An example of a "Twinkling Lights" local extinction event: population dynamics of Gilbert's Whistler at The Charcoal Tank Nature Reserve, New South Wales

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A banding project at The Charcoal Tank Nature Reserve in central west New South Wales has accumulated data on the bird populations utilising this small, isolated patch of remnant mallee-ironbark/box woodland for more than thirty years. The Reserve supported a small, resident sub-population of Gilbert's Whistler *Pachycephala inornata* when the study commenced, but several years later this sub-population went into decline and eventually became extinct. Although individual dispersing Gilbert's Whistlers have been recorded at the Reserve on several occasions since then, a self-sustaining population has not been re-established. Banding data indicate that the population began experiencing very low annual recruitment rates in 1993-4 (well before the local onset of major drought in 2001) and that this decline persisted until the last remaining adults died and the species became locally extinct around 2000-01. This seems to be an example of a so-called "Twinkling Lights" extinction event. There is widespread concern over the recent decline of many woodland bird species in this region, and a better understanding of the population dynamics underlying local extinction events is critical for testing and validating existing ecological models of population dynamics, as well as refining the knowledge base underpinning conservation efforts directed at woodland birds.

INTRODUCTION

There is increasing concern over the declining populations of many bird species inhabiting the inland woodlands of eastern Australia (Olsen 2007; Ford 2011a). These woodlands have undergone substantial fragmentation and reduction in area due to land clearing for agriculture over the past century or more. This significant loss and degradation of habitat is generally identified as the primary factor driving the decline of the woodland birds (e.g. Watson et al. 2003), but it is also compounded by increases in a range of other disturbance factors. These factors include introduced predators, increased competition from native species (such as the Noisy Miner Manorina melanocephala), disrupted patterns of dispersal, and climate change effects such as increases in the intensity, frequency and duration of drought and periods of extremely high ambient temperatures (Reid 1999, 2001; Ford et al. 2001; Watson et. al 2003; Ford 2011a; Stevens and Watson 2013; Gardner et al. 2014). Small, isolated populations are particularly susceptible to extinction resulting from such stochastic events (Gilpin and Soulé 1986). Viewed in its entirety, the situation currently facing the woodland birds of this region is a classic example of the "Extinction Debt" scenario first described by Tilman et al. (1994), in which species continue to disappear from the remaining fragments of habitat left in a landscape long after the initial isolation of these patches occurred, due to the slow, but inexorable, operation of the ecological processes that have been unleashed.

Whilst there is an emerging consensus on the overall nature and scale of the problem of declining bird populations in inland New South Wales (NSW) and its likely root causes, there is also recognition that there is much complexity in the ways that the various threatening processes interact at different scales and in different circumstances, and in turn in how individual species will be affected. An example of this is provided by Ford (2011b), who outlines two distinct mechanisms by which woodland fragmentation and loss might result in extinctions of woodland bird populations with different ecological characteristics - the "Twinkling Lights" and the "Dimmer Switch" models. The former model applies to species with poor dispersal abilities, in which the overall population consists of numerous subpopulations of varying size isolated from one another in habitat fragments. In this model, the population is thus visualised as a collection of twinkling lights, the "twinkles" being the variation in the intensity of the lights (sizes of the sub-populations) as various stochastic factors impact upon them. Every now and then one of the sub-populations, usually a smaller one, will "twinkle out" and be extinguished when a larger-than-usual downward oscillation touches the zero baseline. In contrast, the "Dimmer Switch" model visualises a wide-ranging species, whose members easily and regularly disperse among areas of habitat, as a single source of illumination; the illumination's intensity (i.e. the size of the population) undergoes a general dimming when it is adversely affected by one or more landscape-scale factors (e.g. increasing populations of Noisy Miners in woodland patches). Ford (2011b) designates the Brown Treecreeper

Climacteris picumnus as an example of a species experiencing the "Twinkling Lights" effect and the Regent Honeyeater *Anthochaera phrygia* as one experiencing the "Dimmer Switch" effect. In the context of these two models, the Gilbert's Whistlers at the Charcoal Tank Nature Reserve (CTNR) in central western New South Wales (NSW) are interpreted as a sub-population exhibiting the properties associated with susceptibility to the "Twinkling Lights" effect. Improving our understanding of how these putative extinction mechanisms work and which species may be affected most requires detailed, preferably long-term, data from studies encompassing as many permutations of the variables as is practicable (Olsen 2007; Suthers *et al.* 2007; Bennett and Watson 2011; Rayner *et al.* 2014).

The CTNR banding study has been operating consistently for over 30 years and has generated an invaluable set of life history data that provides a source of detailed, long-term insights into the lives of the members of many species of woodland birds that inhabit the site. As a small patch of remnant vegetation isolated from large areas of continuous woodland for several decades, the Reserve represents a model setting in which to examine the operation of Extinction Debt mechanisms in detail. Fortuitously, the study has captured a snapshot of the population dynamics of a small, remnant sub-population of an "at risk" species (*sensu* Reid 2001), the Gilbert's Whistler *Pachycephala inornata*, in the years leading up to the local extinction of that sub-population. This provides an excellent, albeit retrospective, opportunity to examine some of the population dynamics underlying this type of event.

Gilbert's Whistlers are distributed widely in the drier parts of southern Australia in three disjunct populations (Higgins and Peter 2002). The eastern population is spread across NSW, Victoria and South Australia, with the CTNR being near to the eastern edge of its distribution. The species is typically found in semi-arid mallee woodland and occasionally in taller, semi-arid eucalypt woodland or forest, usually where a dense understory is present (Higgins and Peter 2002). The whistlers feed on the ground and in understorey layers, primarily on invertebrate prey, although they also eat fruit and seeds (Higgins and Peter 2002). They breed in pairs, usually nesting in dense shrubs and sometimes in the roof of an old babbler nest (Higgins and Peter 2002), and are usually described as being resident and/ or sedentary. They are generally difficult to observe, but in spring calling males establishing breeding territories are easily detected (Higgins and Peter 2002).

The landscape surrounding the CTNR contains numerous small patches of habitat apparently suitable for Gilbert's Whistlers, although most of the woodland that once covered this landscape has been cleared for agriculture. Whilst many of these patches are comparable in size to the study site, being tens or hundreds of hectares in extent, there are only three large (thousands of hectares) patches, namely Cocoparra National Park (NP) ~ 85km to the southwest, Weddin Mountains NP ~75km to the east, and Round Hill/Nombinnie Nature Reserve (NR) ~ 140km to the northwest. Of these, only Round Hill/ Nombinnie NR is known to contain a resident breeding population of Gilbert's Whistlers, although there have been numerous occasional records of the species from many other locations in the region, including both Cocoparra NP and Weddin Mountains NP (NSW Office of Environment and Heritage 2017).

METHODS

Study Site

The CTNR is a small patch of remnant, native vegetation, primarily Mugga Ironbark *Eucalyptus sideroxylon* – Inland Grey Box *E. microcarpa* woodland and Mallee *E. viridis/E. polybractea* – Broombush *Melaleuca uncinata* woodland, located on the west side of the Newell Highway, approximately twelve kilometres south of West Wyalong, in central-western NSW (Figure 1). The reserve is rectangular and 86 ha in area (NSW NPWS 2012), although the area locally occupied by this habitat is a little larger than this, as there are small areas of additional native vegetation adjacent to the reserve boundaries on all sides.

During this study from 1986-2016 the mean annual rainfall in the area was ~460 mm, which was consistent with the longer-term average of 480 mm (Bureau of Meteorology 2018). However, there was considerable annual variability, with an extended drought occurring from 2001 to 2008-09. This drought period included the driest year on record at Wyalong (2006), when only 180 mm of rainfall was recorded. It was widespread across almost all south-eastern Australia and is now widely referred to as "the Big Dry". It appears that the period 1997-8 to 2007-8 may have been the driest decade in the area in the last 200 years (Cockfield 2011; van Dijk *et al.* 2013). There are no historical records of fires occurring in the Reserve (NSW National Parks and Wildlife Service 2012).

Bird banding programme

The banding programme at the CTNR was initiated in July 1986 and is ongoing. One hundred and sixty banding trips, each lasting 2-3 days, were conducted in the 30 years from July 1986 to June 2016, with 2-7 trips (mean 5.3) occurring annually. Birds were captured using standard 31 mm mesh mist nets, approximately 3 m high and 6 to 18 m long. Nets were typically deployed at daybreak and usually kept open through to lateafternoon. They were placed in a combination of standard and opportunistic locations to maximise the likelihood of capturing birds, with specific net locations being selected at the discretion of each bander to suit the prevailing conditions. All birds captured were marked with numbered metal bands supplied by the Australian Bird and Bat Banding Scheme (ABBBS). Using standard methods (Lowe 1989), morphometric data and condition data (moult status, brood patch status) were collected and, where possible, the age and sex of the birds were determined. All banding data were recorded on a central database in a consistent format, with regular checks for data integrity being performed by the banding study coordinators.

Sampling effort undoubtedly varied significantly among years during the study. Unfortunately, records of the lengths of nets used and the time for which nets were deployed on each banding day were not collected, so the information required to calculate the sampling effort expended annually is unavailable. For this reason, the annual catch rates reported herein are the raw data; no attempt has been made to normalise them or otherwise correct for variations in sampling effort.

Gilbert's Whistler exhibits distinct sexually dimorphic adult plumage, which in males is acquired early in the third year of life (Higgins and Peter 2002). The sex of younger birds cannot be reliably determined, so these individuals were recorded as 'sex



Figure 1. Map location and aerial view of the Charcoal Tank Nature Reserve.

unknown'. Younger birds can be aged, on plumage characters and soft parts, as juvenile (J), first year (1) or second year (2-) birds. Birds in adult plumage when first caught were aged as 2+ years.

Banding data were supplemented with observational data, obtained primarily by the team during banding visits, but supplemented by a few observations made by other people visiting the CTNR independently. This data set has been collated from field notebook entries and a search of the NSW Office of Environment and Heritage's *Atlas of New South Wales Wildlife*, which holds data consolidated from several other databases (NSW office of Environment and Heritage 2017).

RESULTS

Capture statistics

Eighty-eight captures of Gilbert's Whistlers were made in the 30-year period from July 1986 to June 2016, involving a total of 49 individuals. Thirty-two of these individuals were only caught once. Of the 17 whistlers that were recaptured during the study (34.9%), 7 were re-trapped just once and 10 more than once. Of the latter 10 birds, two were recaptured on two occasions, five on three occasions, two on four occasions and one on six occasions. Overall, recaptures constituted 44.3% of all captures of Gilbert's Whistlers during the study.

The probability of an individual Gilbert's Whistler being captured during an individual banding trip was estimated using data from individuals captured on more than one occasion, as these individuals are thus known to have been present on all sampling occasions after time of first capture up to (and including) time of last capture. The average probability of recapture, P, for each of the n individuals captured on more than one occasion was calculated as:

$$\boldsymbol{P} = \left(\begin{array}{c} \underline{X}_1 + \underline{X}_2 + \underline{X}_3 + \dots \\ Y_1 & Y_2 & Y_3 \end{array} \right) / n$$



Figure 2. Number of Gilbert's Whistlers captured in each 12-month interval from July 1986 to June 2016, with the number of banding trips in each year in parentheses.

where X is the number of recaptures for each individual and Y is the number of recapture opportunities (i.e. banding trips) in the interval between the first the trip after first capture to the trip of last capture, inclusive. P was 0.31, with a standard deviation of 0.32 (n=17).

Of the 49 Gilbert's Whistlers captured during the study, 18 were designated females, 15 males and 16 'sex unknown' (i.e. too young to be sexed on plumage characters). Of the birds captured before 2001(i.e. up to the time when the subpopulation went functionally extinct), two were classified as juveniles (age J) and twelve as first-year immatures (age 1), based on plumage and soft parts. The presence of individuals in juvenile plumage is taken as evidence of breeding occurring at the study site. Seven individuals were known to be alive for at least three years during the study period and all of them were adults (2+) at time of first capture.

Figure 2 shows the number of Gilbert's Whistlers captured in each 12-month interval during the study period. The number captured annually was low compared to the numbers of many other species captured in the Reserve; for example, almost 2500 White-plumed Honeyeaters *Ptilotula penicillatus* were banded in the Reserve in total over the study period. However, the proportion of banded Gilbert's Whistlers recaptured on subsequent occasions was consistent with rates for a range of other commonly captured passerine species (see Table 1), indicating that the banding programme was sampling this subpopulation effectively, despite the low numbers captured.

The number of Gilbert's Whistlers captured annually began to slowly decline from the early 1990s, finally reaching zero in 2001-2, which appears to be the time, or very close to the time, at which the sub-population became extinct. Solitary birds were captured on two subsequent occasions, one each in 2005-6 and 2015-16 (see Figure 3), but these are presumed to have been dispersing birds from sub-populations located elsewhere due to the long (multi-year) intervals between the captures.

Observational data

Figure 4 summarises observational data for Gilbert's Whistler at the CTNR. It indicates that Gilbert's Whistler has been present there since at least the early 1970s, as evidenced by a single sighting in 1971. The long time that elapsed between this sighting and the next in 1983 is probably due to a lack of visiting observers over this period, rather than an absence of the species per se. Regular visits by observers began occurring with the initiation of the banding programme in 1986 and sightings consequently became more frequent, particularly after 1990 when the banding team began making more systematic, supplementary observations. Regular sightings of Gilbert's Whistler were recorded until 1999 when the number began to decrease, and then sightings essentially ceased after 2000, except for intermittent records widely separated in time. This overall pattern accords with that revealed by the banding data (see Figure 2).

Seasonality of occurrence

Figure 5 shows the mean number of Gilbert's Whistlers captured per banding trip in each month prior to 2001-02 when the sub-population became functionally extinct. The data indicate that Gilbert's Whistlers were present at the CTNR in all months and that the sub-population was almost certainly a resident one. This consistent presence contrasts dramatically with that of the two other whistler species recorded at the site, the Golden Whistler *Pachycephala pectoralis* and the Rufous Whistler *P. rufiventris*, which respectively are winter and summer migrant

Table 1

Recapture rates in % recaptured order for commonly caught species at The Charcoal Tank Nature Reserve, 1989-2016.

Species	No	%
	Captured	Recaptured
White-throated Treecreeper Cormobates leucophaeus	29	79
Brown Treecreeper Climacteris picumnus	87	62
White-browed Babbler Pomatostomus superciliosus	256	53
Chestnut-rumped Thornbill Acanthiza uropygialis	47	49
Inland Thornbill Acanthiza apicalis	396	41
Eastern Yellow Robin Eopsaltria australis	504	40
White-plumed Honeyeater Lichenostomus penicillatus	2475	36
Gilbert's Whistler Pachycephala inornata	49	35
Brown-headed Honeyeater Melithreptus brevirostris	618	32
Variegated Fairy-wren Malurus lamberti	139	31
Grey Shrike-thrush Colluricincla harmonica	90	28
Peaceful Dove Geopelia striata	264	26
White-eared Honeyeater Lichenostomus leucotis	638	26
Golden Whistler Pachycephala pectoralis	97	26
Weebill Smicrornis brevirostris	75	25
Yellow Thornbill Acanthiza nana	117	25
Rufous Whistler Pachycephala rufiventris	235	24
Yellow-rumped Thornbill Acanthiza chrysorrhoa	56	21
Grey Fantail Rhipidura albiscapa	143	16
Red-capped Robin Petroica goodenovii	171	16
Willie Wagtail Rhipidura leucophrys	150	13
Spiny-cheeked Honeyeater Acanthagenys rufogularis	857	11

visitors (unpublished banding records). The mean number of Gilbert's Whistlers recorded per month was generally stable, except possibly for a reduction in early winter (May-June,), when the average capture rate fell by > 50% compared to all other months. There are three plausible explanations for this apparent seasonal decline: (1) there may have been some local dispersal of members of the sub-population at this time, (2) the species became less "catchable" during winter, perhaps due to variations in behaviour and/or habitat preferences exhibited in the non-breeding season, and (3) the decline simply reflects the fact that some months were 'under-sampled' relative to others (e.g. over the thirty-year study period, only seven banding trips occurred in June, compared to nineteen in July. A correlation coefficient of 0.7 between the number of sampling trips per month and the total number of captures recorded in that month provides strong support for the third hypothesis.

Age structure and survival

The 'trajectory' of the Gilbert's Whistler sub-population at the CTNR over the 30 years of the study, as revealed by the known life history details of the 49 individuals banded during that period, is illustrated in detail in Figure 6. As expected for a resident species, during the first decade of the investigation many individuals were recorded in multiple years and many of them were recaptured regularly. During this first decade, the slope of an approximate visualised line-of-best-fit connecting



Figure 3. A young (first year) Gilbert's Whistler caught at The Charcoal Tank Nature Reserve on 21/05/2016, presumed to be a dispersing bird. Photo: Richard Allen

the month when each individual was first recorded in each year (shown as a dotted line in Figure 5) is relatively consistent from 1986-87 to 1998-99; this suggests that the rate at which new individuals were recruited into the sub-population during this period was fairly consistent. It was impossible to determine whether the new recruits to the sub-population detected by the banding program had been bred locally or were immigrants dispersing from other sub-populations, although the regular capture of young birds (aged J or 1) suggests that locally-bred birds were involved.

However, it is also noticeable that whilst the recruitment rate into the CTNR Gilbert's Whistler sub-population (as indicated by the slope of the line alluded to above) appeared to remain constant until the summer of 1998-99, very few of the new recruits first encountered after the summer of 1993-94 were ever recaptured, and none were re-trapped more than a year after they were first captured. This suggests that a period of low long-term survival of young (or newly recruited) birds began after the summer of 1993-94, resulting in a steady decline in the proportion of long-lived birds in the sub-population.



Figure 4. Number of separate observations of Gilbert's Whistler recorded in each year from 1971 to 2016 at the Charcoal Tank Nature Reserve.



Figure 5. Overall number of Gilbert's Whistlers captured in each month, with the number of banding trips made in each month in parentheses.

The starkest feature of Figure 6 is, of course, the 'disappearance' of the sub-population. This local extinction event occurred during the summer of 2000-01 (or shortly thereafter), although it seems clear that the circumstances leading up to the 'disappearance' had been in operation for several years prior to that. It appears that after the summer of 1993-94, the established long-lived individuals in the sub-population (that presumably formed the core of the breeding adults) were not being replaced, apparently due to poor survivorship of the new birds recruited into the sub-population, so that when the breeding individuals died the sub-population died out soon afterwards.

Over the remaining 15 years of the study, only two further Gilbert's Whistlers were captured and two others observed, all at widely spaced intervals. Neither of the individuals captured (one in 2006 and the other in 2016) has been recaptured or seen subsequently. It seems reasonable to assume that these were dispersing birds originating from other locations. Whilst there is only limited evidence of long-range dispersal movements by Gilbert's Whistlers, there is at least circumstantial evidence that some dispersal movements may occur (Higgins and Peter 2002). Moise (2009), using radio-tracking at Gluepot Reserve and Ngarkat Conservation Park in South Australia, showed that Gilbert's Whistlers were relatively mobile at a local scale,



Figure 6: Age structure of the CTNR Gilbert's Whistler population, July 1986 to June 2016 (June each year marked). Each row represents a different individual bird, with the coloured bar indicating the period in which that individual was known (from recapture history) to be alive. Males shaded blue; females shaded green; immature birds of indeterminate sex shaded yellow; capture events shaded red. The dotted line is drawn through the month of first encounter of each individual. The shaded period in the centre indicates the main period of drought in the area, running from 2001 through to 2009.

regularly shifting home ranges both within and between seasons, although no long-distance movements were recorded.

DISCUSSION

Gilbert's Whistler was a year-round (breeding) resident at the CTNR from 1986-2016, although there may have been some local dispersal of members of the sub-population in winter. The sub-population was stable in size, but was always small, and it eventually reached a point at which it was no longer selfsustaining. Unfortunately, this relatively small size meant that the number of individuals captured was also too small to obtain reliable estimates of population size, recruitment and mortality using standard statistical methods, such as Jolly-Seber (Dettman 1995). Despite this limitation, some useful, tentative inferences can be made about the demography of the CTNR sub-population from the available banding data.

The data suggest that the sub-population of Gilbert's Whistler was in serious decline well before the local commencement of the "Big Dry" drought in about 2001, and probably even before the 1997 inception of this major drought regionally. The CTNR Gilbert's Whistler sub-population began experiencing very low recruitment rates in 1993-4 and this persisted until it 'petered out' around 2000-01, when the few remaining, longerlived individuals (which presumably contributed most of the breeding output) had expired and had not been replaced by new recruits. Without any "experienced" breeding adults left in the sub-population, local extinction became inevitable.

Conceivably the onset of the drought at about the time that the sub-population became extinct may have been the 'last straw' leading to its demise. However, it is unlikely that it was the root cause of the decline, which appears to have started well before the onset of drought. The reason(s) for the decline in recruitment into this sub-population can only be surmised. Reduction in habitat quality, loss of genetic diversity, competition from other species, predation by both native and introduced species and even simple stochastic factors (such as chance mortality of key breeding individuals) all have the potential to induce the variations in populations dynamics observed in this study, variations that can ultimately bring a small, isolated sub-population to the point of extinction (Gilpin and Soulé, 1986). Whatever the cause(s) of the subpopulation's decline and extinction, it seems likely that ultimately this habitat fragment was simply too small to support a sufficiently large sub-population of a resident species with limited dispersal ability, such as the Gilbert's Whistler, in a viable condition in the long-term. In this respect, the loss of Gilbert's Whistlers from the CTNR is consistent with the specific predictions of Reid (2001) and the "twinkling lights" scenario described by Ford (2011b), as well as with 'Extinction Debt' theory in general.

A few Gilbert's Whistlers still pass through the CTNR, apparently dispersing from other sub-populations. Despite the comparatively low sampling intensity, four such birds in transit have been recorded (two by misting netting, two by observation) in the 15 years since the resident sub-population was first presumed extinct. To date, such transits have not led to re-establishment of a breeding sub-population. This may be due to numbers simply being too low and transits too widely separated in time for breeding pairs to become established, or because the dispersing birds find the habitat unsuitable and either die or leave the site and continue their dispersal. However, the evidence suggests that even if a breeding pair (or pairs) do establish themselves at the site, ultimately this habitat patch is unlikely to be sufficiently large to maintain a viable sub-population in the long-term, and eventually the lights will 'twinkle out' once again.

Given the dynamics of the (now extinct) sub-population at the CTNR described here, the overall status of Gilbert's Whistler in the central western region of NSW appears problematic. Whilst there are reports of Gilbert's Whistlers occurring in many of the habitat fragments in the landscape, they are nearly always thinly dispersed in time. This could be just a product of a relatively low frequency of site visits, combined with the relatively small size of local sub-populations. However, it could also be consistent with the observations of transient Gilbert's Whistlers and/or of small, short-term sub-populations "twinkling" in and out of existence, fed by dispersing birds from a small number of viable, long-term sub-populations inhabiting sufficiently large habitat patches, such as Round Hill/Nombinnie NR. If this latter scenario is the case, the long-term future of this species in the region may be dependent on a very small number of critical locations.

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