Using traits of species to understand responses to land use change: Birds and livestock grazing in the Australian arid zone

Kendi F. Davies [a,b,*], Brett A. Melbourne [a,b], Craig D. James [b,c], Ross B. Cunningham [d]

[a] Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA
[b] CSIRO Centre for Arid Zone Research, P.O. Box 2111, Alice Springs N.T. 0871, Australia
[c] CSIRO Sustainable Ecosystems, GPO Box 284, Canberra, ACT 2601, Australia
[d] The Fenner School, Australian National University, GPO Box 4, Canberra, ACT 0200, Australia

ARTICLE INFO

ABSTRACT

The expansion of the artificial water-point network and livestock grazing in arid and semi-arid Australia has significantly increased access to water by water limited herbivores and thus has potential to seriously negatively affect the unique endemic flora and fauna. We examined the effects of the expansion of the water-point network on the arid and semi-arid zone bird community, using data from the Atlas of Australia bird surveys of 1977–1981 and 1996–2001. We examined whether traits of species could be used to uncover the critical ecological processes altered by this land use change. We detected large scale declines in individual species. Species reliant on water for nesting and feeding declined more than other groups in the presence of high water-point density, likely through direct effects of livestock degrading habitat of both natural and artificial water points. The arid zone has no natural hoofed animals and livestock have significant impacts. Species that forage and nest on the ground also showed large declines, likely because of trampling and removal of vegetation by livestock and potentially through the indirect effect of water limited predators, dingos and foxes, expanding their ranges in response to the expanding network of water points in the landscape. This result was also apparent at large spatial scales so that these local-scale responses to water points translate into continental-scale population declines. Using traits of species to understand declines of bird species helped us to uncover which critical changes associated with the expansion of the water-point network most affected the bird community and therefore which species are most at risk.

1. Introduction

Ecologists are often interested in how a given land use change affects the population dynamics of a suite of species (e.g. birds). Linking traits of species to changes in population dynamics caused by changes in land use can greatly increase ecologist's understanding of which altered processes are most critical. This in turn can allow for more targeted management strategies to reduce impacts.

Animal ecologists have used traits of species to predict vulnerability to extinction. Some life-history traits are related to the dynamics of populations, including colonization ability and extinction risk, which means that traits may act as surrogates for extinction risk when we lack detailed population dynamics data (Cole, 1954; Elton, 1958; MacArthur and Wilson, 1967; McKinney, 1997; Fagan et al., 2001; Henle et al., 2004). For example, Fagan et al. (2001) were able to predict the general extinction vulnerability of 60 out of 72 mammals simply by knowing body size, age at first reproduction, and average number of offspring. Worldwide, the extinction vulnerability of bat species was correlated with small geographic ranges and low wing aspect ratios (Jones et al., 2003). Declining amphibian species in Central America had large body sizes, restricted elevational ranges and aquatic habitats (Lips et al., 2003). Rare, specialized beetle species declined in response to forest fragmentation (Davies et al., 2000, 2004). Finally, UK farmland bird species using rare resources and with relatively small brains were most likely to decline (Shultz et al., 2005).

In plant based studies, a more sophisticated framework exists that distinguishes between response and effect based traits (Lavorel and Garnier, 2002; Suding et al., 2008). Response based traits are considered in terms of their response to environmental factors, while effect based traits are considered from the perspective of the effect that they have at a community scale on ecosystem properties (Lavorel and Garnier, 2002; Suding et al., 2008). For example, in subalpine grasslands in the central French Alps, fertilization led to a community composed of species with greater specific leaf area and leaf nitrogen content (response traits), which, in turn, led to

greater community productivity and faster leaf decomposition (impact of effect traits) (Quetier et al., 2007). For another good example see Gross et al. (2008). While, animal ecologists have successfully used response based traits to predict species' responses to a given land use change, few animal studies have considered effect based traits.

In this study, we examine whether response traits of species can be used to uncover the critical processes that have been altered in the face of a major land use change, through correlations of traits with species' population increases and declines. Here we examine arid zone birds and their response to livestock grazing in arid Australia. What additional information does the study of life-history traits provide about how artificial water points and livestock grazing affect bird populations? Further, while we do not explicitly consider effect traits, our approach may also provide insight into how the loss of particular species may affect ecological processes.

The arid and semi-arid zones comprise 70% of the Australian continent, and in this landscape there are few natural permanent sources of water. Rainfall is unpredictable in space and time, historically creating environmental variation in the grazing pressure of native herbivore species (James et al., 1999; Landsberg et al., 2003). Over evolutionary timescales, this landscape likely had relatively light exposure to grazing by large herbivores (Landsberg et al., 2003). More recently, this landscape has undergone a fundamental change. A profitable commercial livestock grazing industry now relies on an extensive network of artificial water points in the arid and semi-arid zones. Natural water sources are associated with deep, permanent pools on river systems and temporary pools that are scattered through the landscape after heavy rain (James et al., 1995; James et al., 1999). Temporary sources may last from a few days to weeks and the frequency of their creation varies: in the northern and southern fringes of the arid zone, they are seasonally present (winter in the south and summer in the north); whereas in the large central belt the occurrence is unpredictable in association with infrequent rainfall (Stafford Smith and Morton, 1990). At a landscape scale, water-dependent fauna have vastly more access to water from artificial sources than would be possible from natural sources in both geographic extent and permanence (temporal extent). The creation of this network of artificial water points was necessary for the growth of a commercial livestock industry. This network provides high densities of permanent water points to optimize access to forage by livestock. Water points are now numerous over large areas, to the extent that little land area remains that cannot be accessed by sheep, cattle and other water-dependent herbivores like feral goats and kangaroos (James et al., 1999; Landsberg et al., 2003).

The impact of artificial water points is dramatic; they create a gradient of grazing impact that extends several kilometers and diminishes away from the water point. Studies of the effects of water points and grazing pressure on both native plant and animal species have consistently found that the majority of native species have low abundances or are absent near water points but are abundant far from water points (Landsberg et al., 2002, 2003) – and see (Fensham and Fairfax, 2008). Artificial water points can change predator prey relationships by expanding the distributions of water limited predators (Harrington et al., 1999), and can increase pressure on vegetation (Thrash, 1998; Parker and Witkowski, 1999). We predict that for bird species, the effects of artificial water points may be both positive and negative, direct and indirect, depending on the species. Direct effects include allowing species that are limited by water to expand their ranges. Indirect effects include the competitive effects of these range expanders on species that do not directly benefit from the increased availability of water in the landscape, trampling and disturbance of habitat by livestock (including loss of plant cover and introduction of exo-

tic species), and increased abundance of water limited predators like dingos and foxes.

Our aims were to discover: (1) how intensification of land use affects bird populations, and (2) to link population changes due to changes in land use to species traits to determine which altered processes are most critical. We used data from the Atlas of Australian Birds, a survey conducted by the Royal Australian Ornithologists Union, now Birds Australia, from two survey periods, 1977 to 1981 and 1996 to 2001. We considered nine traits: ecological niche, clutch size, nesting behavior, nest site, vertical feeding level, feeding habitat, food and bodyweight. We expected that the greatest effects of water points and grazing on bird species would be through habitat modification, with predictable affects on species with different nest sites, vertical feeding levels, feeding habitats and food. For example, we predict that species that nest and/or feed on the ground will be most detrimentally affected because livestock eat and trample their habitat. Species that nest and/or feed on the ground are also prone to predation (Rayner et al., 2007; Pescador and Peris, 2007; Purger et al., 2008; Bonnaud et al., 2009). We also predicted that aquatic birds would increase in abundance with the increase in water in the landscape. Finally, we predicted that traits like body weight, food (trophic level) and clutch size should provide information about population dynamics and risk of extinction in the face of habitat change that reduces population size. For example, large-bodied species are predicted to be at a greater risk of extinction than small-bodied species (Gaston and Blackburn, 1996) and species at the top end of food chains are more prone to extinction than those at lower levels because they tend to have more unstable population dynamics and are less likely to persist in a fluctuating environment (Holt, 1996; Lawton, 1995; Pimm and Lawton, 1977). Similarly, time to extinction should decrease with increasing clutch size because of the larger stochastic components in the population dynamics of such species (Saether et al., 2005).

2. Method

2.1. Spatial sample units

The smallest unit for statistical analysis was a grid square of 1° latitude and longitude. We first produced summarized data for birds and environmental variables at the scale of this sample unit. One degree grid squares were excluded if more than half of the grid was in the sea, more than twenty percent of the grid had an inappropriate land use type (woodland was excluded to avoid habitat observer effects), or had poor water-point data (see Fig. 1a). One degree grid squares were further nested within bioregions (from the Interim Biogeographic Regionalisation of Australia, a classification based on climate, vegetation and soil; (National Land & Water Resources Audit, 2001); see Fig. 1c) because bioregions are at a larger spatial scale.

2.2. Environmental data

Our study area was the arid and semi-arid zones of Australia, which make up approximately 70% of the Australian continent (Fig. 1a). Using ANUCLIM 1.8 (ESOCLIM) we calculated a moisture index as the ratio of monthly rainfall to evaporation averaged over the twelve months in a year, with spatial resolution of 0.08° (Hutchinson et al., 1998). We defined the arid zone as areas that have a moisture index less than or equal to 0.2, and the semi-arid zone as areas with a moisture index less than or equal to 0.3 (Fig. 1a). One degree grid cells were included in the arid/semi-arid zones if the centre of the grid satisfied these criteria. The area encompassing both the arid and semi-arid zone has annual rainfall
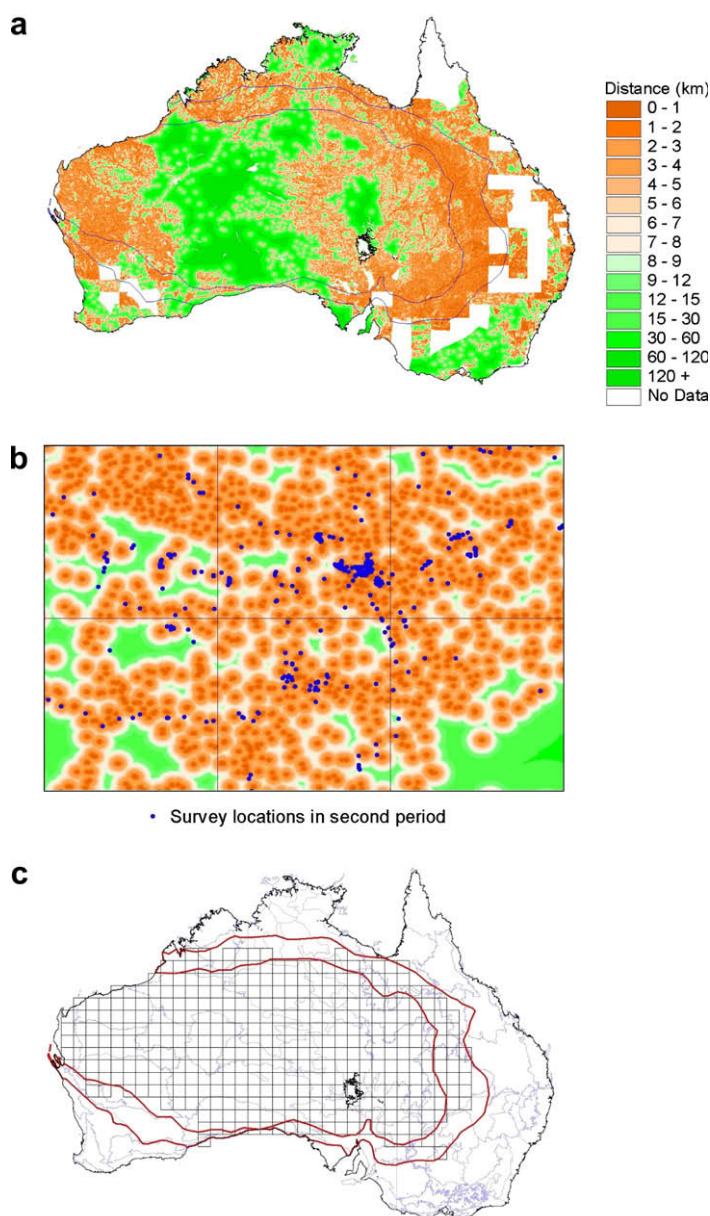
Fig. 1. (a) Measurements of distance to an artificial water point. Orange sites are close to water and green sites are far from water. In large parts of the arid zone, there are now few areas far from permanent water. (b) Detail for the location around Alice Springs, in the heart of the arid zone, illustrating that the influence of water points depends both on their density and configuration in the landscape (Key as for (a)). Blue dots represent survey locations. The squares are 1° of latitude and longitude (approximately 100 km by 100 km). (c) We looked at changes in bird populations in time at three spatial scales: the continental scale – across the entire semi-arid (outer red line) and arid zones (inner red line); the bioregional scale (demarcated by the grey lines); and the 1° grid scale (the small squares).

values that range from roughly 200 mm in the south to 600 mm in the north.

We measured the great circle distance to an artificial water point (a point location), from the centre of any 0.005° grid in the landscape, from a database of water point locations (Fig. 1a and b). The locations of all artificial water points in each 1° grid square were taken from topographic maps (by the Wilderness Inventory of the Australian Heritage Commission). While this method does not produce a precise map of all active water points because water points come and go, we assume that derived grid scale averages are indicative of the true situation. For use in analyses, we calculated the variable *DistWater*, equal to the mean of $\ln(D + 1)$, where D is the distance to water (in degrees) of a 0.005° grid, and the mean is calculated across all 0.005° grids in a 1° grid (*DistWater* mean

0.0507, s.d. 0.0546, range 0.0135–0.6777). For reference, *DistWater* = 0.05 corresponds to 5.7 km.

Because rainfall is so important in the arid zone it is potentially an important explanatory variable for population change. We included data for rainfall change (variable *Rainfall* Table 1) between the two survey periods for each 1° grid square (National Land & Water Resources Audit, 2001). Forty-one percent of Ibra regions showed no change in rainfall between Atlas survey periods, while 59% showed increases in rainfall between Atlases.

2.3. Bird data

We used data from two Australian Bird Atlas periods 1977–1981 and 1996–2001 (http://www.birdsaustralia.com.au/atlas/

Table 1
Initial (full) statistical model used to asses population change for individual arid zone bird species between survey period one (1977–1981) and two (1996–2001). A linear mixed-effects model (REML) was used.

Term	Explanation
$E\ [(logit(p))] = constant$	
+ln (# surveys)	Adjusts for survey effort
+Period	Continental scale change in population
+Period × ln (# surveys)	Adjusts for survey effort
+Bioregion	Spatial variation in abundance due to bioregions
+Rainfall	Accounts for rainfall change
+Bioregion × Period	Regional scale change in population
+Rainfall × Period	Population change due to rainfall change
+DistWater	Spatial variation in abundance due to water points
+DistWater × Period	Population change due to water points

index.html). These data were collected by volunteer observers. The Royal Australian Ornithologists Union, or Birds Australia as they are now known, oversees and organizes the data collection.

Our analyses were devised to detect a change in the frequency of occurrence of a species between the two survey periods, measured as the ratio of the number of sightings to the number of surveys submitted to the Atlases. However, survey methods used in the two Atlases were heterogeneous necessitating rigorous filtering of the Atlas data to provide matching datasets: (1) to match spatial scales we selected only 10' grid surveys from Atlas 1 and 500 m or 5 km transect surveys from Atlas 2; (2) we selected only surveys done within 1 day thereby eliminating the problem of interdependence created by combining single-day surveys done on consecutive days; (3) we used only surveys in which more than three species were detected thereby excluding "incidental" records (especially in Atlas 1, where incidental records were not explicitly identified); (4) we assumed that surveys conducted on the same day in the same 10' grid were not independent, so we selected the first survey on that day; (5) we used only the 1° grids that had at least five surveys in each atlas thereby creating a minimum resolution for the sighting frequency of 0.2. This filtering resulted in a set of 184 one degree grids, which is about half of the arid zone but includes most of the livestock zone. The final dataset included 9210 surveys, split roughly evenly between the two survey periods (3925, 5285 respectively).

We looked for population changes in only arid zone species. First, we selected species from the arid zone bird species lists of Reid and Fleming (Reid and Fleming, 1992). To this we added any species whose distribution in the Atlases made up more than half of the arid zone or had more than half of its total continent wide distribution in the arid zone. There were 225 species that satisfied these initial criteria. From this list we selected only those species for which there were sufficient independent records to analyze. We selected species that would have residual degrees of freedom of more than 20 in our regression analyses. This gave us 133 species for which to model changes in the frequency of occurrence between time periods (Supplementary Table 1).

2.4. Data structure: spatial scale

We looked at changes in bird populations at three spatial scales (Fig. 1c): the continental scale (across the entire arid zone), the bioregional scale, and the 1° grid scale, (the smallest spatial unit in our models). Estimates of change at these three nested scales were made using a linear mixed-effects model, as explained below.

2.5. Data analysis - individual species

Our measure of population change was the change in the probability of sighting a bird species in a 1° grid between the 1977–1981 and 1996–2001 atlases. This was measured on a logit scale, which is standard for proportions data, and is also a natural measure of population dynamics:

$$\text{Population change} = \ln \left(\frac{p_2}{1-p_2} \right) - \ln \left(\frac{p_1}{1-p_1} \right), \qquad (1)$$

where p_1 and p_2 are the probability of sighting the species in period 1 (1977–1981) and period 2 (1996–2001) respectively. In practice, we modeled the probability of sighting a bird using the empirical logit, which transforms the frequency data to a continuous, linear scale.

$$logit(p) = \ln \left(\frac{Sightings + 0.5}{Surveys - Sightings + 0.5} \right) \qquad (2)$$

This allowed us to model variance arising from heterogeneity among observers and surveys. We also used this measure because we did not expect surveys to be independent trials. Such heterogeneity and non-independence violates the assumptions of the Binomial distribution, which is often used to model proportions data.

We used a linear mixed-effects model to model the variance structure correctly. Since surveys were aggregated at the 1° grid scale, we had two components of variance, variance within and between grid squares, while our effect of interest was between periods. We also allowed for spatial autocorrelation of grid squares by specifying the spatial correlation structure as an exponential decay with distance. We used residual maximum likelihood to estimate variance components and autocorrelation and we used weighted least squares to estimate fixed effects, weighting by the inverse of the expected variance in the empirical logit to account for the fact that the variance depends on survey effort (number of surveys).

Table 1 specifies our full (initial) model for each species. The key points of the model are that there were terms that adjusted for a systematic effect of survey effort (ln(*Surveys*)), and there were terms that modeled population change at the continental scale (*Period*), the regional scale (the interaction term *Bioregion* × *Period*), and due to water points (the interaction term *DistWater* × *Period*). Finally, the distance to water effect could be manifested at two spatial scales: the bioregion scale, or between grid squares within bioregions. We examined this by looking at the order dependence of *Bioregion* and *DistWater* terms in the model.

2.6. Data analysis – traits of species

We conducted an analysis of species' responses using the collection of analysis results from the individual species. From the analyses of individual species, we calculated two different response metrics for each species. The first metric summarized the continent-wide population change of a species between the two time periods. It was the difference in the predicted means between period one and period two from the final model for each species (Eq. (1)). The second metric was a local scale metric that summarized the effect of water-point density on population change. We calculated this metric as the negative of the initial slope of population change versus the distance to water (*DistWater*) for a geometric mean distance to water as large as 4.5 km (examples Fig. 2). We used these two different response metrics as two different response variables in regression analyses to examine the effect of species' traits. In the regression analyses of traits, we weighted the response metrics by their standard errors to account for the uncertainty in each of the responses.

We compiled a database of arid zone species' traits from the literature (Supplementary Table 2, Garnett et al., 1992). We used these traits as independent variables in an analyses in two ways,
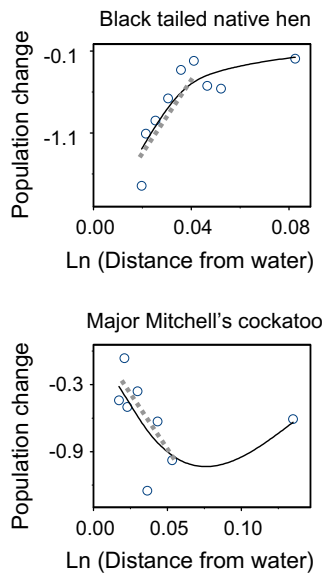
Fig. 2. Examples illustrating how the local scale metric was calculated for the trait analysis. The metric summarizes the effect of water-point density on population change as the slope of population change versus distance to water between 0 and 4.5 km from water points (4.5 km equals 0.04 on the transformed scale of the *x*-axis). Population change is the change in logit transformed sighting frequency between the two survey periods adjusted for the other effects in Table 1. For example, the black-tailed native hen declined less in frequency of occurrence with greater distance to a water point. The slope is represented by the grey hashed line (solid lines show smoothing splines fitted to all of the data); this slope was calculated for all 133 bird species. Since a positive slope indicates a negative effect of water-point density, we reversed the sign of the slope so that the metric is negative when the effect of water-point density is negative. This metric then became the response variable in a regression analyses of traits of species.

first in a summarized form as species groups that shared similar traits, and second as individual traits. We numerically classified species into trait groups using the unweighted pair group method with arithmetic mean (UPGMA). We formed 12 groups. We then used a linear model to examine mean populations responses of these groups using both local and continent scale response metrics. Each of the two metrics (local and continental scale) was considered in separate analyses. In two further multiple regression analyses, we considered all of the trait variables against each of the response metrics (local, continental). We used *Genstat* (Version 6.1, VSN International Ltd, Hemel Hempstead, U.K.) for all statistical analyses.

3. Results

3.1. Changes in bird populations

Without considering the effect of water point intensification and looking only at changes in bird populations between surveys at a continental scale, of 133 arid and semi-arid zone species, 17% of species declined significantly, while 32% increased significantly. At a bioregional scale, for 52% of species, change varied significantly among bioregions, so that in some bioregions a given species increased in occurrence while declining in occurrence in other bioregions. For 30% of species, increases and declines at the bioregional scale were related to changes in rainfall between the two survey periods.

Intensification of land-use, in the form of livestock grazing and artificial water points, was related to declines in bird populations at both bioregional and local scales. In total, 38% of species declined in the presence of high water-point density (23% at the bioregional scale; 15% at the local scale) relative to low water-point

density. In contrast, only 2% of species showed increases in the presence of high water-point density at the bioregional scale, and 2% showed increases at the local scale.

3.2. Bird population responses and traits of species

3.2.1. Local scale – trait groups

At the local scale, land use intensification, in the form of increased water-point density and livestock grazing caused declines in most bird trait groups (Fig. 3a; $p = 0.03$; R^2 0.09; regression d.f. 11, residual d.f. 121). However, the four groups of aquatic birds, declined more, overall, than the eight groups of terrestrial birds in response to increased water-point density. Within the four aquatic
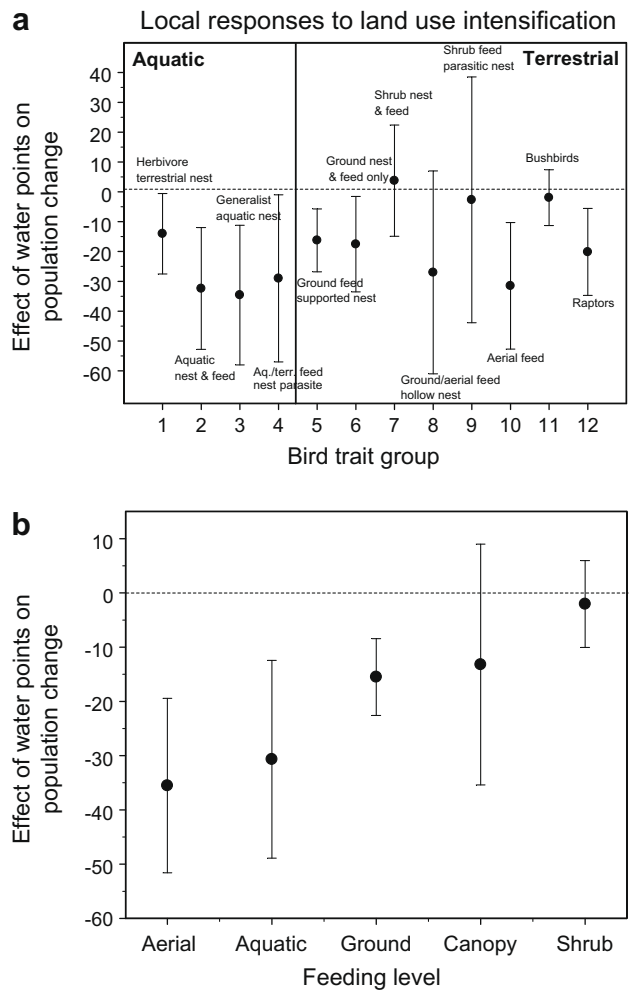

Fig. 3. Traits of bird species and their local-scale responses to land use intensification (increases in the number of artificial water points, livestock grazing) in the Australian arid- and semi-arid zone. Effect of water-point density on population change was calculated as in Fig. 2. A large negative value for the effect of water points indicates that population change was more negatively affected close to water. The results in (a) and (b) come from two different analyses. In (a) bird species were classified into 12 groups according to their traits using UPGMA. In (b) traits were considered independently in a multiple regression analysis. Only vertical feeding level was related to the responses of species to land use intensification. Error bars represent confidence intervals. Thus, only those means with confidence intervals that do not include zero represent significant increases or declines. Legend for bird trait groups: Aquatic birds – 1. herbivores, terrestrial nesters, 2. aquatic nesters and feeders, 3. generalist feeders, aquatic nesters, 4. aquatic/terrestrial feeders, nest parasites. Terrestrial birds – 5. ground feeders, supported nests, 6. strictly ground feeders and nesters, 7. shrub nesters and feeders, 8. ground/aerial feeders, hollow nesters, 9. shrub feeders, parasitic nesters, 10. aerial feeders, 11. bushbirds, 12. raptors.

bird groups (Fig. 3), the group that was the least affected relies least on artificial water points. It includes the Gruiformes (cranes, coots and rails) and Anseriformes (geese, ducks and swans). These are large birds that feed in water and on the ground on herbs and seeds. However, species in this group nest on the ground. In contrast, the three groups of aquatic birds that declined most dramatically (Fig. 3) are more dependent on water. For example, two of the groups nest over water, and one of these feeds exclusively in water. The third group includes species that feed both on the ground and in water but are nest parasites.

Of the eight terrestrial bird species groups, four groups showed large declines associated with high water-point density (Fig. 3). One of these groups, the ground feeders and nesters, relies solely on ground habitat for feeding and nesting. The other three groups included the hollow nesters, raptors and aerial birds. All three of these groups contain aerial feeders, which means that they feed on the wing on invertebrates, although all of the raptors also feed on small vertebrates (9 of 13 raptors are aerial feeders).

3.2.2. Local scale – traits as independent variables

Our regression analysis that considered traits as independent variables supports and clarifies the findings from the trait group analysis (Fig. 3b). Of the nine traits considered, only vertical feeding level was significantly related to water point impact on population change ($p = 0.001$; R^2 0.11; regression d.f. 4, residual d.f. 128 – raw data and categories can be seen in Supplementary Table 2). The three groups that declined under high water-point density were birds that feed in the water, birds that feed on the wing, and birds that feed on the ground, whereas canopy and shrub feeders were unaffected (Fig. 3b).

3.2.3. Continental scale – trait groups

At the continental scale, fewer trait groups showed overall declines ($p = 0.002$; R^2 0.14; regression d.f. 11, residual d.f. 121), and the magnitude of the declines were much smaller (Fig. 4a). The main result is that birds in trait groups with statistically significant declines feed or nest on the ground.

The four groups that declined between the two surveys included two of the aquatic bird groups and the group of birds that rely solely on the ground for both feeding and nesting sites, indeed the latter group declined more than any other group (Fig. 4a). These species feed in chenopod shrubland, spinifex and grassland, and feed on terrestrial invertebrates, seeds, and herbs. Raptors also declined significantly (Fig. 4a); raptors tend to be predators of vertebrates and invertebrates. Of the species considered, most feed aerially, taking insects and birds on the wing; a large proportion also feed on the ground.

Three groups showed overall increases in abundance (Fig. 4a), including one aquatic bird group: the generalist feeders, aquatic nesters. This group is largely made up of the Ciconiiformes (herons, ibis, spoonbill), which feed in freshwater on fish and invertebrates, and in grasslands on vertebrates and invertebrates. They tend to be large birds (>500 g) that are colonial. The second group was shrub nesters and feeders, made up almost entirely of Psittaciformes, the parrots and cockatoos, which are seed feeders on the ground and in the shrub layer, and nest in the shrub layer. The third was bushbirds, who, in general, use the middle shrub layer to feed and nest. They tend to be insectivores, and nectar and pollen feeders.

3.2.4. Continental scale – traits as independent variables

The analysis at the continental scale, considering traits as independent variables again supports and clarifies the findings of the trait group analysis. Only vertical feeding level and nest-site level were significantly related to continental-scale population change (vertical feeding level $p = 0.006$, d.f. 4; nest-site level $p = 0.05$, d.f. 3; R^2 0.11, residual d.f. 123). Ground feeders and nesters declined,
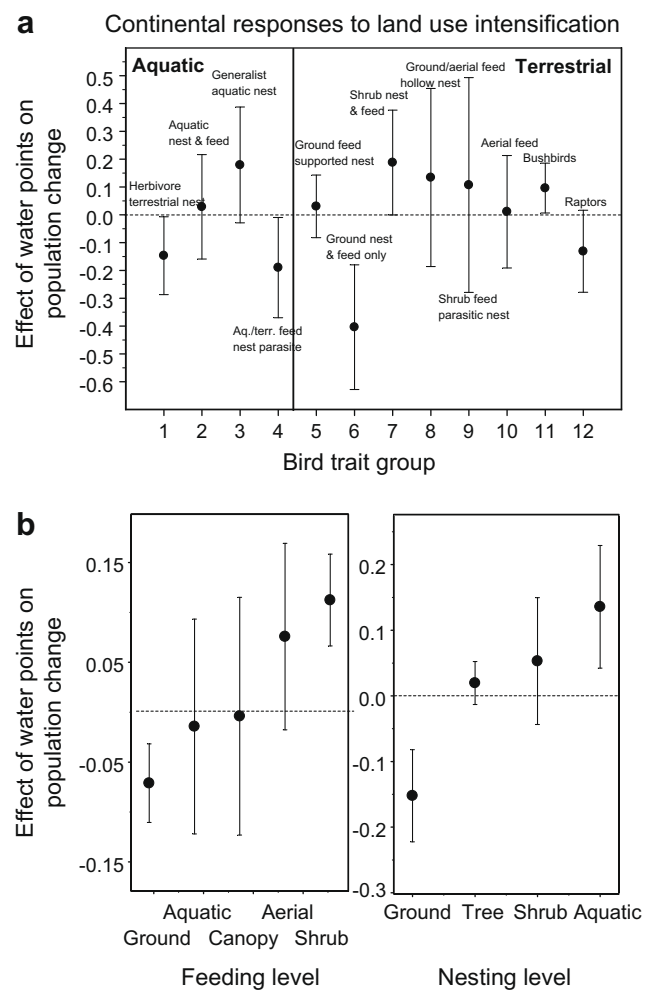

Fig. 4. Traits of bird species and their continental-scale population change in the Australian arid- and semi-arid zones. Population change (plotted on the *y*-axis) is the change in logit transformed sighting frequency between the two survey periods adjusted for the other effects in Table 1. The results in (a) and (b) come from two different analyses. In (a) bird species were classified into 12 groups according to their traits using UPGMA. In (b) traits were considered independently in a multiple regression analysis. Only vertical feeding level and nesting level were related to population change. Error bars represent confidence intervals. Thus, only those means with standard errors that do not include zero represent significant increases or declines. Legend for bird trait groups: Aquatic birds – 1. herbivores, terrestrial nesters, 2. aquatic nesters and feeders, 3. generalist feeders, aquatic nesters, 4. aquatic/terrestrial feeders, nest parasites. Terrestrial birds – 5. ground feeders, supported nests, 6. strictly ground feeders and nesters, 7. shrub nesters and feeders, 8. ground/aerial feeders, hollow nesters, 9. shrub feeders, parasitic nesters, 10. aerial feeders, 11. bushbirds, 12. raptors.

while ground feeders increased (Fig. 4b), confirming the results of the trait group analysis. Aquatic, canopy and aerial feeders were unaffected, as were tree and shrub nesters (Fig. 4b).

4. Discussion

We predicted that aquatic birds would increase in abundance with the increase in water points in the landscape because adding water points to a water limited landscape should benefit species that require water for feeding or nesting. However, aquatic birds declined more than terrestrial birds at both local and continental scales (Figs. 3 and 4) suggesting that adding artificial water points to landscapes is detrimental to these species. This is likely because water points support free roaming livestock, which then also use existing natural water points (James et al., 1999; Landsberg et al., 2003). Livestock

have large environmental impacts in these landscapes, which have no naturally occurring hoofed animals. Livestock trample vegetation, and muddy and foul water holes (James et al., 1999; Landsberg et al., 2003). Thus, for bird species that rely on fresh water holes for food (for example, aquatic invertebrate and fish populations may be affected) and nesting sites, the presence of livestock can have serious consequences. Eutrophication may also be a potential effect that could affect bird populations by, again, affecting food resources. Notably, the group of aquatic birds that was the least affected (group 1 "herbivore, terrestrial nest", e.g. Grey Teal, Pacific Black Duck) relies least on water, whereas the three groups of aquatic birds that declined most dramatically are more dependent on water for nesting and feeding (Fig. 3a, groups 2, 3, and 4, e.g. Hoary-headed Grebe). Thus, the addition of water points and livestock grazing to the landscape affects aquatic birds directly by degrading feeding and nesting habitat.

Some of the terrestrial bird species that declined most near water points included birds in trait groups that rely solely on ground habitat for feeding and nesting (Fig. 3a, group 6, e.g. Singing Bushlark and Richard's Pipit). Again, degradation of habitat through herbivory and trampling by livestock is the likely mechanism, mediated by artificial water points. It is also possible that the addition of water points to landscapes may have indirect effects, by increasing the number of predators in the landscape. The distributions of dingos and foxes are limited by availability of water. Thus, increasing water availability in this landscape allows these predators to increase their ranges and/or the duration of occupancy of parts of the landscape that they would otherwise abandon earlier (James et al., 1999; Landsberg et al., 2003). Other potential indirect effects include the facilitation affects of non-predatory mammals. For example, the presence of water is critical for the establishment of rabbits and allows herbivores such as kangaroos and goats to maintain higher populations than possible with less permanent or sparser water sources. Kangaroos, goats and rabbits degrade habitat through over-grazing and their presence may facilitate hyperpredation (Newsome et al., 2001).

The other groups that declined near water points were raptors and aerial feeders (Fig. 3a, groups 10 and 12, e.g. Little Eagle and Black Falcon). These groups feed on invertebrates and vertebrates, and share in common the habit of feeding on the wing. Previous studies in the arid zone show that invertebrate richness and abundance decline close to water points because of changes in floristic composition and structure (James et al., 1999). Thus, these groups may be declining near water points because of a decline in their food resources. However, water points may also attract vertebrate prey, and thus may also be attractive to some raptors. The analysis of individual traits supports these findings, with only feeding level being an important variable determining how species responded to proximity to water points (Fig. 3b). Again, aerial and water feeders declined most close to water points, and ground feeders also declined. Canopy and shrub foragers were not affected.

When responses are viewed at the continent scale, bird species that rely on ground habitat for feeding and nesting were most affected and aquatic birds were no longer greatly affected. The analysis of individual traits showed that both ground nesters and feeders declined significantly, but most other groups were unaffected. Thus, we detected the greatest declines in aquatic birds at the local scale and ground nesters and feeders at the continent scale. This difference reflects the scale of our metrics. At the local scale our focus was between zero and 4.5 km from water. We expect to see the direct effects of livestock at this scale, close to water. The continental scale metric incorporates all distances from water and therefore is likely to average out direct effects seen close to water.

While the discussion so far has focused on response traits (Lavorel and Garnier, 2002; Suding et al., 2008), changes in the abundance and composition of species with particular traits might also affect ecosystem processes. For example, the reduction in abundance of predatory water bird species that feed on fish or invertebrates has potential to alter the composition of water point communities, through the disruption of trophic chains. In addition to altering the composition of fish and invertebrates in these aquatic communities, the reduction in abundance of water birds may also affect the composition and abundance of aquatic primary producers, affect nutrient levels and water quality (e.g. Carpenter et al., 2001; Beisner et al., 2003).

Traits of species helped us to uncover which processes affecting the persistence of bird species in the arid and semi-arid zones were altered with the expansion of the artificial water-point network and livestock grazing. Bird species were affected directly through the impact of livestock (trampling, muddying, fouling) on natural and artificial water points, with species reliant on water for nesting and feeding sites demonstrating the greatest population declines near water points. Bird species may have also been affected indirectly through the increase in abundance of predators, foxes and dingos, with species reliant on ground habitat for nesting, especially, and feeding, at risk of population declines. By examining traits of species and species' responses at both local and continental scales we discovered that the direct effects of livestock are seen in close proximity to water points but an important potential indirect effect of artificial water points, increased predator ranges, may be seen at larger spatial scales suggesting that it is a larger scale and more general phenomenon. This is likely because both dingos and foxes forage over large areas, whereas the detrimental effects of livestock on habitat are most acute close to water and ameliorate with distance from water (James et al., 1999; Landsberg et al., 2003). Examining species' traits provided us with more information about how water points and livestock grazing affect the arid and semi-arid bird community than looking at changes in species' population dynamics alone.

Livestock grazing has been linked to declines of bird species in previous studies (Popotnik and Giuliano, 2000; Recher, 1999). Further, traits of bird species have been used to understand population and community responses to impacts ranging from habitat fragmentation (Yamaura et al., 2006; Lees and Peres, 2008), to expansion of farm land in the UK (Shultz et al., 2005), to grazing (Martin and Possingham, 2005). For example, in primary forest patches in a region of the Amazonian 'Arc of Deforestation', bird species that were small-bodied, flock-following and terrestrial insectivores were most at risk of extinction from the fragmentation of their primary forest habitat (Lees and Peres, 2008). Martin and Possingham (2005) showed that woodland and riparian birds declined with increased grazing pressure and that foraging height preference predicted species' susceptibility to grazing. Our study adds to this literature, showing that traits can help us understand large-scale landscape change like the expansion of the network of artificial water points and livestock grazing in the Australian arid zone, and most importantly why these changes affect bird species the way that they do.

Our results presented here for birds, and in other places for plants and other animal groups (Landsberg et al., 2002, 2003; James, 2003) have identified the need for actions to plan for the potential deleterious impact of high densities of artificial water points. Traditional land acquisition approaches to secure areas of low water-point density across representative habitats as 'reserves' seem unlikely to be adopted politically and inadequate for the purpose of maintaining diffuse natural processes at large scales (Klein, 1989). Instead stewardship approaches which encourage land managers to act in the public interest on private land, often associated with publicly-funded stipends, may be more effective but are slow to be adopted in arid lands. The effectiveness of such measures, if implemented, is not yet clear.

In summary, many arid and semi-arid zone bird species declined in response to the expansion of the artificial water-point network and intensification of livestock grazing. Aquatic birds were most strongly affected close to water, likely through direct effects of livestock on both natural and artificial water sources (trampling and muddying). Species that forage or nest on the ground also showed large declines. Direct degradation of habitat through herbivory and trampling by livestock is the most likely mechanism for these declines. However, they may also be the result of an indirect effect whereby the expansion of the water-point network allows predators like dingos and foxes that are water limited to increase their duration of occupancy of parts of the landscape that they would otherwise abandon earlier. Examining traits of species helped us to undercover which process that were altered in the landscape most affected the bird community and therefore which species are most at risk.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.09.006.

References

Beisner, B.E., Dent, C.L., Carpenter, S.R., 2003. Variability of lakes on the landscape: roles of phosphorus, food webs, and dissolved organic carbon. Ecology 84, 1563–1575.

Bonnaud, E., Bourgeois, K., Vidal, E., Legrand, J., Le Corre, M., 2009. How can the Yelkouan shearwater survive feral cat predation? A meta-population structure as a solution? Population Ecology 51, 261–270.

Carpenter, S.R., Cole, J.J., Hodgson, J.R., Kitchell, J.F., Pace, M.L., Bade, D., Cottingham, K.L., Essington, T.E., Houser, J.N., Schindler, D.E., 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecological Monographs 71, 163–186.

Cole, L., 1954. The population consequences of life history phenomena. The Quarterly Review of Biology 29, 103–137.

Davies, K.F., Margules, C.R., Lawrence, J.F., 2000. Which traits of species predict population declines in experimental forest fragments? Ecology 81, 1450–1461.

Davies, K.F., Margules, C.R., Lawrence, J.F., 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology 85, 265–271.

Elton, C.S., 1958. The Ecology of Invasions. Methuen, London, UK.

Fagan, W.F., Meir, E., Prendergast, J., Folarin, A., Karieva, P., 2001. Characterizing population vulnerability for 758 species. Ecology Letters 4, 132–138.

Fensham, R.J., Fairfax, R.J., 2008. Water-remoteness for grazing relief in Australian arid-lands. Biological Conservation 141, 1447–1460.

Garnett, S.T., Crowley, G.M., Fitzherbert, K., Bennett, S., 1992. Life History Database for Australian Birds. Royal Australasian Ornithologists Union, Melbourne.

Gaston, K.J., Blackburn, T.M., 1996. Rarity and body size: importance of generality. Conservation Biology 10, 1295–1298.

Gross, N., Robson, T.M., Lavorel, S., Albert, C., Le Bagousse-Pinguet, Y., Guillemin, R., 2008. Plant response traits mediate the effects of subalpine grasslands on soil moisture. New Phytologist 180, 652–662.

Harrington, R., Owen-Smith, N., Viljoen, P.C., Biggs, H.C., Mason, D.R., Funston, P., 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. Biological Conservation 90, 69–78.

Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J., 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conservation 13, 207–251.

Holt, R.D., 1996. Food webs in space: an island biogeographic perspective. In: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York, USA, pp. 313–323.

Hutchinson, M.F., Nix, H.A., Houlder, D.J., McMahon, J.P., 1998. ANUCLIM Version 1.8 User Guide. Centre for Resource and Environmental Studies, The Australian National University, Canberra.

James, C.D., 2003. Response of vertebrates to fenceline contrasts in grazing intensity in semi-arid woodlands of eastern Australia. Austral Ecology 28, 137–151.

James, C.D., Landsberg, J., Morton, S.R., 1995. Ecological functioning in arid Australia and research to assist conservation of biodiversity. Pacific Conservation Biology 2, 126–142.

James, C.D., Landsberg, J., Morton, S.R., 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. Journal of Arid Environments 41, 87–121.

Jones, K.E., Purvis, A., Gittleman, J.L., 2003. Biological correlates of extinction risk in bats. American Naturalist 161, 601–614.

Klein, B.C., 1989. Effects of forest fragmentation on dung and carion beetle communities in central Amazonia. Ecology 70, 1715–1725.

Landsberg, J., James, C.D., Maconochie, J., Nicholls, A.O., Stol, J., Tynan, R., 2002. Scale-related effects of grazing on native plant communities in an arid rangeland region of South Australia. Journal of Applied Ecology 39, 427–444.

Landsberg, J., James, C.D., Morton, S.R., Muller, W.J., Stol, J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. Journal of Applied Ecology 40, 1008–1024.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16, 545–556.

Lawton, J.H., 1995. Population dynamics principles. In: Lawton, J.H., May, R.M. (Eds.), Extinction Rates. Oxford University Press, Oxford, UK, pp. 147–163.

Lees, A.C., Peres, C.A., 2008. Avian life-history determinants of local extinction risk in a hyper-fragmented neotropical forest landscape. Animal Conservation 11, 128–137.

Lips, K.R., Reeve, J.D., Witters, L.R., 2003. Ecological traits predicting amphibian population declines in Central America. Conservation Biology 17, 1078–1088.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Martin, T.G., Possingham, H.P., 2005. Predicting the impact of livestock grazing on birds using foraging height data. Journal of Applied Ecology 42, 400–408.

McKinney, M.L., 1997. Extinction vulnerability and selectivity: Combining ecological and paleontological views. Annual Review of Ecology and Systematics 28, 495–516.

National Land & Water Resources Audit, 2001. Landscape Health in Australia. A Rapid Assessment of the Relative Condition of Australia's Bioregions and Subregions (report). Commonwealth of Australia, Canberra.

Newsome, A.E., Catling, P.C., Cooke, B.D., Smyth, R., 2001. Two ecological universes separated by the dingo barrier fence in semi-arid Australia: interactions between landscapes, herbivory and carnivory, with and without dingoes. Rangeland Journal 23, 71–98.

Parker, A.H., Witkowski, E.T.F., 1999. Long-term impacts of abundant perennial water provision for game on herbaceous vegetation in a semi-arid African savanna woodland. Journal of Arid Environments 41, 309–321.

Pescador, M., Peris, S., 2007. Influence of roads on bird nest predation: an experimental study in the Iberian Peninsula. Landscape and Urban Planning 82, 66–71.

Pimm, S.L., Lawton, J.H., 1977. Number of trophic levels in ecological communities. Nature 268, 329–331.

Popotnik, G.J., Giuliano, W.M., 2000. Response of birds to grazing of riparian zones. Journal of Wildlife Management 64, 976–982.

Purger, J.J., Csuka, S., Kurucz, K., 2008. Predation survival of ground nesting birds in grass and wheat fields: experiment with plasticine eggs and artificial nests. Polish Journal of Ecology 56, 481–486.

Quetier, F., Thebault, A., Lavorel, S., 2007. Plant traits in a state and transition framework as markers of ecosystem response to land-use change. Ecological Monographs 77, 33–52.

Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K., Clout, M.N., 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. Proceedings of the National Academy of Sciences of the United States of America 104, 20862–20865.

Recher, H.f., 1999. The state of Australia's avifauna: a personal opinion and prediction for the new millennium. Australian Zoologist 31, 11–27.

Reid, J., Fleming, M., 1992. The conservation status of birds in arid Australia. Rangelands Journal 14, 65–91.

Saether, B.E., Engen, S., Moller, A.P., Visser, M.E., Matthysen, E., Fiedler, W., Lambrechts, M.M., Becker, P.H., Brommer, J.E., Dickinson, J., Du Feu, C., Gehlbach, F.R., Merila, J., Rendell, W., Robertson, R.J., Thomson, D., Torok, J., 2005. Time to extinction of bird populations. Ecology 86, 693–700.

Shultz, S., Bradbury, R.B., Evans, K.L., Gregory, R.D., Blackburn, T.M., 2005. Brain size and resource specialization predict long-term population trends in British birds. Proceedings of the Royal Society B – Biological Sciences 272, 2305–2311.

Stafford Smith, D.M., Morton, S.R., 1990. A framework for the ecology of arid Australia. Journal of Arid Environments 18, 255–278.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.L., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14, 1125–1140.

Thrash, I., 1998. Impact of water provision on herbaceous vegetation in Kruger National Park, South Africa. Journal of Arid Environments 38, 437–450.

Yamaura, Y., Katoh, K., Takahashi, T., 2006. Reversing habitat loss: deciduous habitat fragmentation matters to birds in a larch plantation matrix. Ecography 29, 827–834.