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Undetected Allee effects in Australia's threatened birds: implications for conservation

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ABSTRACT

Allee effects occur when survival or reproductive success declines with decreasing population size or density. Species most severely impacted by Allee effects may be the very species for which these effects will be hardest to detect and overcome. This impedes effective conservation through a lack of evidence to drive management actions. We review the literature to identify (1) component Allee effects (components of fitness) which could lead to a demographic Allee effect (effect of all components on the population growth rate) in bird populations; and (2) traits that make species susceptible to component Allee effects. Concurrently, we assess the potential for undetected Allee effects to negatively influence the population growth rate of 14 critically endangered Australian bird species or subspecies. Whilst some (e.g. Helmeted Honeyeater) are unlikely to suffer from a demographic Allee effect, several (e.g. Great Knot, Orange-bellied Parrot) are susceptible to a number of component Allee effects and, hence, a demographic Allee effect. However, traits of the Regent Honeyeater suggests this species' decline in particular is accelerated by an undetected demographic Allee effect. For this species and others, an inability to detect Allee effects need not preclude efforts to account for their potential presence through precautionary conservation management.

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Introduction

Individuals of many species increase their fitness by associating with conspecifics (Allee 1931; Odum and Allee 1954; Krause and Ruxton 2002). The concept of dependence on group living was formalised as the Allee effect: a positive relationship between components of individual fitness and the number or density of conspecifics (Allee 1931; Stephens *et al.* 1999). In a conservation context, the Allee effect describes how population growth rates decrease with decreasing population size or density, accelerating the decline and extinction of small or sparse populations (Stephens and Sutherland 1999; Stephens *et al.* 1999). Component Allee effects (hereafter CAEs) influence components of individual fitness, but do not necessarily affect population growth rates. Rather, one or more CAEs can contribute to the existence of a demographic Allee effect (hereafter DAE): the overall effect of reduced population size or density on the population growth rate (Figure 1).

The detrimental impact of Allee effects on threatened species is widely acknowledged in theory (Courchamp *et al.* 2008), and as global biodiversity declines (Butchart *et al.* 2010), Allee effects are likely to increase in both frequency and magnitude (Courchamp *et al.* 2008; Gascoigne *et al.* 2009).

However, Allee effects pose a challenge for conservation. Despite their potential role as a driver of extinction (Halliday 1980; Hung *et al.* 2014), empirical evidence of Allee effects in threatened species remains limited (Kramer *et al.* 2009; Gregory *et al.* 2010), and so too are the strategies for redressing them (Gilroy *et al.* 2012). For example, despite ongoing declines in Australian avifauna (Cresswell and Murphy 2017), CAEs have been implicated in just three species (Cuthbert 2002; Grünbaum and Veit 2003; Gardner 2004) and in no Australian species has a DAE been demonstrated to negatively influence population growth rates.

Substantial conservation resources are invested in preserving small populations, but measuring the trajectory of fitness as a function of population size or density in such populations is extremely challenging (Gilroy *et al.* 2012). Traits that make a species difficult to monitor, such as high mobility and small population size, may also make them susceptible to a DAE (Courchamp *et al.* 2008). Time spent proving the existence of an Allee effect may see a declining population pass the 'Allee threshold', beyond which extinction may be unavoidable (Berec *et al.* 2007; Figure 1). Thus, Allee effects can hinder conservation success

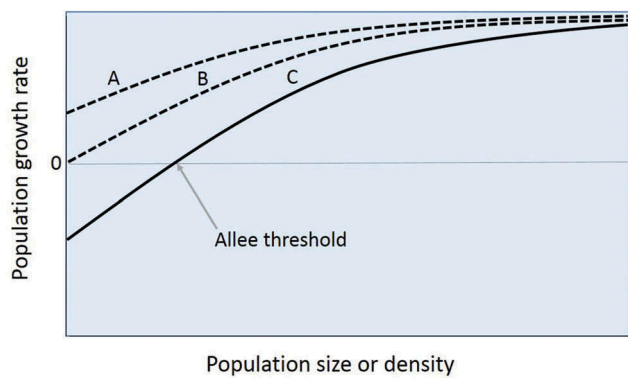


Figure 1. Simplified schematic of two component Allee effects (A and B) that give rise to a demographic Allee effect (C). Once population size or density decreases below the Allee threshold, population growth is negative and the population declines to extinction. Figure adapted from Berec *et al.* (2007). For a comprehensive summary of component and demographic Allee effects, see Stephens *et al.* (1999) and Berec *et al.* (2007).

because their impact on population growth rates may be greatest in species for which they are least likely to be detected and most difficult to overcome.

The presence, strength and potential to overcome a DAE should therefore inform optimal management decisions (McDonald-Madden *et al.* 2010; Armstrong and Wittmer 2011). The trend-detection approach to management has been criticised for delaying management action (Martin *et al.* 2009), as undetected DAEs may already inhibit population recovery. Consequently, applying the precautionary principle and taking immediate management action when there is a strong case for the existence of a DAE (Cooney 2004; Courchamp *et al.* 2008) may prove most effective in achieving conservation goals (Martin *et al.* 2009; McDonald-Madden *et al.* 2010).

Here, we review the literature to identify: (1) potential CAEs that may impact small or sparse bird populations (Table 1), and (2) life-history, ecological and demographic traits (hereafter ‘traits’) that may increase a species’ susceptibility to each CAE (Table 1). To demonstrate this, we concurrently evaluate the potential for undetected CAEs, and hence a DAE, to exist in 14 of the 16 species or subspecies (hereafter ‘taxa’ where both are considered) currently listed federally as critically endangered in Australia (Commonwealth of Australia 2017; Table 2). We omit the Mount Lofty Quail-Thrush (*Cinclosoma punctatum anachoreta*), which is presumed extinct (Garnett *et al.* 2011) and jointly evaluate Herald and Round Island Petrels (*Pterodroma arminjoniana/heraldica*) given the similarity of their traits in the context of Allee effects. The 14 case taxa, spanning 7 families and 12 genera, represent a non-arbitrary sample with which to evaluate the

potential impact of undetected Allee effects on Australia’s threatened birds (Table 3). Many, though not all, have suffered a rapid decline (Garnett *et al.* 2011), but, as for most threatened bird populations, a lack of detailed monitoring data for these taxa makes confirming the presence of a DAE extremely challenging (Gilroy *et al.* 2012). We then discuss the feasibility of accounting for undetected Allee effects via precautionary conservation management of the data-deficient case taxa (Table 4).

Review of component Allee effects

Habitat selection

Selection of quality breeding habitat is critical to breeding success (Gunnarsson *et al.* 2005; Fletcher 2006). Adaptations to select high-quality habitat include philopatry (Part 1991; Gunnarsson *et al.* 2005), imprinting (Teuschl *et al.* 1998) and conspecific attraction (Fletcher Jr. 2006; Schmidt *et al.* 2015). However, conspecific attraction can result in a DAE because socially acquired information on habitat quality can be unreliable at low population density (Schmidt *et al.* 2015), particularly in highly variable environments (Stodala and Ward 2017). Individuals use the presence of small numbers of conspecifics as an inaccurate cue that occupied habitat is of high quality (Schmidt *et al.* 2015). Cues that historically provided reliable information on habitat quality can also become unreliable following habitat modification (Kokko and Sutherland 2001). At low density, competitive exclusion from poor-quality, modified habitat by conspecifics is reduced and a larger proportion of individuals settle there, setting an ‘ecological trap’ for the population (Kokko and Sutherland 2001). Despite theoretical support, Allee effects pertaining to habitat selection are challenging to detect empirically and the relative influence of social information in determining an individual’s assessment of habitat quality is poorly understood (Fletcher Jr. 2006; Schmidt *et al.* 2015).

Species that exhibit high conspecific attraction, have low philopatry in highly variable environments and small populations that are sparsely distributed across wide areas, should be at risk from a habitat selection CAE. Given their semi-nomadic movement patterns and tendency to aggregate when breeding (Ford *et al.* 1993; Webb *et al.* 2014), Swift Parrots and Regent Honeyeaters are the most susceptible of the case taxa to a habitat selection CAE. The very small breeding ranges of the King Island Scrubtit, Helmeted Honeyeater and the Herald/Round Island Petrels

Table 1. Component Allee effects in birds and ecological, demographic or life-history traits that increase susceptibility to each at small population size or density

Component Allee effect	Rationale for susceptibility to component Allee effect	Susceptible life-history/ demographic/ecological traits	Examples
Habitat selection	Lack of exclusion from poor-quality habitat leads to ecological trap	Low philopatry/high mobility	Models (Kokko and Sutherland 2001)
	Small nesting aggregations provide unreliable social information on habitat quality, leading to suboptimal habitat selection	High conspecific attraction	Models (Schmidt <i>et al.</i> 2015)
Mate-finding	Reduced capacity to find mates at low densities	High environmental variability	Least Flycatcher (Fletcher 2009)
		High or female-biased dispersal	Models (Stodala and Ward 2017)
	High susceptibility to male-biased operational sex ratio	Large range	Models (Gilroy and Lockwood 2012)
		Aggregative nesting	Willow Warbler (Morrison <i>et al.</i> 2016)
		Historically common	Theory (Gascoigne <i>et al.</i> 2009)
Mate choice/facilitation	Lack of mate choice leads to less, or less successful, breeding activity	Socially monogamous	Models (Berec <i>et al.</i> 2017)
	Lack of nesting conspecifics reduces female impetus to nest	Highly monogamous	Models (Shaw <i>et al.</i> 2017)
		High female mortality	Glossy Black Cockatoo (Lee <i>et al.</i> 2015)
		Aggregative or colonial nesting	Black-eared Miner (Ewen <i>et al.</i> 2001)
Nest success	Lower nest survival	Aggregative or colonial nesting	Swift Parrot (Stojanovic <i>et al.</i> 2014)
		Open nesting	Models (Møller and Legendre 2001)
	High susceptibility to stochastic events, e.g. storms or heatwaves	Aggregative or colonial nesting	Puerto Rican Parrot (Brock and White 1992)
Dispersal	Reduced efficiency of dispersal movements	High mobility	Passenger Pigeon (Halliday 1980)
		Movement in flocks	Fieldfare (Andersson and Wiklund 1978)
	Reduced capacity for optimal location of food resources	High variability of food resources	Lesser Kestrel (Serrano <i>et al.</i> 2005)
	Reduced capacity to overcome a DAE once established	Low population structure	Passenger Pigeon (Halliday 1980)
Foraging and anti-predation	Reduced foraging efficiency	Group feeding	Little Tern (Medeiros <i>et al.</i> 2007)
	Increased predation risk	Obligate intraspecific flocking	Theory (Gascoigne <i>et al.</i> 2009)
Interspecific competition	Reduced competitiveness for access to common resources	Relatively small body size in guild	Whooping Crane (Mueller <i>et al.</i> 2013)
Genetics	Reduced hatching success	Small effective population size	Domestic Pigeon (Biro <i>et al.</i> 2006; Pettit <i>et al.</i> 2015)
	Reduced disease resistance	Low dispersal	Black-browed Albatross (Grünbaum and Veit 2003)
	Reduced survival		Models (Boukal and Berec 2002)
Cultural adaptation, social learning and song-learning	Reduced capacity to learn, or slower spread, of socially acquired adaptations	High sociality	Speckled Warbler (Gardner 2004)
		Long generation time	Redshank (Cresswell and Quinn 2011)
	Song-learning errors/small vocal repertoire hinder mate/territory acquisition	Close-ended song-learning.	Honeyeaters (Ford 1979; Ford <i>et al.</i> 1993)
Anthropogenic	Disturbance by eco-tourists reduces nesting success	High species profile	Meta-analysis (Heber and Briskie 2010)
	Illegal harvesting for food or animal products	Value or demand increase with rarity	Galapagos Hawk (Whiteman <i>et al.</i> 2006)
			Darwin's Finches (Keller <i>et al.</i> 2002)
			Great Tit (Morand-Ferron and Quinn 2011 ; Aplin <i>et al.</i> 2015)
			Models (Kokko and Sutherland 2001)
			Florida Grasshopper Sparrow (Ragheb <i>et al.</i> 2015)
			Dupont's Lark (Laiolo and Tella 2008)
			Humboldt Penguin (Ellenberg <i>et al.</i> 2006)
			Helmeted Hornbill (Beastall <i>et al.</i> 2016)
			Indonesian songbirds (Harris <i>et al.</i> 2017)

Table 2. The 14 Australian case taxa listed federally as critically endangered, their estimated population size, cause of population decline (declining population paradigm, Caughley 1994) and quality of available monitoring data in the context of detecting Allee effects (Gilroy *et al.* 2012)

Species	Estimated population size	Declining population paradigm	Quality of available monitoring data
Round Island/Herald Petrel (<i>Pterodroma arminjoniana/heraldica</i>)	25–50	N/A (range-restricted)	Poor
Plains-Wanderer (<i>Pedionomus torquatus</i>)	250–1000	Habitat loss + degradation	Poor
Eastern Curlew (<i>Numenius madagascariensis</i>)	<20 000	Habitat loss + degradation	Poor
Bar-tailed Godwit (<i>Limosa lapponica menzbieri</i>)	150 000–170 000	Habitat loss + degradation	Poor
Great Knot (<i>Calidris tenuirostris</i>)	<250 000	Habitat loss + degradation	Poor
Curlew Sandpiper (<i>Calidris ferruginea</i>)	50 000–100 000	Habitat loss + degradation	Poor
Swift Parrot (<i>Lathamus discolor</i>)	2000	Habitat loss + introduced predator	Poor
Western Ground Parrot (<i>Pezoporus flaviventris</i>)	<100	Habitat loss + degradation	Poor
Orange-bellied Parrot (<i>Neophema chrysogaster</i>)	20–40	Habitat loss + introduced predator	Poor
Grey Range Thick-billed Grasswren (<i>Amytornis modestus obscurior</i>)	10	Habitat loss + degradation	Poor
Regent Honeyeater (<i>Anthochaera phrygia</i>)	300–350	Habitat loss + degradation	Poor
Helmeted Honeyeater (<i>Lichenostomus melanops cassidix</i>)	<100	Habitat loss	Moderate
Capricorn Yellow Chat (<i>Epthianura crocea macgregori</i>)	200–300	Habitat loss + degradation	Poor
King Island Scrubtit (<i>Acanthornis magnus greenianus</i>)	<50	Habitat loss + degradation	Poor

make these taxa least susceptible to a habitat selection CAE.

Mate-finding, mate choice and facilitation

Selection of a high-quality mate is central to maximizing individual fitness (Andersson 1994), but finding or choosing between potential mates can be limited in species that have become anthropogenically rare, sparsely distributed (Veit and Lewis 1996; Gascoigne *et al.* 2009; Berec *et al.* 2017), or in which the operational sex ratio (OSR; the local ratio of fertile females to sexually active males) has become biased (Clout *et al.* 2002; Donald 2007). Dispersal in birds is typically female-biased (Dale 2001), which at low densities or in small populations may cause females to become lost to the effective population, if potential mates are distributed sparsely across large areas. High female mortality can also lead to an OSR bias (Ewen *et al.* 2001). A mate-finding CAE can be exacerbated if unpaired males disturb breeding pairs by attempting to steal mates (Goodburn 1984), harassing females (Ewen *et al.* 2011) or increasing nest exposure to predators (Taylor *et al.* 2001). Species can avoid a mate-finding CAE by evolving strategies to enable the location of mates at low densities (Berec *et al.* 2017), or by avoiding low population density during breeding via aggregative nesting (Gascoigne *et al.* 2009). If species that adopt avoidance strategies *do* find themselves at low densities, however, their ability to find mates and recover from low densities can be severely limited (Gascoigne *et al.* 2009; Berec *et al.* 2017). Component Allee effects can also occur if individuals do not nest or have low reproductive success through the poor quality of available mates in small populations (Møller and Legendre 2001). Many social species also require the

presence of conspecifics to initiate breeding, which limits reproduction at low density via a ‘facilitation’ CAE (Stephens and Sutherland 1999).

Species that have low breeding philopatry within a large breeding range, nest in aggregations and have high dispersal should be susceptible to a mate-finding CAE. Regent Honeyeaters should therefore be most at risk from a mate-finding CAE. Species with monogamous breeding strategies that have a male-biased sex ratio should also be susceptible to a mate-finding CAE (Shaw *et al.* 2017). Evidence from Orange-bellied Parrots (4 males per female; Stojanovic *et al.* *in review*), Swift Parrots (estimated 2 males per female; D. Stojanovic unpub.), Regent Honeyeaters (1.4 males per female; R. Crates *in review*), Curlew Sandpipers and Bar-tailed Godwits (Nebel 2007) suggests that these species should all be susceptible to a mate-finding CAE through a male-biased OSR. Low breeding participation in Orange-bellied Parrots may be due to the poor quality of potential mates (Holdsworth *et al.* 2011).

Nesting success

Nesting success can be positively influenced by the size or density of nesting aggregations (Halliday 1980; Redondo 1989). Small or sparse nesting aggregations are less able to defend against predators or competitors through mobbing (Andersson and Wiklund 1978; Oro *et al.* 2006). A nest success CAE may be compounded if predators preferentially target small aggregations (Cuthbert 2002).

Species that build open nests in dense aggregations should therefore be susceptible to a nesting success CAE. Regent Honeyeater nest survival has declined by 30–40% since the 1990s (Crates *et al.* *in review*), at which

time pairs nested in aggregations of 2–11 nests spaced just 40–80 m apart (Geering and French 1998; Oliver *et al.* 1998). In contrast, no monitored Regent Honeyeater nests had >1 pair nesting within 100 m of a focal nest in 2015–2017 (Crates *et al.* *in review*). Eastern Curlews can also nest in aggregations of 2–3 pairs (Del Hoyo *et al.* 1992), which may assist nest defence against Corvids (Gerasimov *et al.* 1997). Although Swift and Orange-bellied Parrots also nest in aggregations (Holdsworth *et al.* 2011; Webb *et al.* 2014), both species nest in hollows, do not defend nests by mobbing predators and are therefore unlikely to be at risk from a nest success CAE.

Dispersal

Dispersal encompasses a range of movements as a three-part process of departure, transience and settlement (Clobert *et al.* 2009). Dispersal decisions are influenced by multiple social, environmental and genetic factors (Pasinelli *et al.* 2004). A dispersal CAE may occur if dispersal is influenced by a collective decision-making (i.e. social) process, with dispersal efficiency (departure time, direction/duration of transience, settlement location) a function of group size (Couzin *et al.* 2005). The ‘many wrongs hypothesis’ proposes that navigation accuracy increases with group size (Simons 2004), as a smaller proportion of informed individuals is required for accurate navigation as group size increases (Couzin *et al.* 2005; Biro *et al.* 2006). Experienced individuals reduce the distance and duration of migratory flights (Mueller *et al.* 2013), so the loss of experienced individuals from flocks should disproportionately affect dispersal efficiency. In addition, highly mobile species typically have less population structure (few or no sub-populations) than more sedentary species (Newton 2006), which means that single, panmictic populations of mobile species have no buffer against a DAE should one become established (Boukal and Berc 2002; Gilroy *et al.* 2012).

Highly mobile species that disperse in flocks should therefore be susceptible to a dispersal CAE. Nomadic species may be particularly susceptible to a dispersal CAE in small flocks, because the location of food resources that they depend upon are highly variable in space and time (Grünbaum and Veit 2003). Of the case taxa, all four shorebirds and both parrots may be susceptible to a dispersal CAE as they migrate in flocks between their breeding and wintering grounds (Del Hoyo *et al.* 1992). Given their semi-nomadic dispersal patterns, Swift Parrots and Regent Honeyeaters may be particularly susceptible to a dispersal CAE with decreasing flock size. Although Herald and Round

Island Petrels are also highly mobile, both species typically undertake solitary movements (Commonwealth of Australia 2015a) and are unlikely to suffer from a dispersal CAE.

Foraging and anti-predation

Flocking or group living are adaptations to increase foraging efficiency and decrease predation risk (Krause and Ruxton 2002). Cooperative species benefit from obligate group living because helpers increase reproductive output or survival via augmentation (Kokko *et al.* 2001). Similarly, interspecific flocking facilitates efficient resource location, higher foraging rates and lower rates of predator vigilance (Sridhar *et al.* 2009). Although species that form obligate cooperative groups or join interspecific flocks are susceptible to foraging or anti-predator CAEs from a reduction in group size (Courchamp and Macdonald 2001), both formations may serve to prevent the emergence of such CAEs. A reduction in group or flock size can be compensated for by immigration or group fusion, thus maintaining high local density despite a reduction in overall population size (Angulo *et al.* 2013). Consequently, birds that form obligate *intraspecific* flocks may be among the most susceptible to a foraging or anti-predation CAE (Gardner 2004; Cresswell and Quinn 2011).

All four shorebird species, but particularly the Great Knot and Curlew Sandpiper, form large flocks during the non-breeding season (Del Hoyo *et al.* 1992) and should therefore be at risk from a foraging/anti-predation CAE. So too should Orange-bellied Parrots, Swift Parrots and Regent Honeyeaters, which all form non-breeding, single-species flocks (Franklin *et al.* 1989; Saunders and Heinsohn 2008). Historically, Regent Honeyeater flocks numbered in the thousands (Geering and French 1998), but contemporary flocks containing more than 10 individuals are extremely rare (BirdLife Australia unpub.). In contrast, the Plains-Wanderer, Grey Range Thick-billed Grasswren and Capricorn Yellow Chat have not evolved to form obligate large flocks (Baker-Gabb *et al.* 1990; Houston *et al.* 2013), resulting in a low risk from a foraging/anti-predation CAE at low population size or density for these taxa.

Interspecific competition

Species that compete for access to common resources are susceptible to a CAE if access to resources depends upon local conspecific density (Connell 1983). For many species that compete for patchy resources (Ford 1979; Ford *et al.* 1993), access is positively correlated with body size (Ford and Paton 1982). Thus, high local conspecific

density of smaller species can facilitate access to rich patches by overcoming the territorial defences of larger competitors (Foster 1985; Dubois *et al.* 2003).

Species that have a relatively small body size within their feeding guild and compete for food resources that are spatially aggregated may therefore be at risk from an interspecific competition CAE with decreasing group size. Regent Honeyeaters should be most susceptible to an interspecific competition CAE, as they compete with multiple larger-bodied species for access to rich nectar patches (Ford 1979; Franklin *et al.* 1989). Historically, Regent Honeyeaters likely overcame their body size disadvantage by 'swamping' larger competitors with many individuals occurring at high density (Ford *et al.* 1993). Assuming that heterospecific competition exceeds conspecific competition, the co-occurrence of many Regent Honeyeaters at rich nectar patches should make displacement by larger competitors uneconomical (Dubois *et al.* 2003), diluting individual displacement and increasing the efficiency of foraging bouts (Ford *et al.* 1993). As the local density of Regent Honeyeaters declines, so too could their foraging efficiency (Kvistad *et al.* 2015).

Genetics

The negative genetic effects of small effective population size on fitness have been widely documented (Allendorf *et al.* 2012). Loss of genetic diversity through inbreeding or genetic drift (Lande 1976) in small effective populations can reduce hatching success (Heber and Briskie 2010), survival (Keller *et al.* 2002) and increase susceptibility to disease (Whiteman *et al.* 2006). For a detailed review of the negative genetic impacts of small effective population size on population growth rates, see Frankham (2005).

Whist by definition all small effective populations may be susceptible to a genetic CAE, Grey Range Thick-billed Grasswrens, King Island Scrubtit, Helmeted Honeyeaters, Orange-bellied and Western Ground Parrots may be most at risk from a genetic CAE given their very small effective populations (Table 2) or limited dispersal capabilities. High incidence of infertility and disease outbreaks in recent years (Peters *et al.* 2014; Stojanovic *et al.* in review) suggests that the Orange-bellied Parrot in particular may suffer from a genetic CAE.

Cultural adaptation, social learning and song-learning

Behavioural plasticity provides an important mechanism for adapting to environmental change,

particularly in long-lived species (Kokko and Sutherland 2001). While many adaptations are acquired through individual experience (Badyaev 2005), the importance of cultural factors in shaping changes to individual behaviour are increasingly apparent (Firth and Sheldon 2015; Firth *et al.* 2015). For example, novel behaviours can be learned through the cultural transmission of information (Aplin *et al.* 2015), which is spread more efficiently in larger groups (Morand-Ferron and Quinn 2011). Bird song is also learned socially in many species (Thorpe 1958; Beecher 2017), and song anomalies can arise in small or sparse populations where isolated individuals have few opportunities to learn accurately songs from conspecifics in early life (Kelley *et al.* 2008). A song-learning CAE may therefore exist in populations of sparsely distributed species, if song anomalies or small vocal repertoires negatively influence mate acquisition or metapopulation dynamics (Laiolo and Tella 2008; Ragheb *et al.* 2015).

Long-lived species that are highly social should be most susceptible to a cultural adaptation CAE at low population size or density. The four shorebirds, both parrots and the Regent Honeyeater should be the case taxa most at risk from a cultural adaptation CAE. Three of the five songbirds (Capricorn Yellow Chat, King Island Scrubtit and Helmeted Honeyeater) have very small ranges, meaning that juveniles of these species are unlikely to be isolated whilst learning songs. In contrast, Regent Honeyeaters are sparsely distributed throughout their vast range and have highly variable vocal repertoires (Veerman 1992; Powys 2010). In some individuals, interspecific song appears to have completely replaced the species' typical song (R. Crates unpub.), which may be caused by a lack of conspecific demonstrators during song-learning (Thorpe 1958). Consequently, the Regent Honeyeater is the sole case species judged to be at risk of a song-learning CAE.

Anthropogenic

An anthropogenic CAE can occur in species of high socio-economic importance if negative human impacts on fitness increase with decreasing population size (Courchamp *et al.* 2006). For species of economic importance (e.g. for the illegal pet trade), negative population growth rates occur as the value (i.e. demand) of species increases as their populations (i.e. supply) decline (Beastall *et al.* 2016; Harris *et al.* 2017). An anthropogenic CAE may also arise through disturbance, as observer pressure increases with species'

rarity (Sekercioglu 2002; Ellenberg *et al.* 2006). Indeed, conservation interventions may themselves inadvertently lead to negative population growth, for example through disease spill-over events from captive to wild sub-populations (Peters *et al.* 2014; Stojanovic *et al.* in review).

Species that have a high profile and are particularly rare or sensitive to disturbance (Blumstein 2006) are at risk from an anthropogenic CAE. In this respect, Orange-bellied Parrots, Eastern Curlews and Regent Honeyeaters should be susceptible to an anthropogenic CAE. Hundreds of observers visit the last remaining breeding site of the Orange-bellied Parrot each year (Commonwealth of Australia 2014). Eastern Curlews are thought to be particularly susceptible to anthropogenic disturbance (Reid and Park 2003; Commonwealth of Australia 2015b), and as one of the most elusive passerines in Australia there is high demand among eco-tourists to observe Regent Honeyeaters. Between 2015 and 2016, 78% of Regent Honeyeater nesting attempts have been in publicly accessible areas (R. Crates unpub.), knowledge of which can potentially spread rapidly through observer networks (Lindenmayer and Scheele 2017). Whilst there is also high demand to observe Plains-Wanderers, the small proportion of the population at risk from anthropogenic disturbance makes an anthropogenic CAE in the Plains-Wanderer unlikely.

Likelihood of multiple CAEs

Although populations become susceptible to an increasing number of CAEs, and hence a DAE, as their size or density decreases (Berec *et al.* 2007; Table 3) there remains relatively sparse empirical evidence of multiple CAEs affecting the population growth rates of threatened species (but see Serrano *et al.* 2005; Berec *et al.* 2007): a likely consequence of the challenge of detecting multiple Allee effects in such populations (Gilroy *et al.* 2012). Nonetheless, many potential CAEs could operate together in a complex and unpredictable fashion, necessitating further management actions to address effectively an Allee-mediated population decline (Berec *et al.* 2007).

The evidence for undetected Allee effects in Australia's critically endangered birds

Our review suggests that the susceptibility of the case taxa to CAEs (and hence a DAE), is highly variable (Table 3). The Round Island/Herald Petrels, Grey Range Thick-billed Grasswren, Helmeted Honeyeater,

Capricorn Yellow Chat and King Island Scrubtit have few traits that make them susceptible to CAEs (Table 3). These taxa are unlikely to suffer from a DAE, supported by the fact that each has persisted at a small population size for a relatively long period. In contrast, the four shorebird and both parrot species exhibit a suite of traits that make them susceptible to a number of CAEs (Table 3). These species have suffered rapid population declines, which may be underpinned by an undetected DAE. However, our review highlights the Regent Honeyeater as the case species most at risk from the greatest number of CAEs, strongly suggesting that this species' decline may be driven by an undetected DAE (Table 3). Regent Honeyeaters have declined at a faster rate than sympatric honeyeater species (Commonwealth of Australia 2016). Despite extensive loss, available habitat suggests that Regent Honeyeaters should occur across large areas of extant woodland (Commonwealth of Australia 2016), implying the species' decline is exacerbated by factors beyond the direct impact of habitat loss (Reed and Dobson 1993).

Implications for conservation

The presence of undetected Allee effects in threatened birds should lead to management actions that (1) address the initial cause of the population decline (Caughley 1994); (2) increase population density; and (3) decrease the negative fitness effects of low population density (Stephens and Sutherland 1999; Deredec and Courchamp 2007). We discuss ways in which potential CAEs, where relevant, could be accounted for in management actions for the case taxa. Given the high susceptibility of the Regent Honeyeater to multiple CAEs (Table 3), we focus in particular on ways in which precautionary conservation actions for the Regent Honeyeater could account for likely undetected Allee effects (Table 4).

Address the declining population paradigm

The declining population paradigm for the case taxa undergoing rapid declines is extensive habitat loss and degradation (Ford *et al.* 2001; Cresswell and Murphy 2017, Table 1). Without habitat restoration, these species will have little chance of long-term population recovery.

Increase local population density

The wild populations of four case taxa (Helmeted and Regent Honeyeater, Plains-Wanderer and Orange-bellied Parrot) are or will soon be supplemented by the introduction of captive-bred birds. To mitigate a DAE, the primary goal of introductions should be to

Table 3. Estimated susceptibility of Australia’s critically endangered bird taxa to undetected component (and hence demographic) Allee effects based on their traits and current population sizes (Table 2). Ticks denote relevance of each trait to the species in the context of each CAE. Shading for each CAE denotes overall estimated susceptibility of each taxon to each CAE (white, not susceptible (0); light grey, moderate susceptibility (1); dark grey, high susceptibility (2)). Each taxon must exhibit all or most traits (ticks present for each) to be considered at risk from each CAE. Overall susceptibility of each taxon to an undetected DAE (bottom row) estimated by summing the risk of each CAE occurring.

CAE	Susceptible traits	Round Island/Herald Petrel	Plains-Wanderer	Eastern Curlew	Bar-tailed Godwit	Great Knot	Curlew Sandpiper	Swift Parrot	Western Ground Parrot	Orange-bellied Parrot	Grey Range Thick-billed Grasswren	Regent Honeyeater	Helmeted Honeyeater	Capricorn Yellow Chat	King Island Scrubtt
Habitat selection	Low philopatry	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Large range	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	High conspecific attraction	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Mate-finding	High/female-biased dispersal	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Large breeding range	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Sparse distribution	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Historically common	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Aggregative nesting	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Mate choice	Socially monogamous	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Facilitation	Male-biased operational sex ratio	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Nest success	Aggregative nesting	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Breeding influenced by conspecifics	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Dispersal	Aggregative/colonial nesting	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Open nesting	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	High mobility	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Dispersal in flocks	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	High variability in food resources	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Low population structure	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Foraging/anti-predation	Large range/sparse distribution	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Group feeding	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Interspecific competition	Obligate intraspecific flocking	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Genetics	Spatial aggregation of food resources	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Small population size	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Cultural adaptation/social learning	Small geographic range	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Song-learning	Low dispersal	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	High sociality	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Long generation time	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	High juvenile dispersal	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Anthropogenic	Close-ended song-learning	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Sparse distribution	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	High species profile (demand)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	High 'observability' when nesting	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Estimated overall susceptibility to a DAE	High susceptibility to disturbance	1	2	8	6	7	8	11	2	12	2	18	2	2	2

maximise local population density (Stephens and Sutherland 1999), which can be achieved by introducing captive-bred birds in the core range, where the majority of wild birds persist. Maximising local population density using introductions should assist wild birds in overcoming potential CAEs relating to interspecific competition and foraging/anti-predation (Table 2). Captive-bred birds often lack socially-acquired knowledge (Caro 1999, 2005) which, in combination with small group size, can inhibit the success of introductions (Fischer and Lindenmayer 2000). Maximising population density can facilitate interactions between wild and captive-bred birds to aid the cultural transmission of information from wild to captive-bred conspecifics (cultural adaptation CAE). The social acquisition of ‘wild knowledge’ may be critical for the survival and successful breeding of naïve, captive-bred birds.

The likelihood of a DAE should also influence the size and procedure of introductions (Deredec and Courchamp 2007; Armstrong and Wittmer 2011). In highly dispersive species such as the Orange-bellied Parrot and Regent Honeyeater, the ‘minimum founding population’ may be substantially larger than the size of introduced groups (Goodsman and Lewis 2016), reducing the benefits of releasing large groups. To maximise breeding density in dispersive species, captive releases should therefore occur either as close to the start of the breeding season as possible, where and when wild birds are present (Table 4).

For species with high conspecific attraction, actions that improve the reliability of habitat cues and encourage settlement in optimal habitat may also be possible (Reed and Dobson 1993; Stodala and Ward 2017). Decoys and acoustic lures can attract birds to settle in optimal habitat where risks can be most effectively managed (Jeffries and Brunton 2001). The targeted release of captive Regent Honeyeaters and Orange-bellied Parrots in optimal breeding habitat (where the abundance of natural food sources is highest) could also attract wild birds and assist them in overcoming habitat selection or interspecific competition CAEs. A mate-finding CAE due to a male-biased sex ratio could be accounted for by introducing proportionally more females, or by temporally segregating captive releases by sex (Wedekind 2002). Recently, the release of female Orange-bellied Parrots has allowed previously unpaired wild males to breed (Stojanovic *et al.* in review). A similar strategy could prove equally effective for Regent Honeyeaters (Table 4).

Decrease the fitness costs of low population density

For taxa at risk of a genetic CAE (e.g. King Island Scrubtit, Capricorn Yellow Chat), the translocation of

individuals amongst isolated sub-populations could facilitate gene flow and reduce the negative genetic effects of small effective population size (Webb *et al.* 2016). For small effective populations lacking population structure (e.g. Helmeted Honeyeater), the introduction of genes from sister taxa could aid genetic rescue (Harrisson *et al.* 2016). For species that may suffer from a nesting success CAE, the implementation of nest protection measures and predator suppression could increase nesting success in small or sparse aggregations (Fulton and Ford 2001; Major *et al.* 2014; Table 4). Careful management of tourists at breeding or wintering sites should overcome potential anthropogenic CAEs.

Conclusion

Allee effects present a major challenge for conservation, because their probability of occurrence and impact on population growth rates may be greatest in the rare and declining species in which they are hardest to detect and overcome. This challenge could explain the lack of empirical evidence for DAEs in threatened species (Kramer *et al.* 2009; Gregory *et al.* 2010). An inability to test for the existence of a DAE in the majority of threatened species is an unavoidable consequence of a lack of comprehensive contemporary and historical population data (Franklin *et al.* 1989; Table 2). Nonetheless, a growing literature can be used to critically evaluate the range of potential CAEs that could lead to a DAE, as well as traits that make species susceptible to each (Tables 1 and 3). Given monitoring constraints (Crates *et al.* 2017) and a race against time (Gilroy *et al.* 2012), adopting a precautionary approach currently offers the most effective means of attempting to eliminate or reduce the strength of Allee effects in threatened bird populations (Cooney 2004; Courchamp *et al.* 2008). Although general, our approach could be used to assess the relative susceptibility of any data-deficient taxa to undetected Allee effects, prioritising early intervention for those deemed most at risk (Drake and Griffen 2010).

Managers must ask three questions to address a potential undetected DAE:

- (1) By which means and over what time scale could a DAE be proven to exist?
- (2) How would the presence of an undetected DAE influence management actions?
- (3) Should a DAE not exist, would accounting for it compromise viability of the target population or success of current management actions?

For example, despite being most at risk from a DAE, we argue that it would not be possible to detect a DAE

Table 4. Potential undetected component Allee effects in the Regent Honeyeater and management options for accounting for their presence based on the precautionary principle

Component Allee effect	Management options to reduce fitness effects at low population size/density
Interspecific competition	Reduce local density of competitors via targeted control Release captive-bred birds in core range when a wild birds are present Increase availability of feeding habitat via habitat restoration Exclude larger competitors by selective caging of critical food resources/supplementary food Increase competitiveness of captive birds by exposing them to competition in captivity
Habitat selection	Release captive birds in high-quality breeding habitat shortly before breeding commences Increase availability of breeding habitat via habitat restoration Use decoys/song broadcast to attract conspecifics to high-quality habitat
Mate-finding	Targeted release of captive-bred females at breeding aggregations with a male-biased sex ratio Release captive-bred birds in core range during early breeding season where wild birds are present Facilitate mate-finding using artificial social cues such as song broadcast
Mate choice/facilitation	Release captive-bred birds in core range when and where wild birds are present Ensure high phenotypic quality of captive breeding stock
Nesting success	Employ nest protection measures such as tree guards, branch collars and nest cages Targeted control or translocation of known nest predators at breeding sites Increase size of breeding habitat patches via habitat restoration
Dispersal	Ensure captive-bred birds interact with wild conspecifics to maximise flock size/group knowledge Increase size and abundance of suitable habitat patches via habitat restoration
Foraging/anti-predation	Maximise flock size by releasing captive-bred birds in core range when wild birds are present Targeted control of predators
Genetics	Ensure genetic integrity of captive stock Maximise mate choice by releasing captive-bred birds in the core range Facilitate gene flow by translocating individuals between regional sub-populations
Cultural adaptation, social learning and song-learning	Release captive-bred birds in core range when and where wild birds are present Ensure interaction of captive-bred birds with wild birds during song-learning Use playback or demonstrator individuals to ensure captive birds have full vocal repertoire
Anthropogenic	Limit human disturbance during breeding by restricting access to breeding areas

in the Regent Honeyeater population in a timescale that would not inhibit the success of recovery actions, should a DAE indeed exist. The presence of an undetected DAE should lead to alterations to current management, as multiple, potentially interacting CAEs could be accounted for by adapting existing actions and employing a small number of new management strategies (Table 4). Given an ongoing population decline despite two decades of recovery effort (Oliver and Lollback 2010), adopting a precautionary approach to account for an undetected DAE in the Regent Honeyeater is unlikely to impede the success of current management actions. Indeed, the Regent Honeyeater population may have already passed the Allee threshold, in which case urgent and intensive population management is required to prevent extinction (Courchamp *et al.* 2008).

We urge conservationists to explicitly consider the potential for undetected Allee effects to influence negatively the population growth rates of threatened species, and to critically assess how management actions could be targeted accordingly. By adopting a precautionary approach, an inability to detect Allee effects in threatened species need not preclude efforts to account for their potential presence in management. Such actions are urgently needed if Regent Honeyeaters, and many species alike, are not to follow the course of the Passenger Pigeon and Paradise Parrot into oblivion.

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