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Monitoring threats to Australian threatened birds: climate change was the biggest threat in 2020 with minimal progress on its management

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ABSTRACT
Most biodiversity monitoring globally tends to concentrate on trends in species' populations and ranges rather than on threats and their management. Here we review the estimated impact of threats and the extent to which their management is understood and implemented for all threats to all Australian threatened bird taxa. The assessment reports the situation in 2020 and how this differs from 2010. The most marked finding was that the impact of climate change has increased greatly over the last decade, and now surpasses invasive species as the threat imposing the heaviest threat load. Climate change has driven recent massive population declines from increased temperatures in tropical montane rainforests and from fire. For both direct climate change impacts and fire management, progress in understanding how to relieve the threats has been slow and patchy. Consequently, little effective management has occurred. By comparison, our analysis showed that the single successful campaign to eradicate introduced mammals from Macquarie Island relieved the total threat load on Australian threatened birds by 5%, and more than halved the load on the birds from oceanic islands. Protection or rehabilitation of habitat, particularly on islands, has also delivered measurable benefit as have, in the longer term, controls on longline fishing. Our approach can be used with other taxonomic groups to understand progress in research and management and to allow quantification of potential benefits from proposed actions, such as the national threatened species plan.

POLICY IMPLICATIONS

- Climate change is now the biggest threat to Australian threatened birds, but almost no research or management to mitigate this threat has been undertaken.
- Most successful threatened species management has been on small islands with invasive species eradication, habitat protection and restoration providing substantial benefits.
- The approach taken can be used to quantify the benefits of both past conservation interventions and potential interventions.
- Monitoring trends in threat load complements indices assessing trends in population size and extinction risk.

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Introduction

The focus of most threatened species monitoring is on the species themselves (Woinarski 2018; Verdon *et al.* 2024). Calculating trends in population size and range then allows estimation of extinction risk, which in turn can be used to calculate change in the International Union for Conservation of Nature's (IUCN) Red List Index (Butchart et al. 2004, 2007). This provides a measure of global or national performance in threatened species management over medium to long time frames, which has happened for Australian birds (Szabo *et al.* 2012; Berryman *et al.* 2024). At shorter timescales, population counts for species and species-groups with adequate monitoring can be incorporated into reporting

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tools such as the annual Threatened Species Index (Bayraktarov *et al.* 2021b). However, useful as such indices are, they are insufficiently detailed to allow targeted investment to influence the population trends they describe (Bayraktarov *et al.* 2021a). For the strategic planning needed to reduce extinction risk, there needs to be information not only on species population trends but also on trends in the threats they face, how to manage those threats and the extent to which that knowledge is being applied successfully to ameliorate those threats (Balmford *et al.* 2005).

One approach, which has been applied to Australian threatened birds (Garnett *et al.* 2019), is to quantify, for each taxon, the estimated individual impacts of all possible threats, and aggregate this information using a set of metrics that are standardised across all taxa, building on existing processes and metrics developed by the IUCN (2012b) and the Royal Society for the Protection of Birds (2017). In Garnett *et al.* (2019), an attempt was made to capture the current state of knowledge about, and management of, each threat so that the status of threat management of each species and the impacts of each threat across multiple species could be assessed on a consistent scale. However, while Garnett *et al.* (2019) provided a status report across all Australian birds considered threatened and Near Threatened at the time, a revised dataset was assembled for the preparation of threatened species accounts in Garnett and Baker (2021). This provides an opportunity not only to compare the existing state with a hypothetical (counterfactual) scenario of what might have happened to threats or species had there never been conservation action (Garnett *et al.* 2019), but also to use the same process to track changes in threat impact, research and management since the last Action Plan in 2010 (Garnett *et al.* 2011).

Analysing trend data on individual species, or groups of species, subject to specific threats and management actions, can make it possible to determine which species and threats are understood and responding to management and which need greater investment (in either threat management and/or research) to reduce extinction risk (Tulloch *et al.* 2023). Importantly, monitoring data must be at an appropriate timescale to enable some form of objective comparison between before and after management (Prowse *et al.* 2021). Collecting monitoring data at time frames that are too short runs the risk of being uninformative to management, or, worse still, providing information that directs allocation of management resources towards management actions that harm rather than recover species (Tulloch *et al.* 2013). This is because responses of species to some management actions occur at timescales of decades rather than months or years, and over short timescales the effects of management are too small to be detected (Maxwell and Jennings 2005; Tulloch *et al.* 2013). Analyses of threat impacts also make it possible to understand which threats need to be managed for extended time frames, and which can be contained more rapidly.

Our analysis for Australian threatened birds over the period of 2010 to 2020 has three aims:

- determine the threats that pose the greatest risk across all taxa and their trends;
- identify factors that have driven changes in threat impact, research and management;
- identify the threats to threatened bird taxa having the highest impact and most in need of research and management.

Methods

Data

Taxa and populations

All Australian bird taxa were assessed at the finest taxonomic level possible; that is, at species level for monotypic species and subspecies for polytypic species (ultrataxa *sensu* Schodde and Mason 1999). The taxonomy followed BirdLife Australia (2022), itself a reflection of BirdLife International (2022), except for a few subspecies that have historically been of conservation concern and for which the taxonomic status is still being assessed (see Table S1). Populations of seabird taxa breeding in Australia were assessed separately from populations of the same taxon visiting from breeding sites outside Australian territory. Of the 1271 extant ultrataxa regularly occurring in Australia, 232 were selected for analysis comprising those currently considered threatened, and those retrospectively considered threatened in 2010, but are no longer.

Geographic scope and extinction risk

The taxa selected for analysis occur regularly within Australian territory, including the islands within the Exclusive Economic Zone (EEZ). For taxa threatened outside Australian territory, including 49 taxa that breed outside Australian territory and 15 taxa that breed inside (9 taxa have populations that breed inside and outside), threat analysis was conducted separately for areas inside Australian territory, where Australian governments can exert control, and areas outside Australia where threat management must be negotiated with foreign entities.

Extinction risk of all taxa and breeding populations of seabirds was quantified using the IUCN extinction risk categories and criteria (IUCN 2001) and was the same as those in the accounts within Garnett and Baker (2021) unless subsequently updated by the BirdLife Australia

Threatened Species Committee (see Berryman *et al.* this issue). Lower categories of status were applied where there was thought to be substantial genetic mixing with populations outside the country, in accordance with IUCN Red List guidelines (e.g. Endangered species might be listed as Vulnerable if replenishment from Least Concern populations was thought likely; IUCN 2012a). The status of taxa in 2010 was assessed retrospectively in 2020 based on new knowledge acquired since that date, as is standard practice for calculating the Red List Index (Butchart *et al.* 2004).

Threats

Threats were defined as causes of mortality that caused a net population decline. All possible threats to birds were first listed at the finest possible level using the IUCN threat taxonomy (IUCN 2013) during preparation of texts in Garnett and Baker (2021) by 263 authorities on extant imperilled birds based on their experience and knowledge of the relevant literature (see Table S2 to individual citations). For example, threats from mining were classified according to the principal ore or other material mined and threats from invasive species, both native and alien, were categorised by the invasive species of concern. Threats from nest hollow competition were classified according to the threat from each of the principal hollow competitor species. For analysis, these 201 individual threats were aggregated using the threat classification of Kearney *et al.* (2023): habitat destruction and degradation (47 individual threat types), biological resource use (13 types), altered fire regimes (3 types), invasive species (114 types), pollution (9 types), climate change (9 types) and other (6 types) (see Table S3).

For each threat, threat impact was classified as very low, low, moderate, high or very high in each of the texts in Garnett and Baker (2021). This classification was derived from application of the methodology of IUCN (2012b), as adapted by Garnett *et al.* (2019; see Table S4) which involved estimation of three metrics:

(i) the timing of the threat (ongoing; in the past and unlikely to return in either one generation/3 years; in the past and unlikely to return in either 2–3 generations/4–10 years, whichever is the longer; only one generation/3 years in the future; only 2–3 generations/4–10 years in the future).
(ii) scope (affects whole population [>90%]; the majority of the population [50–90%]; a minority of the population [1–50%]; a trivial proportion [<1%].
(iii) severity (causing or likely to cause extremely rapid declines where the threat applies [>50% over 10 years or three generations, whichever is the longer]; rapid declines [30–49% over the same time period], significant declines [20–29%], slow but significant declines [1–19%], negligible declines [<1%] and causing/could cause fluctuations).

Threat impact was weighted for impact severity based on Garnett *et al.* (2019; see Table S4), noting that confidence in the information on threat impact varied greatly (see texts in Garnett and Baker 2021).

Impact was assessed for two time periods: (i) 2020 at the time the reports in Garnett and Baker (2021) were prepared; and (ii) 2010 based on Garnett *et al.* (2019), updated with new information assembled for Garnett and Baker (2021). The potential threat impact was also assessed under the counterfactual assumption that no conservation management of the threat had been undertaken (Ferraro *et al.* 2006; Ferraro 2009) since 1900, approximately the date that the first ornithological organisations were established in Australia, extending and updating the same assessment from Garnett *et al.* (2019).

Metrics

Threat impact

Three metrics related to estimated threat impact were calculated for each taxon (Table 1):

(i) Threat impact in 2020.
(ii) Change in threat impact 2010–2020. Following Garnett *et al.* (2019), the weighted value for threat impact was summed across threats, threat classes, individual taxa or species groups with the sum of threat impacts being the threat load for that threat, entity or group. Changes in threat impact, or threat load where impact scores had been summed, were calculated by subtracting scores for one time period from those of another.
(iii) Percent of threat impact relieved by 2020. As in Garnett *et al.* (2019), the percentage difference between the potential threat and the realised threat was also calculated for each taxon for each threat as well as for aggregated data for threats and taxa to determine the percentage of the potential taxon threat load relieved by 2020 ('Percent Threat Reduction' in Garnett *et al.* 2019). A percentage difference between time periods could not be calculated for all taxa because some were newly listed as threatened (e.g. those affected by fires in 2019–2020; Legge *et al.* 2022a) meaning the denominator would be zero.

Table 1. Metrics related to the impact of threats on Australian threatened birds, knowledge of how to manage those threats and the management being implemented.

Metrics for analysis	Calculation method	Characteristics
Threat impact in 2020	Weighted impact based on timing, scope and extent of threat to a taxon (IUCN 2012a; Garnett *et al.* 2018)	For individual threats: 0 (negligible threats causing negligible declines) to 63 (causing very rapid declines across whole range). Can be summed across threats or taxa to estimate total threat load.
Change in threat impact 2010–2020	The difference between the threat impact or threat load in 2010 and that in 2020	Can be negative or positive, unbounded
% of threat impact relieved by 2020	Threat impact/load at a particular time as a percentage of the potential threat impact	0–100%
Knowledge available in 2020	For individual threats: knowledge score (7 levels, scale 0–1; see Garnett *et al.* 2018) x threat impact score	0–63. Can be summed across threats or taxa. Can be summed across taxa or threats to calculate a knowledge score
Change in knowledge availability 2010–2020	The difference between the knowledge score in 2010 and that in 2020	Only positive, assumes knowledge cannot be lost but earlier knowledge scores can be reduced in later assessments
% of knowledge need met by 2020	Knowledge available at a particular time as a percentage of the ideal knowledge for that threat/taxon.	0–100%
Management undertaken in 2020	For individual threats: management score (7 levels, scale 0—1; see Garnett *et al.* 2018) x threat impact score	0–63. Can be summed across threats or taxa. Can be summed across taxa or threats to calculate a management score
Change in management 2010–2020	The difference between the management score in 2010 and that in 2020	Can be positive or negative (i.e. management quality can decline between assessments)
% of management need met by 2020	Management at a particular time as a percentage of the ideal management for that threat/taxon	0–100%

Research and management progress

Similarly, three metrics were also calculated to represent research progress towards understanding how to manage a threat (Table 1): (i) knowledge available in 2020; (ii) change in knowledge availability 2010–2020; and (iii) percent of knowledge need met by 2020. An additional three metrics (Table 1) were calculated representing progress towards effective management of each threat: (i) management undertaken in 2020; (ii) change in management 2010–2020; and (iii) percent of management need met by 2020. As in Garnett *et al.* (2019), scores for all six metrics were based on a set of criteria on a 7-point scale but slightly altered to remove ambiguity (Table S5). They cover the range of understanding and the implementation of research and management from none through to an ideal state. For research, an ideal state was where best practice management was theoretically available *and* had been tested in practice and found to be effective at ameliorating the threat to that taxon at a scale appropriate to the threat and population. For management, the highest score for a threat to a taxon was when effective threat management is being applied so successfully that a threat, as it applies to that taxon, now needs only monitoring and the minimum amount of ongoing management possible (e.g. quarantine for islands where cats have been eradicated; high quality, ecosystem-specific fire management). As with threat impact, scores generated for individual threats as they apply to individual taxa were summed across threats or taxa, or groups of threats or taxa to allow comparisons (Garnett *et al.* 2019). Scores were calculated for 2020, the difference between 2020 and 2010, and between the scores for each of the years and the potential maximum possible if all threats are completely known and managed to the highest standard possible.

Analyses

Generalised linear models (GLMs) were used to examine the effect of 16 predictor variables (see Garnett *et al.* 2019; Table S6 for details and data sources) on each of the 9 metrics (Table 1) for taxa within Australian boundaries. Continuous variables included: (i) population size (log transformed estimated number of mature individuals); (ii) range (log transformed area of occupancy); (iii) generation time; (iv) monitoring score (range 0–100; see Verdon *et al.* 2024); (v) detectability (range 0–10; Table S7); (vi) site accessibility (range 0–10; Table S7); (vii) natural variability in population size over time (range 0–10; Table S7); (viii) weight (log transformed); and (ix) taxonomic distinctiveness (range 2.9–53.7). Categorical variables included: (x) whether a taxon had a Recovery Plan/ Wildlife Management Plan; (xi) whether a taxon had a Conservation Advice (a synopsis of existing information that is usually more succinct than a full recovery plan) before 2015; (xii) extinction risk (IUCN Red List status) in 2020; (xiii) whether a taxon was listed as threatened under the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act); (xiv) geography (i.e. whether a taxon is confined to oceanic or continental islands, is solely marine when in Australian territory or also occurs on the Australian continent); (xv) taxon group (i.e. seabirds, shorebirds, parrots, passerines or other); and (xvi) taxon rank (i.e. whether a taxon is a species or subspecies). The same methods were used to analyse taxa outside Australian boundaries using a subset of six of these predictor variables that had a diversity of values and were independent of political geography: population size, range, generation time, weight, extinction risk and taxon rank. Few populations of Australian taxa are monitored while outside Australia and there was little variation in the scores for detectability, site accessibility, natural population variability, geography or taxon group and whether a taxon had a Recovery Plan/ Wildlife Management Plan, a Conservation Advice or was listed as threatened under EPBC Act would only be expected to have an impact within Australian territory.

We tested for collinearity in the 16 predictors (for taxa within Australian boundaries) and the 6 predictors (for taxa outside Australian boundaries), removing predictors that were highly collinear with other variables of interest. We compared Pearson's correlation coefficients and variance inflation factor (VIF) values using two pre-selected thresholds of < 0.7 and 10 respectively, as per Zuur *et al.* (2010). This led to the removal of weight (from both sets of models) and geography from the models for taxa inside Australian boundaries (Figures S1 and S2, Tables S8 and S9). We then ran a total of 147,744 models (147,456 models and 288 models for taxa within and outside Australian boundaries respectively) representing all possible combinations of predictor variables for each of the 9 response variables (metrics). We used a second-order form of Akaike's Information Criterion (AICc) (Burnham and Anderson 2002) suitable for small sample sizes to rank and identify candidate sets of models (18 sets, representing the 9 metrics within and outside Australian boundaries) within 2 Akaike units of the top ranked model, as models more than 2 units away have less support for explaining the patterns in the data (Burnham and Anderson 2002). We then applied model averaging to the candidate sets to obtain final outputs for further inference. All analyses were conducted in R Version 4.2.1 using the '*lme4*' package (Bates *et al.* 2015) (R script can be provided on request).

To understand the relationship between threat load, knowledge and management, we correlated the potential threat load relieved by 2020 with the percentage knowledge need and management need met using Spearman's Rank-Order Correlation, first normalising all scores to 100.

To understand whether threat load, knowledge availability and management response was related to a taxon's extinction risk, we used a Kruskal-Wallis test to compare the change in IUCN Red List status in any decadal period since 1990 based on retrospective assessments of status in Garnett and Baker (2021) (negative, positive, none) with the threat load and the taxon scores for understanding and management in 2020.

Results

Threat impact status and trends

Across all taxa/populations considered, there were 201 separate threats with an average of 5.3 threats per taxon (see Table S10 and S11). Only 10 taxa were considered to be facing only a single threat whereas the South-eastern Glossy Black-Cockatoo *Calyptorhynchus lathami lathami* was facing 20 threats, the most of any taxon. The 1427 taxon-specific threats represent 4281 opportunities for management to have affected threat timing, extent or severity.

A total of 169 taxa faced threats only inside Australia, 20 did so only outside Australia and 35 taxa faced threats in both. Overall, 80% of the total threat load – the sum of all threat impact scores across all taxa – was for taxa while they are within Australian borders with the remaining 20% affecting birds while they are outside Australian territorial boundaries. There was little change in the total threat load to all species from 2010 to 2020 but the realised total threat load was less than the potential threat load, indicating some management success. Within Australia, the threat load in 2020 was 74.0% of the potential threat load, an improvement of just 0.4% since 2010. Outside Australian borders the threat load was 84.6% of the total potential threat load, an increase in total threat load of 1.4% since 2010.

Within Australia, the greatest threats to birds are now from climate change for which the threat load has increased from 17.3% of the total threat load in 2010 to 20.8% in 2020 (now 34% of the threat load within Australia alone). In contrast, the total threat load within Australia from the threat class having the greatest impact in 2010, invasive species, declined from 18.5% to 14.4% over the same period (Figure 1). Of the other major threat classes affecting Australian threatened birds, there was a slight reduction in the threat load from habitat destruction and degradation (12.8 to 11.8%; the result of some habitat restoration for highly threatened taxa on small islands; see Table S10) but an increase in the threat load from altered fire regimes (10.1% to 11.6%).

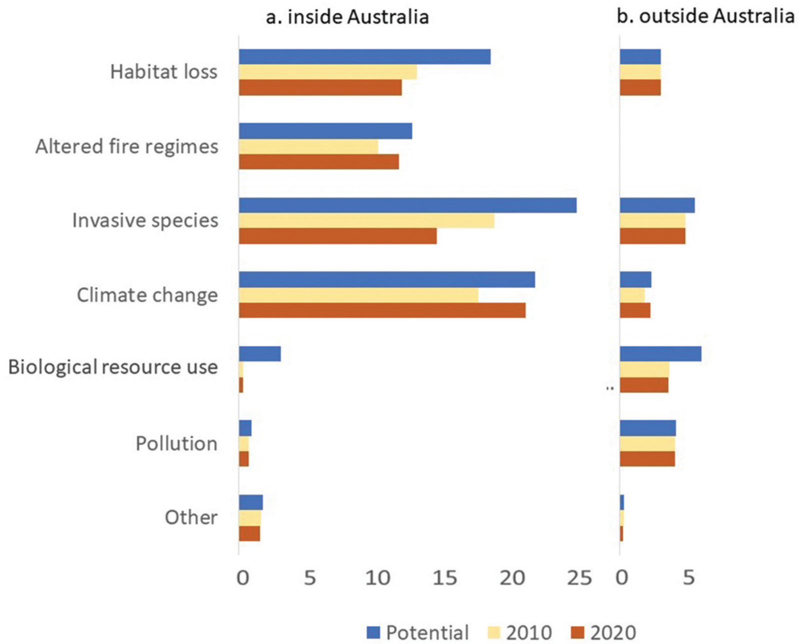

Figure 1. The total potential threat load to Australian threatened and Near Threatened birds inside and outside Australian territory and the realised threat load in 2010 and 2020 for 6 classes of threat (all scores normalised to 100 against total threat load across all taxa/populations; threat classes follow Kearney *et al*. (2023; see Table S3 for how fine-scale threats are condensed into these broader threat classes).

Outside Australia, invasive species have been exerting the greatest pressure, with 26.5% of the threat load on taxa when outside Australia. Pollution (22.2% of the threat load on taxa when outside Australia), biological resource use (20.8%) and habitat loss (16.5%) were also important, with pollution and biological resource use having much greater relative impacts on birds outside Australia than inside (0.7% and 0.3%, respectively, of the threat load in 2020 inside Australia). Climate change currently ranks fifth among the major threat classes outside Australian territory (12.7%) but was the only one in which the threat impact changed by > 2%, its impact increasing by 23% since 2010. Whereas altered fire regimes were responsible for a substantial threat load within Australia, none of the assessed birds were considered threatened by fire when outside Australia.

Research

Research progress and needs

Research had contributed to understanding how to manage 57% of threats to taxa/populations in 2010 and 70% in 2020, leaving 25% of threats to taxa/populations with no formal knowledge on how to manage them in 2020. For 15% of taxon-specific threats, tested best practice management was available for implementation in 2010, rising to 20% by 2020 (Figure 2(a)). The percentage of taxon-specific threats with management trials having either started, looking promising or being successful, also rose between 2010 and 2020, from 26% to 36%.

Within Australia, knowledge need in 2020 was greatest for climate change, which made up nearly half the total need (48% of the total need across all threats) followed by fire management (20%) and invasive species (18%; Figure 2(b)). Knowledge of how to reduce threat impacts was proportionately greatest for biological resource use (81% of the total need for the threat class), habitat loss and degradation (76%) and invasive species (68%) but by far the lowest for climate change (3%). Improvements in knowledge between 2010 and 2020 were greatest for invasive species (improvement of 26%) and for the 15 taxa affected by ‘other threats’ (21%); for 10 of these taxa, low genetic variability is a threat but knowledge of how to manage it, negligible in 2010 (0.6% of total need for the threat), increased to 52% in 2020 (see Table S10). Knowledge of how to manage climate change increased by just 1.4% over the same period.

Outside Australia, knowledge needs were fairly similar across invasive species (28% of the total threat load in 2020 to taxa outside Australia), pollution (21%), habitat loss and degradation (19%), climate change (16%) and biological resource use (15%; Figure 2(c)). Of these, knowledge of how to manage threats was greatest for biological resource use (70% of knowledge need met in

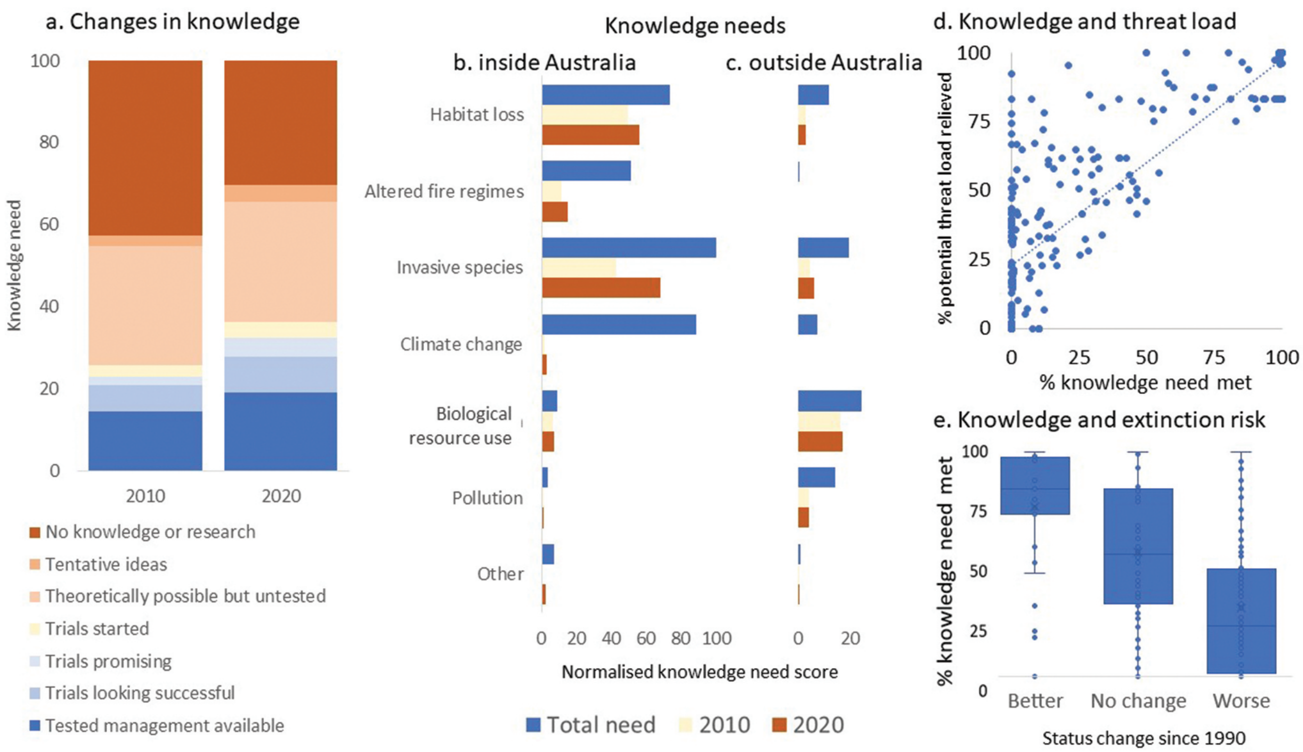

Figure 2. Trends in knowledge of how to manage threats to Australian threatened and Near Threatened birds: (a) % knowledge needs met in 2010 and 2020; comparison between the total estimated current need for knowledge of how to manage threats and that available in 2010 and 2020; (b) in Australia; (c) outside Australia; (d) relationship between % of knowledge need and % threat load relieved; (e) relationship between % knowledge need met and change in extinction risk (International Union for Conservation of Nature's Red List category) in any decade since 1990.

2020), more than twice the level of any other threat class but the only threat class for which knowledge improved from 2010 to 2020 by > 5% was invasive species (7%, from 24% of need in 2010 to 31% in 2020).

Across all taxa there was a moderate correlation between the percentage knowledge need met and the percentage of potential threat load relieved by 2020 (Figure 2(d); $R^2 = 0.667$). Understanding of threats to taxa for which extinction risk declined in at least one of the three decades from 1990 to 2020 was much higher than for either those where IUCN Red List status remained the same or were uplisted to a higher extinction risk category (Kruskal-Wallis $\chi^2 = 205.4$, df = 156, $P = 0.005$, Figure 2(e)).

Management

There was at least some level of management (i.e. scores of 1–6) of 29% of the threats to taxa/populations in 2010 and 41% in 2020. For just 3% of the taxon-specific threats, threat management in 2010 had successfully reduced the impact to a state where only monitoring and passive management was required to alleviate its impact. This figure had doubled to 6% by 2020 (Figure 3(a)). While invasive species continue to have the greatest need for management within Australia, this was also the threat class where management improved most over the period 2010 to 2020 (Figure 3(b)). There was also a slight amelioration of threat load related to habitat destruction and degradation (8% better than 2010). However, this improvement was almost entirely due to improvements for highly threatened taxa on oceanic islands; on mainland Australia, threat load related to habitat destruction and degradation remained unchanged for all but one of the 77 taxa affected (Southern Cassowary *Casuarius casuarius* for which it is now > 3 generations since its habitat was last subjected to large scale clearance). As with research needs, the gap between the need for effective management and its application was greatest for fire management and climate change. Outside Australia, biological resource use has the greatest management need, although that is also where there has been greatest progress (Figure 3(c)).

Across all taxa there was a moderate correlation between the percentage of management need met and the percentage of potential threat load relieved by 2020 (Figure 3(d); $R^2 = 0.7505$). For taxa with more

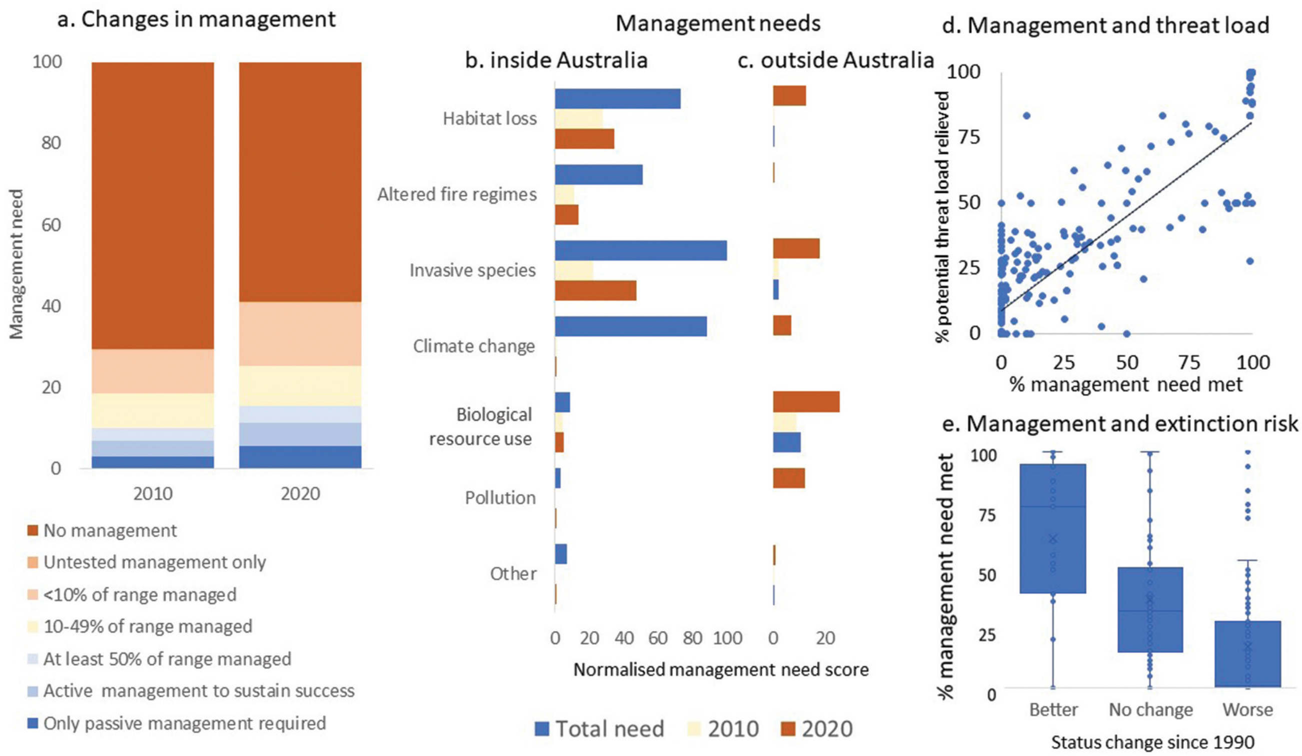

Figure 3. Management trends for Australian threatened and Near Threatened birds: (a) % management needs met in 2010 and 2020; comparison between the total current estimated need for management and that being undertaken in 2010 and 2020; (b) in Australia; (c) outside Australia; (d) relationship between % of knowledge need and % threat load relieved; (e) relationship between % knowledge need met and change in extinction risk (International Union for Conservation of Nature Red List category) in any decade since 1990.

of their management need met, extinction risk was more likely to have been reduced (i.e. the taxon moved to a lower risk IUCN Red List category) in at least one of the three decades between 1990 and 2020, whereas taxa moved to a higher extinction risk category tended to have less of their management need met (Kruskal-Wallis $\chi^2 = 178.0$, $df = 130$, $p = 0.003$, Figure 3(e)).

Drivers of change

Modelling relating predictor variables (e.g. area of occupancy, geography) to metrics of threat impacts, threat management knowledge and management implementation indicated that no individual model was superior in explaining the observed data. However, the overall direction and effect size of the estimated relationships (regression coefficients) remained similar for each of the covariates across all models included in each of the candidate sets (i.e. those within 2 Akaike units of the top ranked models), justifying our use of model averaging. Furthermore, predictors that were highly significant (i.e. those where $p < .01$) remained so across all models in which they appeared, and in most cases were present in every model included in the candidate sets.

Taxa within Australia

Four themes can be identified from the results of the analyses (S3 and S4). Unsurprisingly, threatened and Near Threatened taxa in 2020 were generally worse off in terms of threat impact than the taxa that had been threatened in 2010, but were considered Least Concern by 2020 (Figure S3(a)). Threatened and Near Threatened taxa were also less likely to have their threat load relieved (Figure S3(c)) or their research or management need met (Figures S3(f,i)).

Second, monitoring score was positively correlated with management progress and change between 2010 and 2020 (Figures S3(g,h)), with better-known birds also more likely to have positive trends in knowledge and management of their threats (Figures S3(e,h)). However, the benefits from having a recovery plan or a Conservation Advice were equivocal – taxa with a recovery plan were no more likely to have their percentage of management need met than those without (Figure S3(i)), and were less likely to have had changes in knowledge or management (Figures S3(e,h)).

Similarly, taxa with a Conservation Advice were no more likely to have research or management progress than taxa without (Figures S3(d,g)).

Third, measures of successful threat management were greater for seabirds than for passerines (Figure S3(i)). There were also reductions in threat load for seabirds and other taxa (Figure S3(c)), and improvements in understanding and management for parrots, seabirds and other taxa, when compared to passerines (Figures S3(e,h)).

Finally, characteristics of birds had other positive and negative correlations with metrics of threat impacts, threat management knowledge and management implementation. Threat impact tended to be higher in 2020 for more accessible taxa and those with populations that varied little (Figure S3(a)). Also, percentage threat load relieved was better than average for species with longer generation lengths, and worse for distinctive taxa and those with larger population and range sizes (Figure S3 (c)). Understanding and implementation of management was negatively correlated with detectability (i.e. the harder they are to find, the poorer the indicator trends) and positively correlated with taxa that are listed as threatened under the EPBC Act (Figures S3(e,h)).

Taxa outside Australia

For taxa/populations threatened outside Australia, models were fitted to a smaller sample of 35 seabird taxa, 20 shorebird taxa and one swift, using a much smaller subset of the predictor variables. The main conclusions were that taxa with longer generation lengths were more likely to show progress in understanding and managing threats (Figures S4(d,e,g,h)), and that taxa that were threatened or Near Threatened were less likely to have management change between 2010 and 2020 (Figure S4(h)) or threat and management need met (Figures S4(c,i)) than taxa that were threatened in 2010 but were considered Least Concern by 2020.

Top individual threats

When threats are disaggregated to the finest level under the IUCN classification scheme (Table S3), the top 10 threats may impose over half (51.3%) of the total current estimated impact pressure across all threatened bird taxa, both inside and outside Australia (Figure 4). Of these, the top three are all related to climate change: an increased frequency or length of droughts (10.3% of total potential threat impact), an increase in the frequency, scale or intensity of fire (10.1%) and rising temperatures

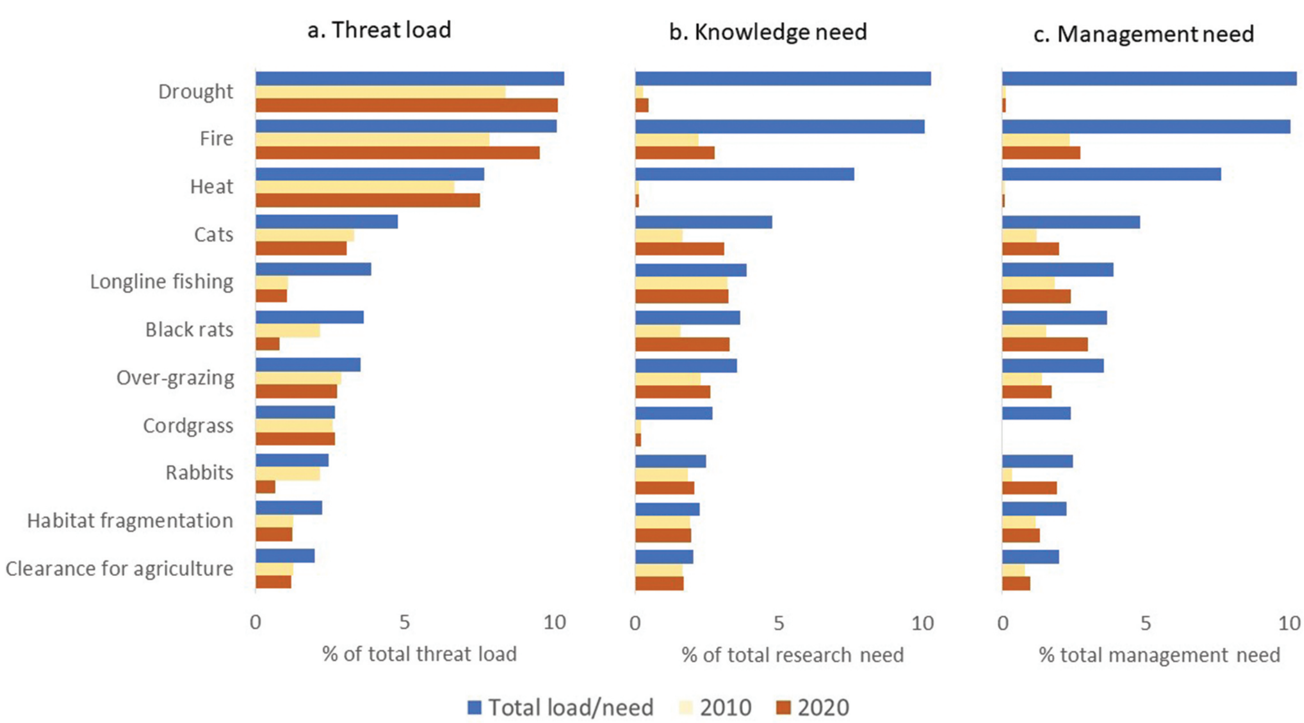

Figure 4. Trends in the management of the 10 most important fine-scale threats to threatened and Near Threatened Australian birds in 2020: (a) % of the total threat load for all Australian birds; (b) % total knowledge need met; (c) % total management need met. Of the 201 threats identified, the top 10 encompassed 51.3% of the total threat load.

and heat waves (7.7%). For all three, the current impacts are only slightly below their potential impact. There is still a great deal to learn about how to manage fire effectively, and there is also almost no knowledge of how to mitigate the impacts of drought or heat, with deficiencies in all three reflected in the level of management. More is known about how to manage the next three most highly ranked threats in terms of their potential impact: predation by feral cats *Felis catus* and black rats *Rattus rattus* on islands, and bycatch from longline fishing. In each case there have been effective reductions in their impact, although in the case of cats and rats, management gains have occurred almost exclusively on islands.

Using our metrics, which emphasise the effect of reducing high-impact threats, the total threat load from black rats and rabbits was higher in 2010 than in 2020 (rabbits 62% to 23%; rats 89% to 28%). For longline fishing there was no change from 2010 to 2020 but the load is now only 15.7% of its potential because of past actions. Of the other threats in the top 10 there was little to no change for cat predation (70% to 64%), overgrazing (78%, 74%), habitat clearance (65.1%, 64.5%) or habitat fragmentation (58.1%, 57.5%) while the impact of invasive cordgrass *Spartina alterniflora* on intertidal flats in East Asia at stopover sites of migratory shorebirds has worsened, and in 2020 had the greatest threat rating for all 20 Australian taxa affected.

Most threatened bird taxa

The rankings of the top 10 taxa for current threat impact, research and management needs (Table 2; see Table S12 for full rankings) include Swift Parrot *Lathamus discolor* at the top of all 3 categories. Subsequent ranks vary greatly with only Regent Honeyeater *Anthochaera phrygia*, Helmeted Honeyeater *Lichenostomus melanops cassidix* and Black-eared Miner *Manorina melanotis* occurring in the top 10 in all 3 lists while Mukarrthippi Grasswren *Amytornis striatus striatus* is on 2.

Discussion

Whereas several recent studies evaluated the relative extent and magnitude of threats to Australian biodiversity (Kearney *et al.* 2019, 2023; Ward *et al.* 2021), our study is the first attempt to monitor changes in threat impact, knowledge of how to manage those threats and the implementation of knowledge. There are four areas where the current analysis provides novel insights.

The primacy of climate change

In 2018, invasive species (collectively) were the threat to Australian threatened birds having the greatest impact, although drought was considered the greatest individual threat (Garnett *et al.* 2019). By 2020, the three greatest threats to Australian birds were climate driven –

Table 2. The 20 threatened or Near Threatened Australian bird taxa ranked highest in 2020 for estimated threat load, the need for knowledge of how to manage threats effectively and for the need to implement known threat mitigation approaches. Scores in brackets are normalised to 100.

Rank	Threat impact	Understanding	Management
1	Swift Parrot (100)[a]	Swift Parrot (100)[a]	Swift Parrot (100)[a]
2	Mount Lofty Ranges Southern Emu-wren (60)	Regent Honeyeater (77)[a]	Houtman Abrolhos Painted Button-quail (72)
3	Regent Honeyeater (60)[a]	Eastern Pink Cockatoo (61)	Mukarrthippi Grasswren (58)
4	Helmeted Honeyeater (56)	Mallee Western Whipbird (55)	Regent Honeyeater (54)[a]
5	Mukarrthippi Grasswren (54)	Heath Western Whipbird (55)	Helmeted Honeyeater (53)
6	Eastern Pink Cockatoo (51)	Helmeted Honeyeater (54)	Australian Fairy Tern (50)
7	Australian Fairy Tern (48)	Black-eared Miner (52)[a]	Mount Lofty Ranges Southern Emu-wren (50)
8	Carnaby's Black-Cockatoo (46)[a]	Northern Eastern Bristlebird (51)	Northern Eastern Bristlebird (47)
9	Plains-wanderer (46)[a]	Mallee Emu-wren (48)	Orange-bellied Parrot (46)[a]
10	Murray Mallee Striated Grasswren (46)	Mount Lofty Ranges Chestnut-rumped Heathwren (47)	Southern Barking Owl (45)
11	Mallee Western Whipbird (46)	Australian Fairy Tern (46)	Mallee Western Whipbird (44)
12	Red-lored Whistler (46)	Noisy Scrub-bird (45)	Eastern Pink Cockatoo (43)
13	Southern Barking Owl (45)	Tasmanian Masked Owl (45)	Heath Western Whipbird (43)
14	Mount Lofty Ranges Chestnut-rumped Heathwren (45)	Southern Barking Owl (45)	Black-eared Miner (43)[a]
15	Northern Eastern Bristlebird (45)	Western Ground Parrot (45)[a]	Western Purple-crowned Fairy-wren (43)
16	Black-eared Miner (44)[a]	Kangaroo Island Glossy Black-Cockatoo (43)	Plains-wanderer (42)[a]
17	Orange-bellied Parrot (43)[a]	South-eastern Hooded Robin (42)	Tasmanian Masked Owl (41)
18	Yellabinna Rufous Grasswren (43)	Yellabinna Rufous Grasswren (41)	Southern Black-throated Finch (40)
19	Western Bassian Thrush (43)	Red-lored Whistler (40)	Noisy Scrub-bird (40)[a]
20	Southern Black-throated Finch (41)	Bar-tailed Godwit (outside Australia) (40)	Mount Lofty Ranges Chestnut-rumped Heathwren (39)

[a]Listed as priority species in the National Threatened Species Action Plan (Department of Climate Change, Energy, the Environment and Water [DCCEEW] 2022).

drought, fire and heat, the last not considered a great threat to many birds in its own right in the earlier study. Overall, climate change and altered fire regimes together constituted nearly a third of the threat load on Australian birds in 2020, affecting 89% of taxa in Australia and 70% overall. That this result for birds contrasts with recent assessments by Ward *et al.* (2021) and Kearney *et al.* (2019, 2023) for Australian threatened taxa, who reported higher threat incidence for habitat loss and invasive species, reflects how quickly evidence is accumulating on the impact of climate change.

A major driver of the change was the wildfires of 2019–2020. Because of climate change, these fires were unprecedented in their scale and intensity (Collins *et al.* 2021) with devastating impacts on fauna (Ward *et al.* 2020) and flora (Gallagher *et al.* 2021). Many birds died as a direct result of the fire or soon afterwards (van Eeden *et al.* 2020; Legge *et al.* 2022a). Population losses of 15 bird taxa, particularly taxa endemic to Kangaroo Island where over half of all the habitat for some taxa was burnt at high intensity, were judged to be so substantial that some taxa previously considered Least Concern or Near Threatened qualified for listing as threatened according to IUCN Red List Criteria solely because of the fires (Legge *et al.* 2022b; Rumpff and Legge 2023). While shifts in fire timing, intensity and extent are not associated solely with climate change, with cessation of First Peoples fire-management practices and invasion by flammable exotic grasses also a significant threat (Miller *et al.* 2010; Kelly *et al.* 2020), climate change is now a major driver of change in fire as a threat.

Second, since the data for Ward *et al.* (2021) and Kearney *et al.* (2019, 2023) were assembled, analysis was completed of the intensive monitoring of birds in the North Queensland rainforest from 2000 to 2016, which identified rapid declines for many species (Williams *et al.* 2021). While a contraction of the ranges of many rainforest species in North Queensland to higher altitudes had been predicted 20 years ago (Williams *et al.* 2003), assiduous monitoring at 1770 carefully chosen and well-dispersed sites across the Wet Tropics region every year from 2000 to 2016 was able to demonstrate the changes that had been occurring and how closely they aligned with predictions. More recently, de la Fuente *et al.* (2023) showed that the decline was driven primarily by increases in temperature, with heat waves even affecting lowland species that have otherwise benefitted from warmer temperatures at higher altitudes. The effect of heat has also been becoming apparent in the semi-arid woodlands of south-eastern Australia (Gardner *et al.* 2022) and climate change is assumed to be contributing to threat loads of taxa in most environments, although much of the empirical data on the deleterious effects of climate change is derived from similar environments around the world, such as the southern oceans (Bestley *et al.* 2020), migratory shorebird breeding habitat in the Arctic (Saalfeld *et al.* 2019) and arid environments in Africa (Conradie *et al.* 2019).

Disturbingly, knowledge of how to manage climate-related threats is in its infancy with virtually no application of that knowledge to threatened Australian birds (Walsh *et al.* 2023). Some important lessons were learnt from the most recent wildfires (e.g. Legge *et al.* 2022b; Rumpff and Legge 2023), and translocation to reduce future risk from fire has been successful for conserving Noisy Scrub-bird *Atrichornis clamosus* (Comer *et al.* 2010) and Eastern Bristlebird *Dasyornis brachypterus* (Baker *et al.* 2012). There is virtually no published research, however, that provides explicit guidance on how to mitigate the direct effects of heat and drought on threatened birds, let alone such management being implemented.

Quantified successful conservation interventions

Three classes of threat impact declined from 2010 to 2020 with an associated increase in the knowledge of how to mitigate the threats, the implementation of that knowledge and the percentage of the threat impact mitigated. The first was taxa affected by invasive species. For these, 82% of the overall reduction in threat load from invasive species since 2010, and 60% of all benefits to Australian threatened birds from invasive species control to date, was derived from the successful eradication of rodents and rabbits from Macquarie Island (Springer 2016). The programme was so successful that it reduced the total threat load across all threatened Australian birds by 5% (even though only 13 of the 223 taxa/populations considered occur on Macquarie Island) and not only ameliorated the decline in the Red List Index value for 2020 (Berryman *et al.* 2024) but also altered the types of biological characteristic shown by birds now threatened within Australia (Olah *et al.* 2024). Another 10% of the reduction in invasive species impact since 2010 can be attributed to programmes on Norfolk, Lord Howe and Christmas Islands with just six mainland taxa benefitting from invasive species control based on the metrics adopted here. The breeding grounds of three taxa – Western Ground Parrot *Pezoporus wallicus flaviventris*, Western Bristlebird *Dasyornis longirostris* and Heath Western Whipbird *Psophodes nigrogularis nigrogularis* – have been the subject of a Red Fox *Vulpes vulpes* control programme in south-western Australia since 1996 which has been expanded to include cats in attempts to reduce two of the greatest threats to persistence of these species (Comer *et al*. 2020).

A reduction in threat impact was also observed for habitat degradation. Given national trends in land condition (Janke *et al*. 2022), and ongoing high rates of land clearing (Ward *et al*. 2019), this result was surprising. However, disaggregation of the results found that, as with invasive species, the benefits were largely derived from actions on oceanic islands, particularly the provision and repair of nestboxes for Green Parrots *Cyanoramphus novaezelandiae cookii* and Moreporks *Ninox novaeseelandiae undulata* on Norfolk Island, an action necessary because so few natural hollows remain and because existing nestboxes had been allowed to degrade , and the moratorium on phosphate mining in unmodified habitats on Christmas Island. The high scores for the two Norfolk Island taxa reflect the severity of the impact from not having hollows, with the Green Parrot narrowly saved from extinction (Gautschi *et al*. 2022).

Our results highlight that, while island taxa tend to be exceptionally likely to be threatened (Manne *et al*. 1999; Olah *et al*. 2024), and are the locations from which most extinctions of Australian bird taxa have occurred (Garnett and Baker 2021; Woinarski *et al*. 2024). They are also the locations where conservation success is most likely to be achieved, especially now techniques for controlling invasive species can be applied to islands as large as Macquarie Island (131 km^2; Springer 2016), with another example being eradication of cats from Dirk Hartog Island (628 km^2; Algar *et al*. 2020). However, there is still much to learn; attempts to eradicate cats are expanding in complexity and scale, including cat eradication attempts from inhabited islands (e.g. Christmas Island, Kangaroo Island, French Island; Commonwealth of Australia 2015).

The third threat class for which there has been an improvement is biological resource use, which makes up about 5% of the total threat load on Australian threatened birds. Almost all the impact can be attributed to the mortality of albatrosses and petrels captured as bycatch in fisheries, a threat so severe that it resulted in the creation of the international Agreement on the Conservation of Albatrosses and Petrels (ACAP) and a Threat Abatement Plan for Australian waters (Commonwealth of Australia 2018). Since ACAP was established in 2001, reductions in losses from fishing bycatch have benefitted 16 of the albatross and petrel taxa nesting in Australia or visiting Australian waters, reducing the potential impact to 64% of its potential (Commonwealth of Australia 2018). However, all but 1.6% of this benefit was realised before 2010 when the longline Threat Action Plan started to be implemented in Australia, most of the longline fishing effort in Australia waters shifted north of 30° S, and tuna fishing effort in Australian fisheries declined (Baker and Robertson 2018). Controls on fishing effort and the widespread uptake of appropriate bycatch mitigation measures in other ACAP countries, which would have potentially been influential on Australian seabirds, are likely to have been minimal (Phillips *et al*. 2016).

Research priorities

Many of the major threats to Australian birds, such as controlling invasive species on islands and reducing seabird bycatch, have been the subject of research for a long time, with benefits realised in terms of management implementation. Other forms of threat management are still the subject of active research. For example, although cats have been successfully eradicated from many islands, cat control at a landscape scale on mainland Australia is challenging and expensive. Nevertheless, research on cat control has expanded in the last decade (Woinarski *et al*. 2019). Similarly, there are active programmes on fire ecology and ecology of threatened species affected by fire, but the complexity of the subject means that much more needs to be learned. Lessons learnt from the catastrophic 2019–2020 fires in particular can be applied to fires in the future (Rumpff and Legge 2023), although the ideas will remain untested until such fires recur. Two major threats operating on species outside Australia are also the subject of intensive research. For cordgrass, this research is relatively recent (Meng *et al*. 2020) but, for longline fishing, the research is mature (Melvin *et al*. 2023) and is being applied. However, as exemplified by Swift Parrots and logging in Tasmania, the research required is on the social and political processes constraining implementation, and on how to secure adequate investment for implementation of management where knowledge is already available (Webb *et al*. 2018; Crates *et al*. 2024).

There are gaps in the research related to uncertainty that are not easily or adequately incorporated into a metric of the type used. For example, the persistence of four taxa (Buff-breasted Button-quail *Turnix olivii*, Coxen's Fig-Parrot *Cyclopsitta coxeni*, Cape Range Rufous Grasswren *Amytornis striatus parvus*, Tiwi Hooded Robin *Melanodryas cucullata melvillensis*; Garnett *et al*. 2022) has not been independently verified, even though judgements on the threats to those taxa, should they survive, can be made based on the change known to have occurred in their former habitat. Similarly, knowledge of the impact of threats is poorly known for some combinations of threat and taxa (see Garnett and Baker 2021 for assessments of certainty of impact for each threat to a taxon) and further research is warranted to ensure action to manage those threats is warranted.

Priority taxa

Many of the highest-ranking taxa in Table 2 have been the subject of sustained conservation effort for many years and are the subject of high-quality research. That they still rank so highly could be seen as an admission of failure. However, that they have persisted at all can be viewed as evidence of at least temporary success, even if the long-term prognosis remains grim (e.g. Regent Honeyeater; Heinsohn *et al*. 2022; Orange-bellied Parrot; Pritchard *et al*. 2021; Stojanovic *et al*. 2023). The reason that these species continue to rank so highly, and are among the bird taxa most likely to go extinct in the next few decades (Geyle *et al*. 2018; Garnett *et al*. 2022), is that the threats they face are not only severe, but the management they require is difficult to implement at any but an experimental scale (e.g. Allee effects; Crates *et al*. 2017). For example, Swift Parrot is known to be highly susceptible to logging of its habitat and predation by Krefft's Glider *Petaurus notatus* (Webb *et al*. 2021), an introduced species, but the social, political, technical and financial constraints on relieving these threats at a landscape scale (see Crates *et al*. 2024) mean that they continue to score highly for both research and management need (Webb *et al*. 2018). Political contestation about Tasmanian forestry means research for solutions is no longer related to the biology of the issue (Woods 2019). Many of the taxa most in need of management solutions are affected by increases in the scale and intensity of fires but the methodology for controlling the sorts of wildfires that occurred in 2019–2020 do not yet exist, while the processes for spreading, and thereby reducing, risk by increasing the number of populations have only been proven and put into practice for a few bird taxa (e.g. Comer *et al*. 2010; Baker *et al*. 2012); such programmes have been attempted without success for others (e.g. Mitchell *et al*. 2021).

The list of taxa In Table 2 facing the highest threat load, in greatest need of research on, and management of, their threats includes 8 of the 22 taxa listed as priorities in the National Threatened Species Strategy (Department of Climate Change, Energy, the Environment and Water [DCCEEW] 2022). Overall, the 22 priority taxa in the Strategy have a mean ranking of 81/261, 96/258 and 84/261 respectively for threat load, research need and management need, so many are well below the top 20. While this is not surprising given the diverse selection criteria employed to select the priority taxa (DCCEEW 2022), it demonstrates that a portfolio of strategies and prioritisation processes is needed to maximise progress towards recovery across all taxa.

Methodological considerations

The results presented here are the first time the methodology developed by Garnett *et al*. (2019) has been used to monitor trends over time, and are the first time, globally, that trends in the threats to an entire continental faunal group have been assessed simultaneously. The approach taken demonstrates utility in understanding broad trends across multiple species but its application to individual taxa should be treated with caution – often more detailed information is needed than can be summarised here. The data collected to assess threat impact, and the current state of research and management related to threat mitigation, at a national level, are necessarily indicative of, and often driven by, data availability of lesser-known taxa. Even for well-known threats and taxa, detailed information is usually available for only a small part of a taxon's range, or its impact is poorly known. The results in Garnett and Baker (2021) show that, while there was medium or better confidence in the impact of 80% of known threats, the evidence for the other 20% was anecdotal. However, while the threats and their impacts could be more accurately measured and monitored (Verdon *et al*. 2024), often usefully so, the return on investment may not be justified, at least to achieve the nation-wide assessment of trends aimed at here – more, and more accurate, information does not necessarily change conclusions or improve outcomes (Maxwell *et al*. 2015).

Another reason for cautious interpretation of the results is that each threat is considered independently, because the interactive effects are too difficult to determine across a taxon's range and across multiple taxa (Doherty *et al*. 2015). Instead, it is assumed that, where there are interactions, the impact of two interacting threats will be equivalent and that threat impact of one will only be reduced if that of the other is also ameliorated. While this may over-emphasise the impacts of, and need to manage, some threats (Auerbach *et al*. 2015), the approach is precautionary because it assumes two threats acting together have the sum of their impact.

It also should be noted that the IUCN (2012b) threat impact metrics were designed to guide the understanding of threats for the IUCN Red List. As a result, the weight of the threats tends to be correlated with extinction risk, many of which can operate at a very fine scale. For that reason, reducing the extinction risk to Critically Endangered taxa will have a greater impact on the indices used here than doing so to more widespread, less threatened taxa. Changes in the indices can be indicative of change at a small scale because shifts in scope are more readily achieved over small areas than large ones. This was apparent in the sensitivity of the indices to restoration or protection of habitat on Norfolk and Christmas Islands. This resulted in a decline in the total threat load from habitat loss and degradation, when such threats continue to operate at a large scale across substantial areas of Australia, and even continue to affect island taxa, such as woodland taxa endemic to King Island. For taxa with large ranges, it is harder to reduce the impact of a threat operating over, for example, 50–90% of its range to 1–50%, than is the case for taxa with small ranges. Other weightings, perhaps based on area occupied, could be used to emphasise declines in abundant, ecologically important taxa (see Baker *et al.* 2019; Bennett *et al.* 2024) but are not built into the current design.

The fourth methodological aspect of the metrics is their use as a rubric for estimating the impact of investments in research or management. For example, the first national Threatened Species Action Plan (Commonwealth of Australia 2015) used expert elicitation to determine its impact (Fraser *et al.* 2022). Using the approach taken here, it was possible to estimate that the total threat load of the 21 focal taxa had declined from 81% to 74% over the decade (2010–2020) in which it was operating for the last 5 years with the threat load declining in 12 taxa. Removing all current threats to the taxa that are the focus of the current National Threatened Species Strategy (DCCEEW 2022) would reduce the threat load to Australian birds by 37%. At the least, the metrics would allow targets to be identified and set for different threats affecting different taxa and allow for research to ascertain the implications of reducing this threat load on species' populations.

Recent attempts to aggregate population trend data at national scales across different taxonomic groups have demonstrated that threatened bird taxa are much better represented in terms of monitoring quantity and quality compared with threatened plant and mammal taxa (Bayraktarov *et al.* 2021a; Tulloch *et al.* 2023). The affection held for birds, and the investment over many decades into their research and management, mean that estimation of threat impact, knowledge and management metrics for any other group will highlight how little is known about the threats they face and their relative impact. Repeating this exercise for other taxonomic groups would be useful for that purpose. Understanding what we do not know is the first step in filling the knowledge gaps. The approach used here can provide framework for that understanding.

Conclusion

Research into and management of Australian threatened birds has improved the outlook for many species (Garnett *et al.* 2018) and prevented the extinction of some (Bolam *et al.* 2021). Here we have placed that achievement in the context of the task required to relieve the threats to all Australian birds and quantify what was achieved in the decade between 2010 and 2020. This was a time when funding for threatened species was less than one-tenth of the estimated requirement (Wintle *et al.* 2019) and when climate change started to make serious inroads into taxon security (e.g. 2017–2019 drought, 2019–2020 megafires, 2021–2022 floods) so the small changes in potential threat impact can, to some extent, be considered as a relative success given the pressures in play. However, they would have been worse without the benefit gained from removing invasive mammals from Macquarie Island (Springer 2016) and as a result, the level of threat reduction achieved across most of Australia (e.g. the mainland) should not be considered more impressive than it actually is.

The analysis highlights the increasing threat posed by climate change, either directly through the increased frequency and intensity of heat waves and droughts or indirectly through its impact on fires. It also exposes the dearth of research being done on practical solutions to the conservation problems being posed by climate change or implementation of the few ideas that exist. At the same time, the research shows where there have been achievements, such as with the reduction of threats on islands and in reducing the impact of longline fishing.

We have demonstrated that our methodology can track broad trends in threats, research and their management as well as having potential to estimate the extent of the benefits that might accrue from future investments. One of the benefits we demonstrate is that taxa that are monitored well are more likely to show improvements. We hope that providing a means to monitor the impacts of threats on a national scale will drive beneficial change.

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Data availability statement

All data are available in the supplementary materials.

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