Mangrove Gerygones *Gerygone levigaster* are short-lived compared to other small Australian passerines

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South temperate Australian passerines are generally long-lived compared to birds of the north temperate region. However, few data are available on the survivorship of tropical and sub-tropical Australian birds. We examined survival in the Mangrove Gerygone *Gerygone laevigaster* at a sub-tropical location in Brisbane, south-east Queensland. Based on a dataset of 414 Mangrove Gerygones banded at three sites separated by a maximum of six kilometres, between 2006 and 2015 we found the species to be highly sedentary, with no movements between sites. No adults were recaptured four or more years after banding, although one bird banded as a juvenile was recaptured 5.5 years after banding. Using a time-dependent Cormack-Jolly-Seber live recaptures model for birds banded as adults, the apparent annual survival rate was 43.8 percent. Using a Time Since Marking model resulted in a slightly higher survival rate (46.7%) – excluding potential juveniles and transients. Banding studies in Darwin, Northern Territory, also indicate that this species rarely lives beyond four years of age. As most small Australian passerines studied to date have apparent annual adult survival rates between 55 percent and 85 percent, apparent survival of the Mangrove Gerygone appears atypically low.

INTRODUCTION

South temperate Australian passerines resemble tropical birds more than north temperate birds in their life history characteristics, which include small clutch sizes, long breeding seasons with multiple broods, and prolonged parental care (Ford 1989; Rowley and Russell 1991; Yom-Tov *et al.* 1992; Magrath *et al.* 2000; Russell 2000). Life-history theory predicts that south temperate and tropical birds compensate for their small clutches by living longer (Martin 1996), and indeed, apparent survival rates of south temperate and tropical birds are generally higher than those of north temperate birds (Johnston *et al.* 1997; Peach *et al.* 2001; McGregor *et al.* 2007; Lloyd *et al.* 2014; but see Blake and Loiselle 2008; Wolfe *et al.* 2014). Consistent with this prediction, Australian birds also appear to be relatively long-lived (Rowley and Russell 1991; Yom-Tov *et al.* 1992), but studies to date are overwhelmingly from south temperate Australia. Few studies have been conducted on the life history characteristics of tropical Australian birds, despite the potential that such studies have to shed light on the generality of the tropical-temperate life history paradigm.

The Mangrove Gerygone *Gerygone levigaster* is found along the coast of tropical northern and sub-tropical eastern Australia, as well as on the tropical southern coast of New Guinea. Of the two subspecies recognised in Australia, the nominate *levigaster* is found in the tropics from the northwest Kimberley region of Western Australia to Cape York in north Queensland, while cantator occurs from Cape York down the east coast to the Sydney region (Higgins and Peter 2002). Over most of its range the species is found exclusively in mangals around estuaries and along tidal rivers, but in Western Australia it also occurs in adjacent tea-tree shrubland (Johnstone 1990).

In this paper we present data on longevity, dispersal and estimates of apparent annual adult survival for the species at a subtropical location, and compare these with published and unpublished data for other species of gerygones and closely related thornbills (*Acanthiza* spp.).

METHODS

From June 2007 to November 2015 Mangrove Gerygones were captured using mist nets and banded at six sites in the Brisbane region, southeast Queensland, as part of a constant effort bird banding programme. The majority were caught at Kedron Wetlands and Nudgee Road cycle track, but the species was also regularly captured at Nudgee Beach (Table 1).

At the Nudgee Beach (27.342249S, 153.097458E) mangroves occupy an extensive area that is inundated with every high tide. The Nudgee Road Cycle Track (27.359188S, 153.101081E; 2 km from Nudgee Beach) and Kedron Wetlands (27.396616S, 153.087820E: 6 km from Nudgee beach) sites contain extensive areas of king tide mangroves which are inundated with seawater only on the highest tides. All three sites are interconnected by mangrove habitat. The dominant mangrove species at all sites was the Grey Mangrove *Avicennia marina*. The climate in the study area is characterised by warm, humid summers with drier, cooler winters.

Birds were captured regularly throughout the year in mist nets measuring 2.6 metres high x 6–18 metres long, with a mesh size of either 12 or 14 mm. Mist netting commenced at dawn and continued for four to six hours. Nets were checked every 10–20 minutes, and any captured birds removed, placed in a calico bag, and taken to a central location for banding and measuring, after which they were released. 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. Each captured bird was banded, measured, and aged according to the plumage criteria defined in De Rebeira (2006). Where possible, the sex of the bird was determined by examining the underparts for evidence of brood patches (females) or cloacal protuberances (males). Mean sampling effort for each site per annum and the mean sampling effort per annum during the breeding season are displayed in Table 1.

Apparent annual survival rates were estimated for birds banded as adults at the Nudgee Beach, Nudgee Road and Kedron Wetland sites, using MARK survival estimation software v2.1 (White and Burnham 1999) with the live recaptures only model (Seber 1970). Birds first captured in juvenile plumage were not included in the survival dataset. Only adult birds caught and banded during the purported breeding season, between June and January (Higgins and Peter 2002) were used in the analysis; juvenile birds and adults caught outside this period were excluded to help reduce the impacts of juvenile mortality and reduce the potential impact of transients. Multiple recaptures in a calendar year were combined to provide a single encounter event for each calendar year rather than using each monthly visit and encounter as a discrete encounter event.

Four basic survival models were tested, with the following assumptions:

Model 1: survival rate and recapture probability time-dependent,

Model 2: survival rate time-dependent and recapture probability constant,

Model 3: survival rate constant and recapture probability time-dependent,

Model 4: both parameters constant.

The best fit models were selected on the basis of Akaike's Information Criterion (AIC) where the lowest value, combined with the fewest parameters used in the model, usually indicates the model that best represents the observed data (Akaike 1973) but also taking account of the AIC weight calculation (AICc) due to the low effective sample sizes used in the analysis. Goodness of Fit (GOF) estimation was used to assess the model fit to the data used and where GOF could not be applied due to low sample sizes the models were recalculated using the actual calculated c-hat value rather than the model value and QAIC and QAICc values compared as above using the alternate method to GOF described in Cooch and White (2015).

To correct for the potential inclusion of juveniles that had attained adult plumage and possible transients in the sample population survival rates were calculated again using a Time since Marking model (TSM). The selected model assumed constant survival of cohort one (potential juveniles) and constant survival of cohort two (assumed adults, with a constant recapture probability (Cooch and White 2015).

RESULTS

Over 6.5 years from 9 June 2007 to 28 November 2015, a total of 414 Mangrove Gerygones were caught and banded, of which 85 (20.5%) were recaptured (Table 1). Of the recaptures, 71 (17.3%) individuals, banded as apparent adults during the breeding season were re-encountered in subsequent years after

Table 1

Banding sites used in this study, inundation frequency, numbers of Mangrove Gerygones captured and recaptured, date when first caught and last visit, and mean visits per annum and during breeding season.

Site	Inundation	No. caught	No. recaptures (No. of individuals)	First visit	Last visit	Mean visits per annum and mean visits (breeding season)
Kedron Wetlands	Rare	213	58 (45)	7/11/2010	28/11/2015	6.7 SE +/- 0.8 (4.5 SE +/-0.5)
Nudgee Beach	Frequent	81	43 (23)	18/10/2007	24/05/2015	4.7 SE +/- 0.7 (3.3 SE +/-0.4)
Nudgee Road Cycle Track	Rare	120	20 (17)	9/06/2007	27/09/2013	6.0 SE +/- 0.8 (4.4 SE +/- 0.5)

Table 2

Statistics for time dependent live recapture models used to analyse survival rates of Mangrove Gerygones banded at Nudgee Beach, Nudgee Cycle Track and Kedron Wetlands. Φ = apparent survival, P = recapture probability. The factors included in each model part are given in parentheses; "t" and '.' mean the respective probabilities are assumed to be time-dependent and constant respectively. Each model summary includes Akaike's Information Criterion adjusted for small sample size (AICc), change in AICc (ΔAICc), Akaike weight (ωi) representing the relative support for a particular model compared with the other models, number of parameters estimated (K), and deviance.

Φ(t)P(t) Survival rate and recapture probability time-dependent

Φ(t)P(.) Survival rate time-dependent, recapture probability constant

Φ(.)P(t) Survival rate constant, recapture probability time-dependent

Φ(.)P(.) Survival rate and recapture probability constant

Model	AICc	ΔAICc	ωi	Model Likelihood	K	Deviation
Φ(t)P(t)	74.0392	10.4529	0.00425	0.0054	7	1.245
Φ(t)P(.)	68.8406	5.2543	0.05717	0.0723	5	1.7261
Φ(.)P(t)	66.9415	3.3552	0.14775	0.1868	4	2.4301
Φ(.)P(.)	63.5863	0	0.79084	1	2	3.8703

banding. The majority of re-trapped individuals used in the analysis (*n*=50) were recaptured only once, but a small number were re-encountered twice (*n*=16), three times (*n*=4) and four times (*n*=1). All re-trapped birds were recaptured at the site where they were banded, despite the Nudgee Road Cycle Track and Nudgee Beach sites being within two kilometres of each other.

A time-dependent live recaptures model, which assumed a constant survival and recapture probability, was selected as the most appropriate model to describe the observed data, based on having the lowest AIC value a high AIC weight and the fewest model parameters (Table 2). This model indicated that the apparent annual survival rate of adults was only 43.8 percent. The TSM live recaptures model produced an apparent annual survival rate estimate of 46.7 percent for adults with the most appropriate model being the one which assumed constant survival of both cohort one (potential juveniles), and cohort two (assumed adults) and a constant recapture probability (Table 3).

A GOF test was conducted and was not significant ($\chi 2$=2.25, df=4, P=0.68) as a result of insufficient sample sizes for the GOF analysis. Therefore we re-ran the analysis according to the method proposed in Cooch and White (2015) using the actual median $\hat{c}$ value of 2.4, calculated in MARK from the model data, rather than using the default value of 1.0 used by MARK. Again the model which assumed constant survival of both cohorts and a constant recapture probability, provided the lowest QAIC value (Table 4) and had the highest QAIC weight and was therefore selected. There were too few data to allow survival analysis to be broken down by sex or banding site, but it is noteworthy that the two longest living individuals in this analysis were sexed as males.

DISCUSSION

Like passerines of tropical regions around the world, Australian passerines of the ancient autochthonous corvine assemblage lay small clutches compared to those of the north temperate region (Rowley and Russell 1991; Yom-Tov *et al.* 1992). Life-history theory predicts that tropical birds balance their low fecundity with higher adult survival (Martin 1996). Consistent with this, most Australian species studied to date are relatively long-lived, typically showing survival rates between 55 percent and 85 percent (Green and Cockburn 1999; Ford *et al.* 2001; Coleman *et al.* 2012). In the present study, however,

Table 3

Summary of model selection results for Time-Since-Marking (TSM) live recapture models, using two TSM-classes for survival (M2) to analyse survival rates of Mangrove Gerygones banded at Nudgee Beach, Nudgee Cycle Track and Kedron Wetlands. The factors included in each model part are given in parentheses; “t” and ‘.’ mean the respective probabilities are assumed to be time-dependent and constant respectively, and, for example, ‘(M2-t/.)’ means survival of the first (‘juvenile’) TSM class is time-dependent and survival of the second (‘adult’) TSM class is constant. Each model summary includes Akaike's Information Criterion adjusted for small sample size (AICc), change in AICc (ΔAICc), Akaike weight (ωi) representing the relative support for a particular model compared with the other models, number of parameters estimated (K), and deviance. Φ = apparent survival, P = recapture probability.

Φ(M2-./.)P(.) Two TSM-classes for survival (M2), survival of both marking classes constant (./.) through time, recapture probability constant

Φ(M2-./t)P(.) Two TSM-classes for survival (M2), first (‘juvenile’) marking classes constant, second (‘adult’) marking class time-dependent (./t) through time, recapture probability constant

Φ(M2-./.)P(t) Two TSM-classes for survival (M2), survival of both marking classes constant (./.) through time, recapture probability time dependent

Φ(M2-t/.)P(.) Two TSM-classes for survival (M2), first (‘juvenile’) marking classes time-dependent, second (‘adult’) marking class constant (t/.) through time, recapture probability constant

Φ(M2-./t)P(t) Two TSM-classes for survival (M2), first (‘juvenile’) marking classes constant, second (‘adult’) marking class time-dependent (./t) through time, recapture probability time-dependent

Φ(M2-t/t)P(.) Two TSM-classes for survival (M2), survival of both marking classes time-dependent (./.) through time, recapture probability constant

Φ(M2-t/.)P(t) Two TSM-classes for survival (M2), first (‘juvenile’) marking classes time-dependent, second (‘adult’) marking class constant (t/.) through time, recapture probability time-dependent

Φ(M2-t/t)P(t) Two TSM-classes for survival (M2), survival of both marking classes time-dependent (./.) through time, recapture probability Time-dependent

Model	AICc	ΔAICc	ωi	Model Likelihood	K	Deviation
Φ(M2-./.)P(.)	166.1271	0	0.85376	1	3	12.2799
Φ(M2-./t)P(.)	170.2562	4.1291	0.10832	0.1269	6	9.7411
Φ(M2-./.)P(t)	173.0938	6.9667	0.02621	0.0307	7	10.2575
Φ(M2-t/.)P(.)	175.1162	8.9891	0.00954	0.0112	7	12.2799
Φ(M2-./t)P(t)	179.4792	13.3521	0.00108	0.0013	10	9.3586
Φ(M2-t/t)P(.)	179.8618	13.7347	0.00089	0.001	10	9.7411
Φ(M2-t/.)P(t)	182.91982	16.7921	0.00019	0.0002	11	10.2575
Φ(M2-t/t)P(t)	190.0107	23.8836	0.00001	0	14	9.3586

Table 4

Summary of corrected model selection results for Time-Since-Marking (TSM) live recapture models, using two TSM-classes for survival (M2) to analyse survival rates of Mangrove Gerygones banded at Nudgee Beach, Nudgee Cycle Track and Kedron Wetlands. The factors included in each model part are given in parentheses; "t" and '.' mean the respective probabilities are assumed to be time-dependent and constant respectively, and, for example, '(M2-t/.)' means survival of the first ('juvenile') TSM class is time-dependent and survival of the second ('adult') TSM class is constant. Each model summary includes Akaike's Information Criterion adjusted for small sample size (QAICc), change in AICc (ΔQAICc), Akaike weight (ωi) representing the relative support for a particular model compared with the other models, number of parameters estimated (K), and deviance. Φ = apparent survival, P = recapture probability.

Φ(M2-./.)P(.) Two TSM-classes for survival (M2), survival of both marking classes constant (./.) through time, recapture probability constant

Φ(M2-./t)P(.) Two TSM-classes for survival (M2), first ('juvenile') marking classes constant, second ('adult') marking class time-dependent (./t) through time, recapture probability constant

Φ(M2-./.)P(t) Two TSM-classes for survival (M2), survival of both marking classes constant (./.) through time, recapture probability time dependent

Φ(M2-t/.)P(.) Two TSM-classes for survival (M2), first ('juvenile') marking classes time-dependent, second ('adult') marking class constant (t/.) through time, recapture probability constant

Φ(M2-./t)P(t) Two TSM-classes for survival (M2), first ('juvenile') marking classes constant, second ('adult') marking class time-dependent (./t) through time, recapture probability time-dependent

Φ(M2-t/t)P(.) Two TSM-classes for survival (M2), survival of both marking classes time-dependent (./.) through time, recapture probability constant

Φ(M2-t/.)P(t) Two TSM-classes for survival (M2), first ('juvenile') marking classes time-dependent, second ('adult') marking class constant (t/.) through time, recapture probability time-dependent

Φ(M2-t/t)P(t) Two TSM-classes for survival (M2), survival of both marking classes time-dependent (./.) through time, recapture probability Time-dependent

Model	Q AICc	Δ QAICc	ωi	Model Likelihood	K	Deviation
Φ(M2-./.)P(.)	72.8686	0	0.91755	1	3	5.1166
Φ(M2-./t)P(.)	78.4785	5.6099	0.05552	0.0605	6	4.0588
Φ(M2-./.)P(t)	81.015	8.1464	0.01562	0.017	7	4.2739
Φ(M2-t/.)P(.)	81.8577	8.9891	0.01025	0.0112	7	5.1166
Φ(M2-./t)P(t)	87.9248	15.0562	0.00048	0.0005	10	3.8994
Φ(M2-t/t)P(.)	88.0842	15.0562	0.00048	0.0001	10	4.0588
Φ(M2-t/.)P(t)	90.8404	17.9718	0.0001	0.0001	11	4.2739
Φ(M2-t/t)P(t)	98.4563	25.5877	0	0	14	3.8994

Mangrove Gerygones in sub-tropical Australia were found to be relatively short-lived, with apparent annual adult survival of only 46.7 percent. Only birds in adult plumage were included in the data analysis, but given the potential for at least some individuals to undergo a full rather than partial post juvenile moult (Higgins and Peter 2002), it is possible that some older juveniles were misidentified as 'adults' and included in the survival dataset. Not only is the survival of juveniles often lower than that of adults (Newton *et al.* 1983; Loery *et al.* 1987; Clobert *et al.* 1988), but juveniles typically have a greater probability of permanently emigrating out of a study area as a consequence of juvenile dispersal (Pradel *et al.* 1997). The inclusion of juveniles in a mark-recapture dataset may therefore violate a critical assumption of Cormack-Jolly-Seber (CJS) models, namely that all individuals have the same probability of subsequent encounter after being marked. However analysis of the dataset using a TSM model, allowing transients and juvenile survival to be identified and excluded from the analysis also demonstrated a low apparent adult annual survival rate of 46.7 percent, supporting the hypothesis that adult Mangrove Gerygones have an unusually low survival rate. This is further supported by the lack of any recaptures of adult birds after the fourth year post-banding and only one juvenile exceeding four years post banding.

Studies of three colour-banded populations of Mangrove Gerygones in the monsoon-tropical city of Darwin, Northern Territory, suggest that a short lifespan may be typical for the species. At Ludmilla Creek, 63 Mangrove Gerygones were colour-banded during 44 sessions over nine years (2000–2009), but only six (10%) were re-encountered, the oldest two (both males) being at least 2.7–2.8 years old when last seen (R. Noske and Y. Mulyani, unpubl. data). Of the 33 individuals banded at Rapid Creek during 28 sessions over eight years, seven (21%) were retrapped or re-sighted, the oldest (a male) being at least 6.8 years old when last recaptured, and the second oldest (also a male) being 4.4 years old (R. Noske and Y. Mulyani, unpubl. data). Finally, of the eleven individuals that were banded near Palmerston Sewage Ponds during 77 sessions over 9.5 years (1985–1994), three (27%) were re-sighted or re-trapped, the oldest (a male) being at least 4.25 years old when last seen (Noske 1996, unpubl. data). In summary, of the 107 Mangrove Gerygones banded at these sites over 149 sessions, only one bird was known to have lived more than 4.5 years.

Although there are no published demographic studies of Australian gerygones, unpublished data from a long-term (12-year), constant effort, banding study at Herdsman Lake, Perth, Western Australia suggest that the Western Gerygone *G. fusca* is also relatively short-lived. Of 729 individuals banded, only ten (1.4%) were re-trapped more than 1.5 years after banding, and of these, eight were last re-trapped less than 2.5 years after banding, the remaining two being over 6.6 and 8.0 years old (W. Rutherford, unpubl. data). In New Zealand, by contrast, Gill (1982) found that that mean annual survival was high (81.5%) for a colour-banded population of the endemic Grey Gerygone *G. igata*. As this study was conducted over only three breeding seasons, the longest-lived individual was last seen 3.2 years after banding, though it was estimated to be at least 3.7 years old, and life expectancy of all birds was estimated to be 4.9 years. Gill (1982) attributed the high survivorship of these birds to their low reproductive rate and lack of intraspecific competition, yet among gerygones, this species has the largest mean clutch size (Higgins and Peter 2002), and breeding success was not particularly low (42%; Gill 1982). High survivorship in this species may also be influenced by the lack of avian and arboreal mammalian predators in New Zealand (Niethammer 1970).

Studies of the phylogenetically closely-related and morphologically similar thornbills (*Acanthiza* spp) indicate that adult survival rates of three species of thornbills are higher than that of the Mangrove Gerygone (Table 5). Maximum longevity records in the Australian Bird and Bat Banding Scheme database were also higher for two of the thornbill species (15–17 years), but these may relate to the much larger sample sizes for these species. The majority of thornbill species are confined to southern Australia, whereas most *Gerygone* species are tropical in distribution (Ford 1985; Keast and Recher 1997; Nyári and Joseph 2012). Most thornbill species forage in small groups and breed cooperatively (Nicholls *et al.* 2000), whereas cooperative breeding has very rarely been recorded among gerygones (Higgins and Peter 2002). Arnold and Owens (1998) found that adult survival is higher among cooperatively breeding species than in non-cooperative species, although in North America, maximum longevity appears not to be affected by either cooperative parental care or group foraging (Blumstein and Møller 2008; Beauchamp 2010).

Both gerygones and thornbills are represented in terrestrial habitats ranging from desert to rainforest, but only gerygones inhabit mangroves (see Higgins and Peter 2002). The Mangrove Gerygone is the most habitat-specialised of all mangrove-dwelling birds, being largely restricted to patches dominated by the Grey Mangrove Avicennia marina (Noske 1996, 2001; Mohd-Azlan *et al.* 2012). Indeed, in the Darwin region, at least 80 percent of its foraging and nesting involves this plant species (Noske 1996). Such a high degree of specialisation partly explains why the species is highly sedentary (Noske 1996; Mulyani 2004; this study) as dispersal may be futile if suitable habitat is saturated. In the present study, neither adults nor juvenile birds were re-captured at sites other than the one at which they had been banded, despite some sites being connected by suitable mangrove habitat.

In both the Brisbane and Darwin populations of Mangrove Gerygones the longest-lived individuals were males, suggesting that the mortality rate of females is higher than that of males. Moreover, an analysis of all recapture data for this species,

Table 5

Longevity and annual adult survival rates for species in the family Acanthizidae. Source is Higgins and Peter (2002) unless otherwise indicated.

Species	No. of birds	Dataset age (Years)[6]	Recovery (%)	Max. longevity	Survival (%)
Brown Thornbill *Acanthiza pusilla*	23 170	48	27.8	17.4	87[2]
Brown Thornbill [1]	136	4	nr	11	73[*]
Striated Thornbill *A. lineata*	14 094	48	36.9	15.6	nr
Buff-rumped Thornbill *A. reguloides*	3460	48	26.2	8.5	54[2]
Yellow-rumped Thornbill *A. chrysorrhoa*	9005	48	14.8	9.5	64[3]
Mangrove Gerygone *Gerygone levigaster*	198	48	18.7	8.6	
Mangrove Gerygone [4]	356	8	19.4	5.5	43.8
White-throated Gerygone *G. albogularis*	245	48	5.3	6.3	
Brown Gerygone *G. mouki*	969	48	9.8	9.9	
Western Gerygone *G. fusca*	1131	48	7.5	5.3	
Western Gerygone [5]	729	12	22.5	8	

[1] Green and Cockburn (1999)
[2] Bell and Ford (1986)
[3] Ford (1963)
[4] this study
[5] W. Rutherford (unpubl. data)
[6] The Data from the 48 year datasets are extracted from the ABBBS banding database excluding one year in which mortality was exceptionally high

provided by ABBBS, revealed that the two oldest birds (> 5 years old), and at least one of the three individuals that were over three years old, were males. Mortality rates of female birds are generally higher than those of males, and this is the main driver of male biased sex ratios (see reviews by Donald 2007; Székely *et al.* 2014). One possible cause of higher mortality in gerygone females relates to their sole role in incubating eggs and brooding young, activities that have been shown to increase metabolic demands (Thomson *et al.* 1998; Barnett and Briskie 2010) and the risk of predation (Conway and Martin 2000). In the ground-foraging and ground-nesting Speckled Warbler *Chthonicola sagittata* adult mortality was significantly higher for females than males, but mainly during the breeding season, when females (the sole incubating sex) are susceptible to predation by ground-dwelling predators (Gardner and Heinsohn 2007).

The Mangrove Gerygone, at least in northwest Australia, is also a major host of the brood-parasitic Little Bronze-cuckoo *Chrysococcyx minutillus* (Noske 2001; Mulyani 2004; Tokue and Ueda 2010), which causes reproductive failure, and may increase the frequency of re-nesting, which in turn, may affect the condition of breeding females. However such considerations do not explain why even male Mangrove Gerygones rarely live beyond four years of age. Further studies will examine mortality of this species in relation to body condition and breeding seasonality.

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