Wynnum Boardwalk, Qld	27.43S, 153.18E	October 2007	July 2008	Frequently inundated mangroves	3

Table 2

Morphometrics of all adult (2+, 1+) and subadult (2, 2-) Mangrove Gerygones caught in the Brisbane (1997–2012) and Darwin (1986-2009) regions. All lengths in mm.

Character	Mean, *SE, n* (Brisbane)	Range (Brisbane)	Mean *SE, n* (Darwin)	Range (Darwin)	t	p
Wing length	56.7 ± 0.1 (255)	50-64	52.8 ± 0.2 (102)	47-60	*-10.1*	<0.0001
Tail length	41.8 ± 0.2 (254)	33-51	39.8 ± 0.2 (97)	32-45	*-3.1*	0.02
Head-bill length	27.3 ± 0.04 (255)	25.2-30.8	26.7 ± 0.1 (74)	24.1-28.3	*-5.9*	<0.0001
Tarsus length	19.0 ± 0.1 (255)	15.9-21.0	19.2 ± 0.1 (74)	17.5-20.6	*-1.3*	0.18
Mass (g)	7.8 ± 0.03 (253)	6.0-9.5	6.7 ± 0.1 (102)	4.7-12.5	*-2.2*	0.02

Table 3

Morphometric comparison of adult male and female Mangrove Gerygones in Darwin region. All lengths in mm, mass in g.

Character	Male (mean, *SE, n*)	Female (mean, *SE, n*)	t	p
Mass	7.1 ± 0.2 (37)	6.4 ± 0.1 (21)	*-2.26*	0.04
Wing length	54.1 ± 0.4 (39)	51.5 ± 0.4 (15)	*-4.4*	0.0003
Tail length	40.8 ± 0.3 (37)	38.3 ± 0.5 (21)	*-3.46*	0.0028
Tarsus length	19.4 ± 0.1 (36)	18.8 ± 0.2 (17)	*-1.54*	0.142
Head-bill length	26.3 ± 0.5 (29)	26.5 ± 0.02 (10)	*-0.42*	0.6832

Table 4

Morphometric comparison of adult male and female Mangrove Gerygones in Brisbane region. All lengths in mm, mass in g.

Character	Male (mean, *SE, n*)	Female (mean, *SE, n*)	t	p
Mass	8.0 ± 0.1 (33)	8.0 ± 0.1 (19)	*-0.1*	0.919
Wing length	58.2 ± 0.4 (33)	56.6 ± 0.5 (19)	*-2.0*	0.06
Tail length	41.7 ± 0.4 (33)	41.3 ± 0.5 (19)	*-0.513*	0.61
Tarsus length	19.2 ± 0.1 (33)	18.7 ± 0.1 (19)	*-2.5*	0.02
Head-bill length	27.4 ± 0.1 (33)	27.0 ± 0.1 (19)	*-2.59*	0.01

In Brisbane, the more regular catching allowed adjusted body mass to be compared among age classes and months. However, as adjusted body mass did not vary among the three age classes used in the analysis (F=0.61, df=17,361, P=0.8), all age classes were combined for further analysis. Adjusted body mass varied significantly among years (F=3.1, df=5,372, P=0.008; Fig. 3), but this was primarily the result just of a noticeable decrease in recorded body mass index in 2009. When this year was removed from the analysis, there was no significant variation among the other years (F=0.76, df=4,316, P=0.551). Adjusted body mass also varied significantly among months (F=2.9, df=11,366, P=0.001); mean mass was highest during March and April, and lowest during May (Fig. 4).

Proportion of juveniles caught in Brisbane

Mangrove Gerygones banded over the study period in Brisbane comprised 195 sub-adults (fledglings, juveniles, and immature birds) and 114 adults. The percentage of sub-adults ranged from 61% to 79% over the six calendar years of the study (Fig. 5), but simple linear regression analysis showed no significant trend over the study period (r^2= 0.03, df =4, P=0.7). The population at Nudgee Road Cycle Track had a consistently higher annual percentage of juveniles (range 64.1–92.3%) than those at Nudgee Beach (range 37.5–62.5%) and Kedron Wetlands (range 50.0–66.6%) in each year of the study (Fig. 5). The differences between Nudgee Beach and Nudgee Cycle Track road were statistically significant (F=23.4, df=1,10, P<0.001). Juvenile birds (Age code 1) constituted more than 30% of all birds caught in each month except February and August, when the percentage dropped below 20% (Fig. 6). The relative abundance of juveniles was highest in April and May, when they constituted more than 50% of all birds caught.

In Brisbane, males with cloacal protuberances (indicating recent breeding activity) were caught in each month from September to March (n=4,7,7,3,4,2 and 6, respectively). Similarly, adult females with brood patches were caught in September (4), October (5), November (4), January (1), February (1), and March (4).

DISCUSSION

Morphometrics

Mangrove Gerygones were sexually dimorphic in both studied regions, males being larger than females in one or more characters, and this appears to be case in other parts of their range (Ford 1981; Johnstone 1990; Higgins and Peter 2002; Mulyani 2004). However, the degree of inter-sexual overlap in all characters makes morphometrics alone unsuitable for discriminating between the sexes. Breeding characters (the presence of brood patches or cloacal protuberances) were the only way to differentiate the sex of at least some individuals. Sexual dimorphism was much more pronounced in the monsoon-tropical population than in the sub-tropical population.

The physical characters in which sexual dimorphism was demonstrated differed between the two populations. Whilst males in Brisbane had longer head-bill and tarsus lengths, these characters did not differ between the sexes in the Darwin population. As Darwin males were larger than females in all other characters, the lack of head-bill length dimorphism suggests that females were relatively long-billed. In the Darwin region, Mangrove Gerygones are highly specialised in their foraging ecology, foraging mostly in Grey Mangroves, whereas coexisting Large-billed Gerygones *G. magnirostris* are more generalised in all foraging dimensions (Noske 1996; Mohd-Azlan *et al.* 2015). However, the latter species shows similar levels of morphological sexual dimorphism, suggesting that dimorphism is unrelated to foraging specialisation and rather may be the result of sexual selection. Moreover, members of Brisbane populations are probably just as specialised, as the Grey Mangrove is overwhelmingly the dominant tree species among the mangroves in the region. Thus, it seems likely that the greater degree of sexual dimorphism in the tropical than in the sub-tropical Mangrove Gerygone populations is related to higher levels of interspecific competition, especially with other gerygone species (absent in Brisbane), and possibly also to the greater diversity of mangrove species or mangrove-dwelling insects.

Ford (1981) collated measurements of Mangrove Gerygones from around Australia and concluded that eastern Australian birds *(cantator)* were larger than northern Australian birds (*levigaster*), which resembled one another. Measurements provided in Higgins and Peter (2002) also suggest that *cantator* averages 4-5 mm and 2-3 mm longer than *levigaster* in the wing and tail, respectively, and measurements of our study populations confirm the size differences described between these two subspecies.

Breeding seasons

The trade-off between fecundity and survival is well documented (e.g. Murray 1985; Johnston *et al.* 1997). Our studies suggest that the Mangrove Gerygone has a shorter lifespan than most Australian passerines studied to date (Coleman and Noske 2017), but the presence of juvenile birds year-round in Brisbane indicates a long breeding season with the potential for several broods. Nevertheless, the relative abundance of juveniles in Brisbane peaked in April–May, with a smaller peak during December–January. Although the phenology of egg-laying of Mangrove Gerygones in the Brisbane region is not known, birds in breeding condition were found from September to March, with the highest numbers for both sexes occurring in September through November, and in March, indicating two widely-separated peaks of breeding activity. The timing of these peaks in juvenile abundance and breeding in adults contradicts the statement of Ford (1981), who said that in south-eastern Queensland and New South Wales the species lays eggs from late August to late January, with a single peak in late October–early November.

The bimodal pattern of abundance of juveniles and breeding adults among Mangrove Gerygones in Brisbane parallels the breeding season in Darwin, Northern Territory (Noske 2001, 2003; Mulyani 2004), where the species breeds biannually, with two egg laying pulses of similar intensity, the first from March to May and the second, from August to October. Mangrove Gerygones are insectivorous, eating (in order of decreasing frequency) bugs, beetles, wasps, moths, spiders, flies and insect larvae (Johnstone 1990; Noske 2003). Egg-laying peaks of Mangrove Gerygones in Darwin were not correlated with rainfall or temperature, but were significantly related to the abundance of small flying insects, especially bugs (Hemiptera) and flies (Diptera) in mangroves around salt flats, the habitat of the species (Noske 2003; Mulyani 2004). Studies of pest insects show that mosquito diversity around Darwin is consistently high from late in the wet season (March) to mid-

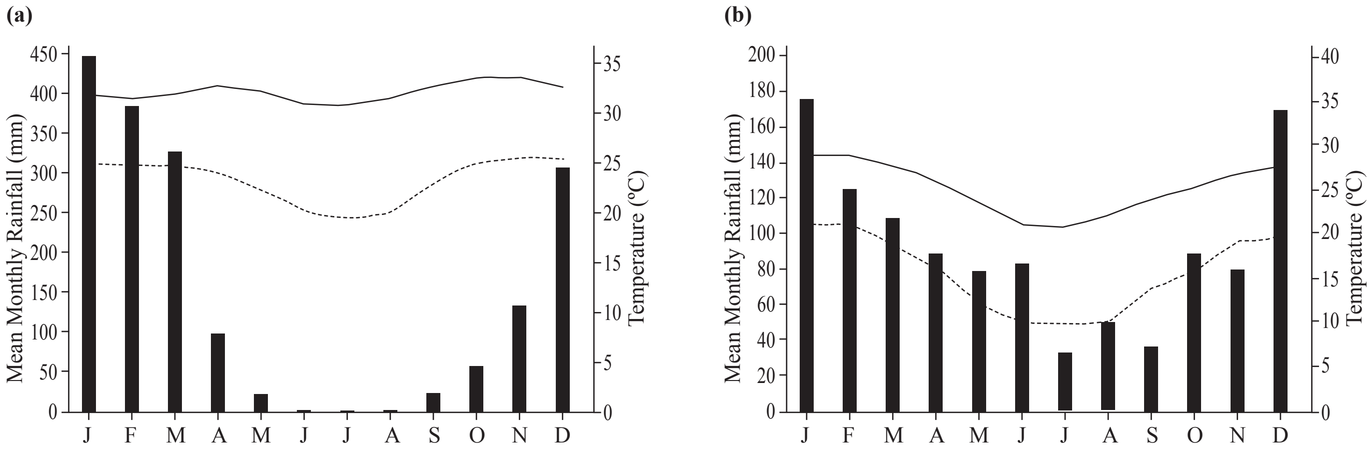

Figure 1. *Mean maximum (solid line) and minimum (dotted line) monthly temperature (ºC) and rainfall (mm, bars) for (a) Darwin and (b) Moreton Bay over the respective study periods. Source of data, Bureau of Meteorology, December 2018.*

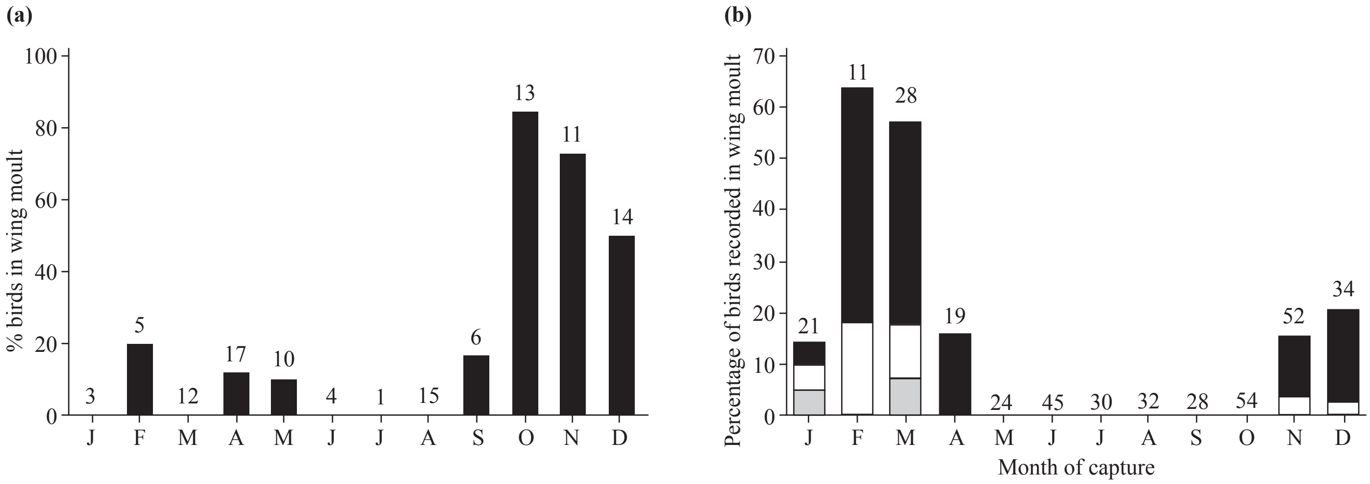

Figure 2. *Percentage of Mangrove Gerygones caught in each month that showed active wing moult in (a) Darwin (n=111) and (b) Brisbane (n= 378) regions. Adults and immature birds not distinguished in Darwin; for Brisbane: black, adults (2+); white, immatures (2-); grey, juveniles (1). Values above the histogram bars are monthly totals caught, including recaptures (n).*

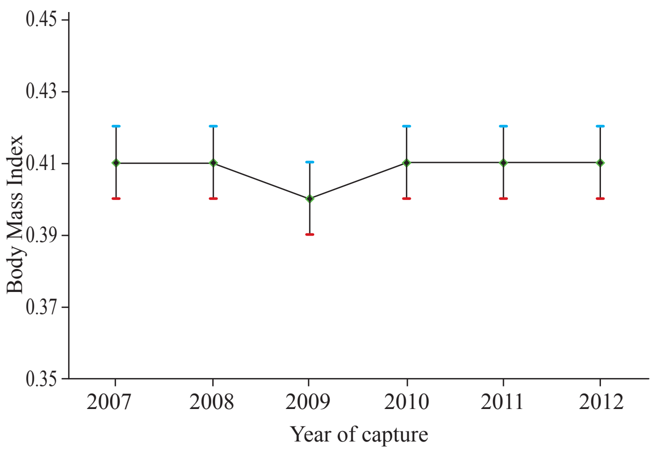

Figure 3. *Annual adjusted body mass index for Mangrove Gerygones caught between 2007 and 2012 in Brisbane. Data combined for all age and sex categories. Bars represent standard errors.*

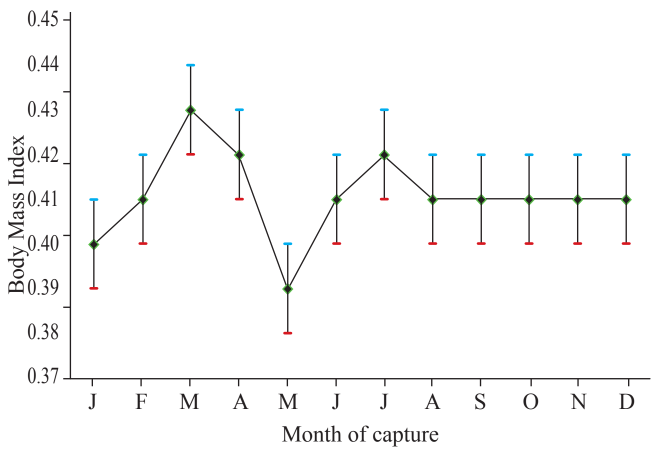

Figure 4. *Mean monthly adjusted body mass index for Mangrove Gerygones caught between 2007 and 2012. Data combined for all age and sex categories. Bars represent standard errors.*

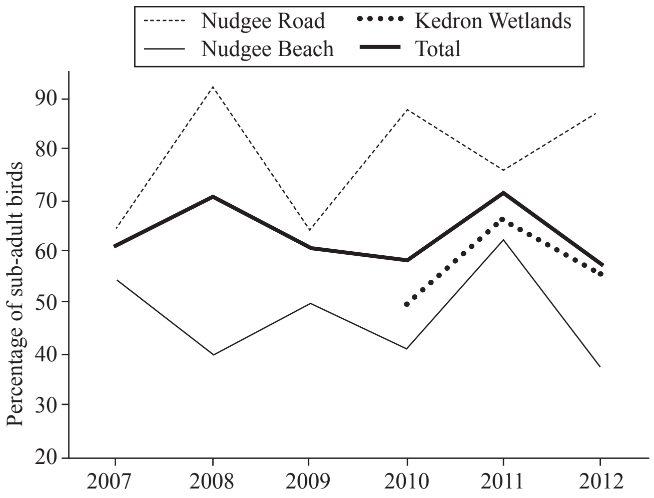

Figure 5. *Mean annual percentage of sub-adult Mangrove Gerygones banded at each location in each year of the study in Brisbane.*

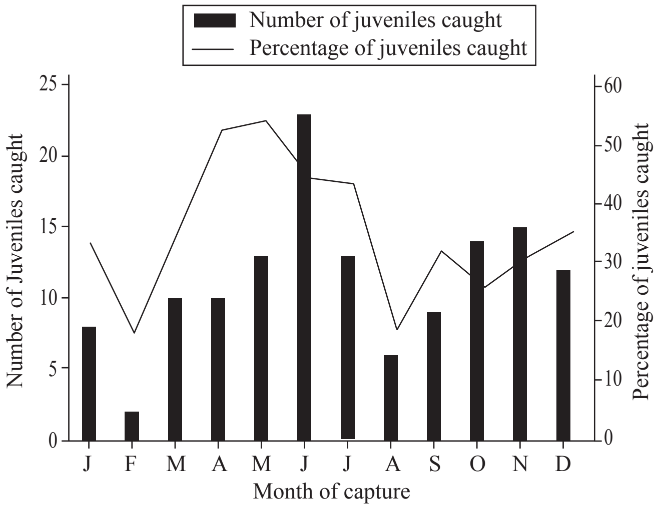

Figure 6. *Number of juvenile (age code 1) Mangrove Gerygones caught in each month of the study period in Brisbane (bars) and expressed as a percentage of the total birds caught in that month in all years (line).*

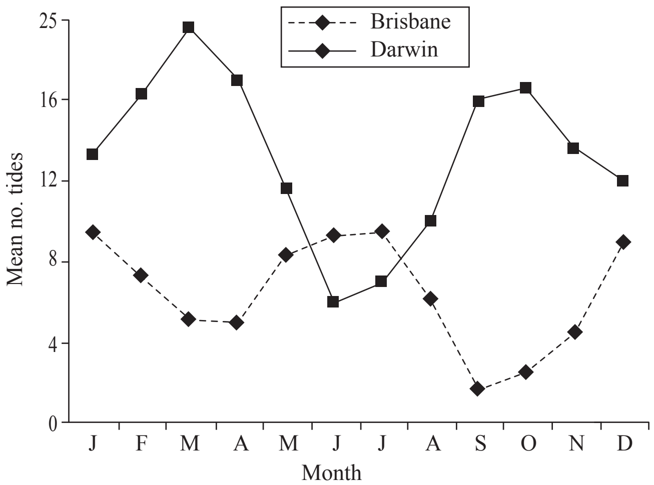

Figure 7. *Mean number of high spring tides by month for (a) Darwin Harbour, 1986-2009, where high spring tide => 7.0 m; and (b) Brisbane, 2007-2012, where high spring tide =>2.4 m. Source of data, Australian Bureau of Meteorology, December 2018.*

late dry season (August), when the abundance of *Anopheles* mosquitoes is also highest (Russell 1987; Franklin and Whelan 2009). The abundance of the Northern Salt-marsh Mosquito *Aides vigilax*, on the other hand, peaks when high tides and rain events coincide, mainly during the 'build-up' (September-November) (Jacups *et al.* 2011). Sessile insects in mangroves around Darwin also showed a biannual pattern of abundance, peaking in July and October (Mohd-Azlan *et al.* 2014).

The bimodal pattern of abundance of small insects in Darwin cannot be explained solely by rainfall, which is unimodal (see Fig. 1), but may be related to the seasonality of high spring tides which inundate salt flats (Noske 2013). The frequency of such tides is markedly biannual, being most frequent in March-April and September-October, and least frequent in June-July (Fig. 7). The frequency of high spring tides in Brisbane also shows a biannual pattern, but it is the converse of the pattern in Darwin, with peaks in June-July and December-January, about 2-3 months after the corresponding peaks in Darwin (Fig. 7). As gerygone fledglings in Darwin are probably most numerous in May and October, the Brisbane population appears to lag about 1-2 months behind the Darwin population in breeding phenology.

In Brisbane, the proportion of juveniles was higher at the less frequently inundated than at the regularly inundated (intertidal) sites. As there was no evidence of movements among sites (Coleman and Noske 2017), this disparity does not seem to be due to the dispersal of juveniles from the former to the latter habitat, although if juvenile birds forage in a different stratum of the vegetation it is possible that their dispersal could be undetected with the sampling methods used. It seems more likely, however, that the disparity reflects higher breeding success in the less frequently inundated sites. It is noteworthy that in Darwin and the Top End generally, this species shows a distinct preference for infrequently inundated mangroves surrounding salt flats, whereas the Large-billed Gerygone prefers taller, frequently inundated mangroves along tidal creeks (Noske 1996; Mulyani 2004).

Moult and Adjusted Body Mass

Like breeding, moulting is quite energy-consuming, so overlap in the timing of moult and breeding is rare in temperate birds (Ginn and Melville 1983; Barta *et al.* 2006) and in most Australian species studied to date, although there are exceptions (Ford 1980; Gardner *et al.* 2008). In Darwin, the incidence of primary wing moult among Mangrove Gerygones peaked in October, overlapping with the second annual pulse of egg-laying, but one month after its September peak (Mulyani 2004). Primary moult was still prevalent in birds captured in November, and to a lesser extent December, but egg-laying was not recorded in either of these months. In January and February, most birds had new primaries with little wear, but by March primaries began showing slight to moderate wear. Four birds showed active primary moult in the first five months of the year – one in February, two in April and one in May. The latter two months correspond to the first annual peak in egg-laying, so it is possible that one or more of these individuals were immature birds hatched during the second annual breeding pulse and undergoing their first moult. Moreover, the absence of birds showing wing moult in the months after the first annual breeding pulse suggests that post-breeding moult is largely limited to the second pulse.

In Brisbane, the earliest records of wing moult were in November, coinciding with the spring peak in the occurrence of juveniles. However, the months with the highest proportions of adults showing wing moult were February and March, 3-4 months after that peak and 4 months before the 'winter peak in juveniles'. Thus, although the Brisbane population appears to lag about 1-2 months behind the Darwin population in breeding phenology (see above), moult appears to lag by c.4 months (cf. Fig. 3a and 3b).

The apparently protracted period over which Mangrove Gerygones moult their primaries in Brisbane is consistent with a long breeding season, as suggested by the year-round presence of juveniles. Virtually all (>95%) the birds recorded in primary moult were adults or sub-adults entering their first complete moult. Notwithstanding the possibility that the age of some birds was incorrectly assessed at the time of banding, the small number of juveniles recorded in moult supports the conclusion of Higgins and Peter (2002) that juvenile birds undergo only a partial post-juvenile moult. Only nine (20%) of the 46 birds recorded as having obvious cloacal protuberances or brood patches were in wing moult, suggesting that in most cases adult birds moult either before or after breeding, rather than the two activities overlapping or occurring concurrently. This supports the suggestion by Higgins and Peter (2002) that adult moult typically occurs post-breeding.

Adjusted body mass in Brisbane was greatest just after moulting (when birds were presumably not breeding) and lowest in May (when the proportion of sub-adults was highest).

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