



Vegetation moderates impacts of tourism usage on bird communities along roads and hiking trails



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ABSTRACT

Bird communities inhabiting ecosystems adjacent to recreational tracks may be adversely affected by disturbance from passing tourism traffic, vehicle-related mortality, habitat alteration and modified biotic relationships such as the increase of strong competitors. This study investigated the effects of tourist usage of roads vs. hiking trails on bird communities in gorges of the Flinders Ranges, a popular South Australian tourist destination in the arid-lands.

High tourist usage along roads decreased the individual abundance and species richness of birds relative to low usage trails. The decrease in species richness, though less pronounced, also occurred at high-usage sites along trails. Changes in the species response to recreational disturbance/impacts varied depending on the ecology of the species. Bigger, more competitive birds with a generalist diet were overrepresented at high-usage sites along roads and trails. Species using microhabitats in lower vegetation layers were more sensitive.

However, structural and floristic complexity of vegetation was a more important factor influencing bird abundance than tourist usage. Sites with a better developed shrub and tree layer sustained higher species abundance and richer communities. Importantly, vegetation qualities moderated the negative effect of high usage on the individual abundance of birds along roads, to the extent that such an effect was absent at sites with the best developed shrub and tree layer.

To protect avifauna along recreational tracks in arid-lands gorges, we recommend the closure of some gorges or sections for vehicle or any access. Further, open space particularly for camping needs to be minimized as it creates areas of high tourist usage with modified habitat that provides birds with little buffer from disturbance.

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1. Introduction

Bird watching is a large component of nature tourism with a high economic value and popularity (U.S. Fish and Wildlife Service, 1996; Valentine, 1984). In the U.S.A. for instance, 47 million people viewed, identified or photographed birds in the 12 months prior to a national survey on recreation and the environment (U.S. Department of the Interior Fish and Wildlife Service et al., 2006). It is also one of the fastest-growing outdoor recreational activities worldwide, including in Australia (Jones and Buckley, 2001).

Bird watching or other tourist activities performed along recreational tracks may affect the abundance of birds via numerous pathways: for example, bird species that are susceptible to visual

and acoustic disturbance become displaced from habitat in proximity to recreational tracks (van der Zande and van der Vos, 1980). Birds may suffer from road mortality (Forman and Alexander, 1998). The vegetation along tracks is often considerably altered, making these habitats less suitable for many bird species (Hammit and Cole, 1998). Relationships between different bird species may be modified along recreational tracks with edge-tolerant bird species displacing other less competitive bird species (Grey et al., 1997). Further, predators may gain easy access to bird habitat via tracks (Miller et al., 1998). These processes may act to reduce avian diversity like other forms of ecological decay such as deforestation and habitat fragmentation (e.g., Brooks et al., 1999).

The severity of the effects and thus the risk to the conservation of bird species depends on whether the changes are temporary or long-term and whether they affect certain individuals, populations (Mallord et al., 2006), the species as a whole or an entire bird community (Knight and Gutzwiller, 1995; Sekercioglu, 2002). Avian communities are very sensitive to changes in habitat (Mac Nally,

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1990). Thus tourism-induced changes in bird habitat need to be recognised within natural variability in vegetation. This may be particularly relevant in arid Australian ecosystems with their typically heterogeneous distribution of vegetation (Dunkerley and Brown, 1995). The structure and species composition ('floristics') of vegetation were in fact more important predictors of bird community structure and species abundance than anthropogenic disturbance in Central Australia (Pavey and Nano, 2009). Structurally (reviewed by Tews et al., 2004) or floristically (Fleishman et al., 2003) complex habitats may provide more niches, and so a greater species richness. They also offer ample possibilities for hiding, whereby birds may perceive human disturbance as less threatening.

Although Australia has many excellent birdwatching sites (Jones and Buckley, 2001), few studies have examined the effects of recreation on bird communities (e.g., as reviewed for non-motorized recreation by Steven et al., 2011). This study was conducted in the Flinders Ranges of South Australia, where gorges provide a particularly rich habitat for a diverse bird community in an arid climate and have many values attractive to tourists. Gorges were divided among those accessible via unpaved but well-maintained back-country roads, and those restricted to hiker access only. Delimiting access to recreation areas is one in a range of tools available to managers of protected-areas to mitigate aversive visitor impacts. However, to our knowledge no study has directly compared the influence of visitor usage of roads with that of hiking trails on bird communities, even though this division in access options is common throughout nature-based tourism destinations in Australia, and presumably worldwide.

Thus, we asked how the mode of access to gorges (roads or hiking trails) and tourism activity within them (high or low usage) would influence bird metrics (total number of individuals, species richness, community composition): (1) We predicted a lower species richness and lower bird abundance at high-usage sites on the assumption that those species intolerant to the more disturbed conditions would be absent from the community. However, we allowed for a counter hypothesis that species attracted to disturbance may balance or outweigh those repelled. (2) We predicted from research examining the nature and intensity of tourism impacts in our study area (Wolf et al., 2012) that high usage effects along roads would be more severe than along hiking trails because these accrued primarily from differences in prolonged camping activities on open space rather than differences in the number of passing visitors. (3) Finally, we took into account the variation in the quality and structure of bird habitat within and between sites in our analyses. The main covariables were the structural and floristic complexity of vegetation and the division of bird usage by vegetation strata to allow for vertical complexity.

2. Material and methods

2.1. Study area

This study was conducted in the central and northern Flinders Ranges in South Australia, from the Flinders Ranges National Park (Wilpena: lat. 31° 30'S, long. 138° 30'E) into the Vulkathunha-Gammon Ranges National Park (Balcanoona: lat. 30° 30'S, long. 139° 30'E). The Flinders Ranges extend northwards into the arid zone, forming a corridor of higher rainfall that allows fauna typical of wetter regions to subsist. The ranges also provide a wide variety of microclimates due to small-scale topography and landforms (Ried et al., 1996). Consequently, the Flinders Ranges, only 4% of the South Australian land area, support a disproportionately high 50% of the total non-marine bird species (Paton, 1980; Ried et al., 1996). These comprise at least 241 bird species belonging to 65 families,

and 70 of these species hold some form of conservation risk rating (Brandle, 2001).

One of the best places to observe birds in the Flinders Ranges are the gorges. These retain water, provide shade, and support a diverse multi-layered vegetation which creates habitat suitable for many bird species. The dominant vegetation community is riparian woodland (Brandle, 2001). Habitats include tall cliff faces and rocky outcrops, a tall canopy of River Red Gums (*Eucalyptus camaldulensis*), a lush mid-storey layer dominated by dense stands of Pointed Mallee (*Eucalyptus socialis*) and shrublands composed of various species along with ephemeral herbs and sedges near the scattered pools of water. Ground cover is heterogeneous, varying from dense vegetation patches with a particularly pronounced shrub thicket to barren areas.

2.2. Study sites

Visitors to the Flinders Ranges access the gorges from a network of roads and trails that also provide ingress to a variety of official and unofficial campsites. We selected seven major gorge systems that were either mainly accessed by vehicles ($n_{\text{vehicle-gorge}} = 3$) or exclusively accessible to hikers ($n_{\text{hiker-gorge}} = 4$). In each gorge type, we started close to the entrance and established belt transects at 40 sites with a typical spacing of about 400 m (minimum 250 m) (Fig. 1a–c). We minimized pseudoreplication, that might have resulted from re-sampling the same birds, by choosing transects in separate meanders of a gorge. In the following, means ± 1 SE are presented unless indicated otherwise. The transects were on average 92.5 ± 3.6 m wide (= average width of gorge sections) and 50 m long. They had to contain a distinct recreational track (roads: 5 ± 0.2 m wide; trails: 1.2 ± 0.15 m wide) and a creek bed (11.6 ± 0.9 m wide), which were separated by at least 30 m (46.9 ± 4.5 m). Roads were unpaved and composed of gravel, dirt or a mix of the two.

Previously each belt transect had been classified into low ($n_{\text{road sites}} = 21$; $n_{\text{trail sites}} = 22$) or high usage ($n_{\text{road sites}} = 19$; $n_{\text{trail sites}} = 18$) (Wolf et al., 2012), thus accounting for local-scale variation in usage along the same roads and trails. The categorisation into usage classes was based on differences in the number of passing tourists, their passing speed, the percentage of stopping tourists, their stop time, the number of day- and night-campers, the average camp-time by day and several proxy indicators of visitor usage. High and low-usage sites along trails mainly differed in their number of visitors passing daily (high: 16.6 ± 1.3 ; low: 3.9 ± 0.9) while camping activity was nearly non-existent within hiker gorges. In contrast, high and low-usage sites along roads received a similar number of visitors passing daily (high: 23.7 ± 1.8 ; low: 16.8 ± 1.7) but strongly differed in camping activity with greater numbers of day (high: 4.82 ± 1.4 ; low: 0.26 ± 0.1) and night campers (high: 2.18 ± 0.6 ; low: 0.07 ± 0.04), their longer daily dwell times (high: 337.53 ± 17.8 min per day; low: 55.10 ± 21 min per day) and largely extended sizes of camping areas (high: $57\,149 \pm 33\,383$ m²; low: 374 ± 202 m²). Visitors were prohibited from bringing dogs or other pets into our study area and we did not observe a single case of non-compliance.

We accepted that, through a long history of pastoralism and then tourism, the whole study area had been subject to anthropogenic disturbance at some time, so we did not seek out sites of 'no usage'. Rather we chose low tourism usage as a baseline and divided the reactions of bird species in high-usage sites to those repelled from, attracted to or behaving neutrally towards them. As we did not intend to measure the environmental effects of camping per se, but of recreational tracks in general independent of their dominant use, belt transects had been placed so there was not more than approximately 10% of overlap with campgrounds (Fig. 1a).

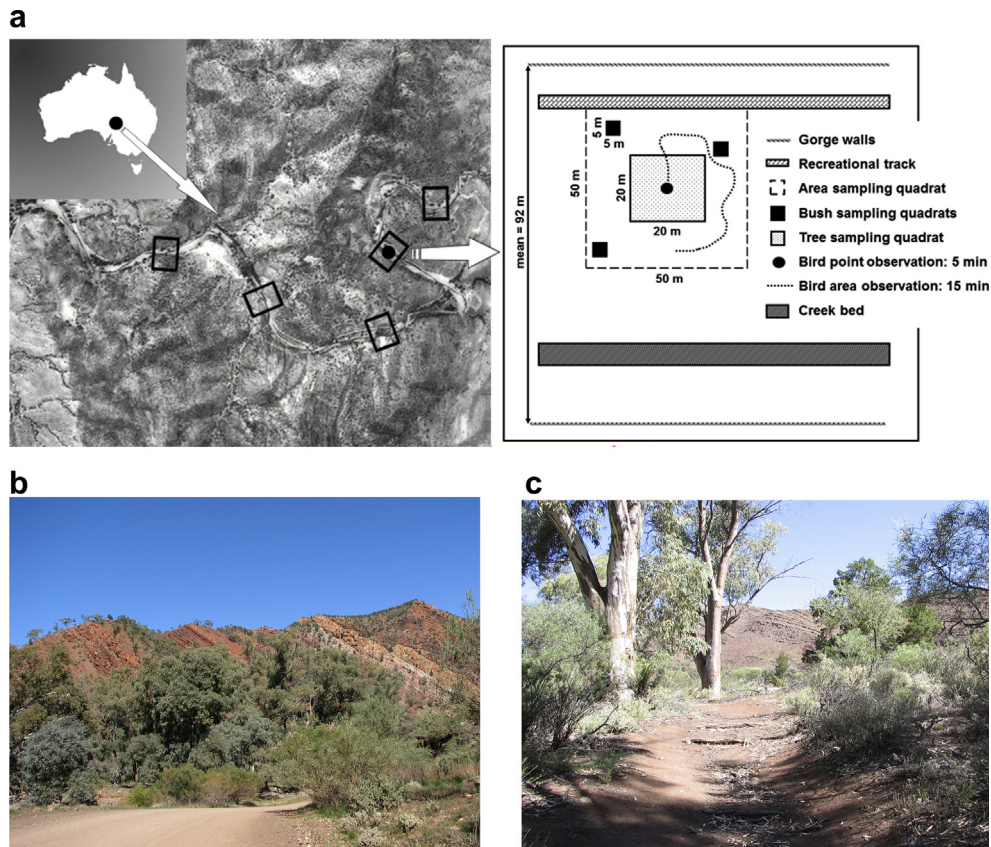


Fig. 1. Illustration of the experimental set up by (a) a sample of study sites in Brachina Gorge (lat. 31° 34'S, long. 138° 56'E; aerial photograph, survey/frame no. 2320/24, reproduced with permission of the South Australian Department of Lands) and the distribution of sampling quadrats within each study site. Representative sections of (b) a road verge, (c) a trail verge.

2.3. Census of the avifauna

Bird sampling was conducted throughout the day during July to December 2006 and 2007. Wet and windy conditions were avoided (Bibby et al., 2000). Drab clothing was worn as birds have reacted to the colour of observers' clothing (Gould et al., 2004). The nomenclature and taxonomy for bird species follows Simpson and Day (2004).

We used standardized area counts (Bibby et al., 2000; Loyn, 1986) during which we counted each bird seen in 20 min while surveying a square plot of 50 × 50 m within the belt transects (Fig. 1a). We further recorded the vertical position of a bird at first notice in five classes: ground, shrub, small trees up to 6 m, tall trees, air/cliff face. The plots were demarcated on one side by the recreational track, from which they extended 50 m in the direction of the creek bed. During the first 5 min of the census a single observer stood still and quiet at the centre of the plot and performed a standard point count using binoculars (10 × 42). In the last 15 min, the observer moved around slowly, stopping at suitable vantage points to look for birds, to access vegetation patches to flush cryptic individuals, and to approach any species that could not be identified from a distance. Through this area sampling approach small birds hidden in patches of dense shrub or the foliage of tall eucalypt trees were unequivocally identified and correctly counted. In contrast, traditional survey methods such as transect or point counts may have caused an inappropriate bias towards sites with less shrub and tree cover where the birds were easier to detect (Craig and Roberts, 2001). Potential errors of the area count method are likely to affect observations at all sites and should therefore not

bias inter-site comparisons (Craig and Roberts, 2001). The flight direction of birds that were flushed was followed briefly to avoid recording the same individuals again.

Each plot was surveyed five times during the study period by two independent observers who had standardized their observation technique. We minimized resampling the same birds within the same or adjacent sites by distributing the observation periods across a considerable time period of two years, and six different months in each year. Further, neighbouring transects were spaced at a considerable distance in separate meanders and not sampled consecutively. Finally, the observation plots were relatively large, and the researchers ensured that they varied their direction of movement during the different observation periods.

Prior to analysis, the individual species-counts of the ten sampling occasions were summed up to the total number of individuals and the total number of species (species richness) per transect. Plotting of species accumulation curves confirmed that an adequate sample had been taken as the species curve levelled off from seven observations onwards.

2.4. Sampling of habitat characteristics

In order to investigate the relationship between bird communities and tourism-induced changes along with natural variation in habitat, data on structure and floristic composition of vegetation were collected on all bird census plots within three 5 m × 5 m quadrats for shrubs and one 20 m × 20 m quadrat for trees.

The shrub sampling quadrats were distributed randomly within each plot. Within these quadrats shrubs were measured with joined

electrical conduit pipes that were marked in centimetre sections. The cover was recorded by measuring the maximum length and width of each shrub and the area calculated as an ellipse. The area that each shrub species covered in total was divided by the total area of the shrub sampling quadrats to calculate a species-percentage cover. We then summed these percentages for the total percentage of overlapping cover per transect. The height of each shrub from its base to the highest part of its bulk (excluding 'outlier' branches) was measured and these values were averaged per species and transect.

The tree sampling quadrat was centred in the bird census plot, where visual estimates of the projected canopy cover were taken and the diameter at breast height (DBH) and the height (optical height meter PM-5/1520 SUUNTO, Finland) of all tree species measured. The multiple stems of eucalypt trees growing as 'mal-lees' were added up and recorded as one tree if they appeared to spring from one underground lignotuber. DBH and height values were averaged per species and site.

Diversity of shrubs and trees per transect was expressed through the heterogeneity diversity index Simpson's $E_{1/D}$ (advantages of this heterogeneity measure over its alternatives are reviewed by Magurran, 2004) based on species-cover values. All these assessments produced a total of eight vegetation variables (Table 1).

To determine how much vertical substrate was available in the habitat, a 2-m long pipe was held vertically beside the vegetation at 120 random sampling points within the bird census plots. The number of 0.1 m-long sections (cylinders) that contained vegetation within a radius of 0.1 m from the pole was counted as a one of 20 possible 'hits' to determine the vertical structure of the vegetation, following the 'pole technique' (Mills et al., 1991). Large numbers of hits per site indicate that hits were obtained from many sampling points and different vertical layers of the vegetation. For smaller numbers, the hits may have been obtained from different sampling points, different vertical layers or both.

Given the aridity of our study area, we also estimated the size of any water pools on our transects as they may influence the abundance and richness of our bird community (Schneider and Griesser, 2009). However, water pools (found at 6 transects) were so rare that we omitted them from our analysis.

2.5. Data analyses

Overall, roads had greater usage than trails and so the distinction between high and low usage was dependant on the mode of

gorge access (Wolf et al., 2012). Therefore, we first analysed how low and high-usage sites behaved in each gorge type, and then compared the emergent patterns between gorge types.

2.5.1. Bird species community and indicator species

To reduce the number of vegetation variables (Table 1), a principal components analysis (PCA) with PRIMER v6 (Clarke and Gorley, 2006) and Euclidean distance as the distance measure was employed. The vegetation variables were replaced by their ranks prior to PCA, which otherwise would be dominated by outlier-values and input variables with the largest measurement scales (Clarke and Gorley, 2006). We admitted the PCA axes scores as continuous variables in several of the following analyses to account for the covariate effect of vegetation variability. In the case of statistically significant effects of a particular PCA axis, the factor loadings determined which of the actual input vegetation variables were instrumental in differentiating our sites.

Bird community composition was compared to tourist usage intensity by conducting a two-way factor permutational multivariate analysis of variance using PERMANOVA+ (Anderson et al., 2008). PERMANOVA (Anderson, 2001) tests the response of variables to experimental factors based on any resemblance measure without assuming that the original variables are normally distributed (McArdle and Anderson, 2001). Prior to analysis, bird count data were square-root-transformed to lessen the impact of high-abundance species. We performed PERMANOVA+ on a Bray–Curtis similarity matrix of the species data with 999 permutations. In our study design, the sites represented replication ($n_{\text{vehicle gorges}} = 40$ levels; $n_{\text{hiker gorges}} = 40$ levels) at the lowest design level and were spatially blocked by the factor 'gorge' (random, vehicle gorges: 3 levels, hiker gorges: 4 levels). The treatment factor of interest was 'usage intensity' (fixed, 2 levels) which was crossed with gorge. Further, the five PCA axes were included as a covariate into the PERMANOVA+ models. Final models were extracted by excluding factors with P -values >0.25 (Underwood, 1997; Winer et al., 1991) from initial models in a manual, stepwise-backward selection procedure (Crawley, 2007). A statistically significant interaction between gorge and usage intensity was followed up with post hoc pairwise tests (999 permutations) which provided simple main-effect tests (Field, 2005).

Finally, multivariate patterns were visualized by ordinating the sampling quadrats in a two-dimensional species-space with non-metric multidimensional scaling (nMDS) in PRIMER v6. As nMDS displays samples without attempting statistical inference, it can be used to identify visual patterns in community composition even in complex, nested designs where the independence of samples may be violated.

To test whether species were under- or over-represented at high vs. low usage conditions, three-way hiloglinear analyses (model factors: gorge \times usage intensity \times bird species) were conducted in SPSS for Windows 17.0 (SPSS, 2008). Given that the triple interaction was not statistically significant, neither for the data from vehicle nor hiker gorges, chi-square tests (usage intensity \times bird species) were calculated on data pooled over the different gorges without violating the assumption of independence. Using species with more than 10 records ensured that no more than 20% of the expected cell frequencies were less than 5 and none below 1 (Field, 2005). For each cell in the dual contingency table, the standardized residual was calculated as the difference between the observed and expected frequencies divided by an estimate of their standard deviation. Values <-1.96 or >1.96 are statistically significant at the $P < 0.05$ level (Siegel and Castellan, 1988), and the frequency of observations in that cell are lower and higher, respectively, than expected. This indicates that a species is associated with high usage (referred to as

Table 1
Factor loadings of the ranked vegetation variables on the component scores of the first two PCA axes obtained from sites ordinated in vegetation variable space. Significant loadings are marked in bold.

| Vegetation variable | (1) Next to roads | | (2) Next to trails | | | | | |
|----------------------------------|-------------------|-----|--------------------|-----|--------------|-----|------------|-----|
| | PCA axis 1 | | PCA axis 2 | | PCA axis 1 | | PCA axis 2 | |
| | r_p | P | r_p | P | r_p | P | r_p | P |
| Vertical structure ^a | 0.140 | | 0.003 | | 0.860 | ** | -0.052 | |
| Shrubs | | | | | | | | |
| Cover (summed %) | 0.789 | ** | 0.161 | | 0.913 | ** | 0.082 | |
| Height (mean cm) | 0.837 | ** | 0.070 | | 0.531 | ** | -0.295 | |
| Diversity (Simpson's $E_{1/D}$) | 0.776 | ** | 0.242 | | 0.019 | | 0.248 | |
| Trees | | | | | | | | |
| Cover (summed %) | 0.584 | ** | -0.036 | | 0.799 | ** | 0.256 | |
| Height (mean m) | 0.447 | * | -0.720 | ** | 0.095 | | 0.280 | |
| DBH (mean cm) | 0.074 | | -0.732 | ** | 0.168 | | 0.112 | |
| Diversity (Simpson's $E_{1/D}$) | 0.156 | | 0.338 | * | -0.112 | | -0.546 | ** |
| Variance explained (%) | 35.20 | | 18.20 | | 47.20 | | 17.20 | |

$P < 0.05$, ** $P < 0.001$, n (sites next to roads) = 40; n (sites next to trails) = 40.

^a Number of 0.1 m \times 0.1 m cylinders of a 2-m pole containing vegetation, sampled at 120 points per site.

'attracted to/indicative of' high usage) or low usage (referred to as 'repelled from' high usage).

To test if birds at high-usage sites were more frequently observed in lower habitat strata we also performed a hiloglinear analysis (gorge \times usage intensity \times height level) with a follow-up chi-square test (usage intensity \times height level). To examine whether birds used strata in proportion to their availability under both high and low tourist usage, we performed a PERMANOVA+ on the cover of shrubs and trees (<6 m and >6 m) in relation to the usage intensity and employed the same design as in the community analysis except that no covariables were input.

2.5.2. Number and species richness of birds

Step-wise multiple regression was used to analyse the relationship of the number of birds and the species richness of the community with the usage intensity and habitat characteristics of the study sites. Usage intensity, gorge and the PCA axes were included as factors in the initial regression model. To test whether the habitat characteristics moderate the relationship between the bird metrics and the usage intensity, the first-order interaction between the usage intensity and the PCA axes was also included by using their cross-products.

The validity of the multiple regression models was justified by checking the model assumptions (Quinn and Keough, 2004). Multicollinearity between the independent variables used in the regression was weak, as indicated by collinearity statistics (Field, 2005) such as variance inflation factors. All univariate statistical analyses were carried out with SPSS for Windows 17.0 (SPSS, 2008). We accepted the 5%-level of alpha as a threshold to decide whether to reject or fail to reject a null hypothesis.

3. Results

3.1. Habitat characteristics

The main vegetation variables were summarized into five statistically independent axes by means of an unrotated PCA, all with eigenvalues >1 (Tables 1.1 and 1.2). Our results focus on the first two axes as they were statistically significant predictors of bird metrics in the PERMANOVA+ and/or regression analysis.

PCA axis 1 (PC1) and 2 (PC2) explained 35.2% and 18.2%, respectively, of the total variation in vegetation characteristics between sites along roads, indicating that the extracted components represent the site relationships reasonably well (Table 1.1). All (ranked) vegetation variables were positively correlated with PC1, and moderate to strong, factor loadings showed up for the cover, height and diversity of shrubs as well as for the cover and height of trees (Table 1.1). This aligns well with our personal observations in the field where sites with a structurally well developed and diverse shrub and tree layer contrasted with sites where these elements of the vegetation were much less developed. PC2 described a gradient in decreasing height and DBH of trees. This is consistent with our observations of sites with a lush mid-storey layer dominated by dense stands of Pointed Mallee compared to sites with a tall canopy of River Red Gums.

Along hiking trails, PC1 and PC2 accounted for 47.2% and 17.2%, respectively, of the total variation in vegetation characteristics between sites, again indicating that the extracted components represented the site relationships quite well (Table 1.2) (Clarke and Gorley, 2001). The cover and height of shrubs as well as the tree cover were positively correlated with PC1 which implies a pattern of site separation similar to what we had observed along roads. In addition, the vertical structure of the vegetation strongly increased along PC1 (Table 1.2). Tree diversity was the main (negative) correlate with PC2.

Campsites adjacent or partially traversing our bird census plots contained $12.9\% \pm 1.3$ of vegetation cover up to 1.5 m in height along roads and $18.6\% \pm 3.9$ along trails, whereas in the camp-free surroundings the values were $32.3\% \pm 2.2$ and $39.2\% \pm 4.3$ cover, respectively.

3.2. Bird species community and indicator species response to tourism usage and vegetation

The community composition of the avifauna observed along roads differed between high and low-usage sites (Table 2.1). Pair-wise comparisons revealed that this effect was not consistent across trails as indicated by the statistically significant interaction (Table 2.2). Both tourist usage and vegetation characteristics differentiated bird communities. The nMDS ordinations displayed a stratification of sites by usage intensity along roads (Fig. 2a) and trails (Fig. 2b) but these results need to be interpreted with caution considering the high stress of the plots (>0.2). Habitats with better developed vegetation (= higher PC1 values) supported a different community than habitats with less developed vegetation along both roads (Table 1.1) and trails (Table 1.2).

Numerous species were repelled from high-usage sites, whilst some species were attracted (Table 3). Examples of species distinctive of high usage conditions were Meliphagidae (e.g., honeyeaters and miners), Artamidae (e.g., Australian Magpie and Grey Butcherbird), Corvidae (e.g., Australian Raven) and Cacatuidae (e.g., Galah, Little Corella). Species more abundant under low usage conditions came from a wide range of families and also included several water birds and doves. Roads and trails shared a considerable percentage of species that were attracted to high-usage sites (75%) and a smaller percentage of species that were repelled from high-usage sites (14.3%).

Beside all roads, high trees were more often used at high-usage sites. The ground and shrubs were more frequented at low-usage sites along one of the three roads, and either ground or shrub usage was more common at low-usage sites along the two remaining roads (Fig. 3a). Along trails, birds predominantly were sighted in shrub layers under low tourism usage but high trees under high usage (Fig. 3b). Location was not biased by the availability of these strata as the cover of shrubs (roads: pseudo- $F_{(1,34)} = 0.42$, $P_{(perm)} = 0.641$; trails: pseudo- $F_{(1,32)} = 0.235$, $P_{(perm)} = 0.838$) and of trees >6 m (roads: pseudo- $F_{(1,34)} = 0.622$, $P_{(perm)} < 0.617$; trails: pseudo- $F_{(1,32)} = 0.218$, $P_{(perm)} < 0.772$) were not statistically significantly different between high and low-usage sites. The

Table 2

Final PERMANOVA+ models including all main terms and interactions which significantly (bold values) explained variation in bird community composition in arid-lands gorges.

| Treatment variable | (1) Next to roads | | | (2) Next to trails | | |
|----------------------------|-------------------|----------|---------------------------|--------------------|----------|---------------------------|
| | df ^a | Pseudo-F | $P_{(perm)}$ ^b | df | Pseudo-F | $P_{(perm)}$ ^b |
| Usage intensity | 1, 35 | 3.16 | 0.001 | 1, 3 | 0.88 | 0.536 |
| Gorge | 2, 35 | 2.95 | 0.001 | 3, 31 | 4.87 | 0.001 |
| Usage intensity x gorge | NA NA | NA | NA | 3, 31 | 2.27 | 0.001 |
| Vegetation variable | | | | | | |
| PCA axis 1 | 1, 35.90 | 2.30 | 0.003 | 1, 31 | 1.92 | 0.016 |

Note: Terms for which $P_{(perm)} > 0.25$ (Winer et al., 1991; Underwood, 1997) were excluded from final models (denoted as 'NA') unless they figured in higher order or nested terms.

^a Denominator degrees of freedom that are not integers are approximated following the Satterthwaite (1946) method.

^b In PERMANOVA (Anderson, 2001), the distribution of the pseudo-F statistic is obtained by using a permutation procedure.

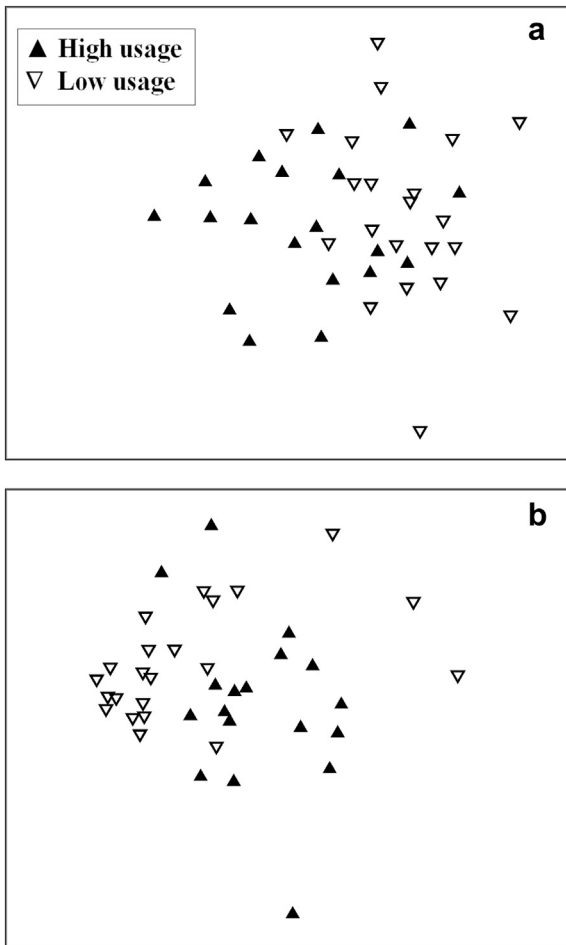


Fig. 2. NMDS plots of sampling quadrats based on avifauna composition, indicating differences in avifauna between high (▲) and low (▽) tourism usage sites next to (a) roads (stress = 2.5) or (b) hiking trails (stress = 2.1) in arid-lands gorges. No scales are shown on the axes as the orientation of a nMDS diagram is arbitrary (Clarke and Gorley, 2006).

number of birds present in low trees or circling in the air/cliff-dwelling was not associated with usage level in either track type.

3.3. Number of birds and species richness in response to tourism usage and vegetation

The bird community comprised 75 species (roads: $n = 6341$ sightings; trails: $n = 5982$ sightings). Road habitat with taller shrubs and trees and a more extensive shrub and tree cover as well as a greater diversity of shrubs (Table 1.1) sustained more birds (Table 4.1a; Fig. 4a) and a richer bird community (Table 4.1b; Fig. 4b). In contrast, high tourist usage reduced the number of birds (Table 4.1a; Fig. 4a) and the bird species richness (Table 4.1b; Fig. 4b). However, the interaction between PC1 and high usage, manifested as a change in the slope of the regression lines for different usage levels, suggests that a more complex vegetation (greater PC1 values) mitigated the effect of high usage (Table 4.1a; Fig. 4a). Consequently, at sites with the best vegetation development similar numbers of birds were counted in high and low usage areas. The species richness of the community was similarly less reduced in more complex vegetation along roads; albeit this was only a trend (Fig. 4b). Along trails vegetation seemed to also have a mildly mitigating effect against high usage but only on bird species richness and not abundance (Fig. 4c–d). The effect was likely not as

strong since the overall usage intensity along trails was lower compared to roads.

According to the factor loadings along trails (Table 1.2), shrub and tree cover and the height of shrubs, as well as the vertical structure of the vegetation, positively influenced bird numbers (Table 4.2a; Fig. 4a) and species richness (Table 4.2b; Fig. 4b). In contrast, high usage did not reduce bird numbers along trails (Table 4.2a; Fig. 4c), but still reduced species richness (Table 4.2b; Fig. 4d) although to a less acute extent, as indicated by less spatial separation between the regression lines at different usage levels. A trend for an interaction effect between PC1 and high usage on species richness was noticeable too, suggesting the same protective effect of vegetation complexity as determined for the road data. Finally, a lower number of birds was apparent in sites where tree diversity was reduced (= higher PC2 values; Table 4.2).

Overall, PC1 explained the greatest percentage of variation (= highest R^2 -values) in the number and species richness of bird communities along both roads (Table 4.1) and trails (Table 4.2): it has a greater predictive importance than tourist disturbance.

4. Discussion

4.1. Habitat effect on bird metrics

The functional relationship between bird metrics and tourist usage (or infrastructure) is complex and cannot be separated from the effect of vegetation characteristics. In our study, structural and floristic vegetation characteristics proved to exert the stronger influence on bird abundance and species richness. Similarly the species richness of a bird community in a large protected area in the Chihuahuan Desert, U.S.A., and the relative abundance of numerous bird species depended strongly, and in some areas solely, on habitat variables along with road and other infrastructure variables (Gutzwiller and Barrow, 2003). In boreal bird communities in Finland bird occurrence was mainly determined by habitat characteristics of the area (Kangas et al., 2010).

Both structural properties (vertical structure of the habitat, cover and height of shrubs and trees) and floristics (the diversity of shrubs and trees) described variation in bird metrics. Structure affects the amount and spatial extent of available resources such as foraging and nesting substrate or shelter from predators (Leimgruber et al., 1994; Urban and Smith, 1989), and ultimately the quantity and types of niches that are available. Higher vegetative diversity typically translates into broader niche dimensions and therefore supports more bird species (Fleishman et al., 2003; Monadjem, 2002; Rotenberry, 1985).

The above results are not novel but an important finding of our study was that the deleterious effect of high tourist usage on the total bird abundance along roads was mitigated if the vegetation was structurally better developed. The interaction between PC1 and 'high usage' constitute what has been referred to as a moderator effect in the context of regression because the slope of the relation between the dependent variable and one explanatory variable (high usage) varies with or is moderated by the values of another explanatory variable (PC1) (Hair et al., 1998). Likely birds benefit from structurally better developed vegetation as a protective barrier against potential predators (Eggers et al., 2008; Jones and Hungerford, 1972).

Structurally better developed vegetation may have also prevented tourists from approaching birds. Murison et al. (2007), for example, found that habitat with denser and shorter vegetation was an effective barrier preventing people and dogs from venturing off the path and causing disturbance to breeding birds. Vegetation also provides a place to escape and hide from people and forms a buffer against direct disturbance from noise. Bird assemblages

Table 3
Bird taxa (and their typical vertical position) indicative¹ of (a) high or (b) low tourist usage sites next to roads and trails in arid-lands gorges.

| Scientific name | Common name | Vertical position | (1) Next to roads | (2) Next to trails |
|-------------------------------------|--------------------------|-------------------|-------------------|--------------------|
| (a) High usage indicators | | | | |
| <i>Manorina flavigula</i> | Yellow-throated Miner | Low trees | High usage | High usage |
| <i>Gymnorhina tibicen</i> | Australian Magpie | High trees | High usage | High usage |
| <i>Cacatua sanguinea</i> | Little Corella | High trees | High usage | High usage |
| <i>Cacatua roseicapillus</i> | Galah | High trees | High usage | High usage |
| <i>Ocyphaps lophotes</i> | Crested Pigeon | Ground | High usage | High usage |
| <i>Barnardius zonarius barnardi</i> | Australian Ringneck | Shrub | High usage | High usage |
| <i>Cracticus torquatus</i> | Grey Butcherbird | Low trees | High usage | High usage |
| <i>Lichenostomus ornatus</i> | Yellow-plumed Honeyeater | Low trees | High usage | High usage |
| <i>Manorina melanocephala</i> | Noisy Miner | Shrub | High usage | High usage |
| <i>Corvus coronoides</i> | Australian Raven | High trees | High usage | Nonsignificant |
| <i>Lichenostomus plumulus</i> | Grey-fronted Honeyeater | Low trees | High usage | Nonsignificant |
| <i>Psephotus haematonotus</i> | Red-rumped Parrot | Low trees | High usage | Not tested |
| (b) Low usage indicators | | | | |
| <i>Malurus lamberti</i> | Variiegated Fairy-wren | Shrub | Low usage | Low usage |
| <i>Pardalotus striatus</i> | Striated Pardalote | Low trees | Low usage | Low usage |
| <i>Anas gracilis</i> | Grey Teal | Ground | Low usage | Low usage |
| <i>Merops ornatus</i> | Rainbow Bee-eater | High trees | Low usage | Low usage |
| <i>Geopelia striata</i> | Peaceful Dove | Ground | Low usage | Low usage |
| <i>Pachycephala rufiventris</i> | Rufous Whistler | Low trees | Low usage | Low usage |
| <i>Zosterops lateralis</i> | Silvereye | Shrub | Low usage | Not tested |
| <i>Acrocephalus stentoreus</i> | Australian Reed-warbler | Ground | Low usage | Not sighted |
| <i>Anas castanea</i> | Chestnut Teal | Ground | Low usage | Not sighted |
| <i>Dicaeum hirundinaceum</i> | Mistletoebird | Shrub | Low usage | Nonsignificant |
| <i>Dromaius novaehollandiae</i> | Emu | Ground | Low usage | Nonsignificant |
| <i>Anas superciliosa</i> | Pacific Black Duck | Ground | Low usage | Nonsignificant |
| <i>Acanthiza chrysorrhoa</i> | Yellow-rumped Thornbill | Shrub | Nonsignificant | Low usage |
| <i>Acanthiza apicalis</i> | Inland Thornbill | Shrub | Nonsignificant | Low usage |
| <i>Petroica goodenovii</i> | Red-capped Robin | Shrub | Nonsignificant | Low usage |
| <i>Geopelia cuneata</i> | Diamond Dove | Ground | Nonsignificant | Low usage |
| <i>Climacteris picumnus</i> | Brown Treecreeper | Shrub | Nonsignificant | Low usage |
| <i>Falco berigora</i> | Brown Falcon | Air, cliff | Nonsignificant | Low usage |

¹Marked in bold are the significant greater abundances of certain bird species under particular tourism usage conditions based on a three-way hierarchical analysis (model factors: gorge × tourism usage × bird species) and subsequent chi-square analysis of the interaction effect between tourism usage and bird species (Road: $\chi^2(46) = 608.16$, $P < 0.001$; Trail: $\chi^2(42) = 973.4$, $P < 0.001$). Species with less than 10 observations ('not tested') were not included in the chi-square test.

protected by dense shrubbery in coastal New Jersey, for example, persisted in spite of on-going disturbance by human observers (Burger et al., 1995). A protective barrier may reduce alert distances of birds in the proximity of pathways (Fernandez-Juricic et al., 2001), and thus may ultimately prevent birds from taking flight unnecessarily. Conversely, cover and resulting visibility does not always influence escape decisions by birds as these may be traded off against other essential behaviour such as foraging (Boyer et al., 2006).

4.2. Impacts of tourist usage on bird metrics

4.2.1. Number of individuals

High-usage sites along roads had substantially fewer birds than low-usage sites. Fewer birds could be a consequence of birds avoiding high usage road sites (Buckley, 2004; reviewed by Liddle, 1997) or a lower survival or reproductive output of birds at these sites (e.g., Pearce-Higgins et al., 2007). Results elsewhere vary. Visitor activity reduced the number of birds over a disturbance gradient in Australian rainforest (Jones and Neelson, 2005), in response to pedestrians in parklands (Fernández-Juricic, 2000), and in the presence of bird watching groups (Remacha et al., 2011). In contrast, a greater density of birds has been observed at some camping and picnicking sites (Densmore and French, 2005) and in urbanized areas (Marzluff et al., 2001) relative to the surrounding natural or less developed areas. These patterns are often ascribed to the presence of a few, highly abundant species that successfully exploit anthropogenically-generated resources such as food and outweigh the number of birds that are repelled by the accompanying disturbance (e.g., Emlen, 1974).

If tourist usage is a main driver of variation in bird abundance, then the lack of a substantial decrease along trails in our study suggests that tourist impacts were less intrusive there than adjacent to roads. The differential between high and low-usage sites along roads at our study site was greater than trails likely because of (1) elevated levels of direct disturbance due to the greater presence of prolonged camping usage and higher noise emissions associated with vehicle traffic, (2) the effect of road-kill (evidenced by bird corpses found along roads), and (3) the stronger, more pervasive modification of the immediate high usage roadsides as well as the larger number of campgrounds with their open-space character (Wolf et al., 2012).

4.2.2. Species richness and community composition

High tourist usage reduced the species richness of bird communities along both roads and trails. Unlike bird abundance, a reduction in species richness has more consistently been found in other studies of disturbance effects. For example, Densmore and French (2005) counted fewer species (67% of grand total) in Australian recreation areas than in the surrounding natural hinterland (87%) which is consistent with Jones and Neelson's (2005) observations. Urbanization also reduces bird species richness in what McKinney (2006: 247) has referred to as "biotic homogenization" under disturbed conditions which was apparent for instance in Leveau and Leveau's (2012) comparison of urban, suburban and periurban areas.

Many of our high-usage indicator species are common inhabitants of urban and recreation areas or edge habitat throughout Australia (Densmore and French, 2005; Luck et al., 1999; Parsons et al., 2003; Piper and Catterall, 2006; Sewell and Catterall, 1998).

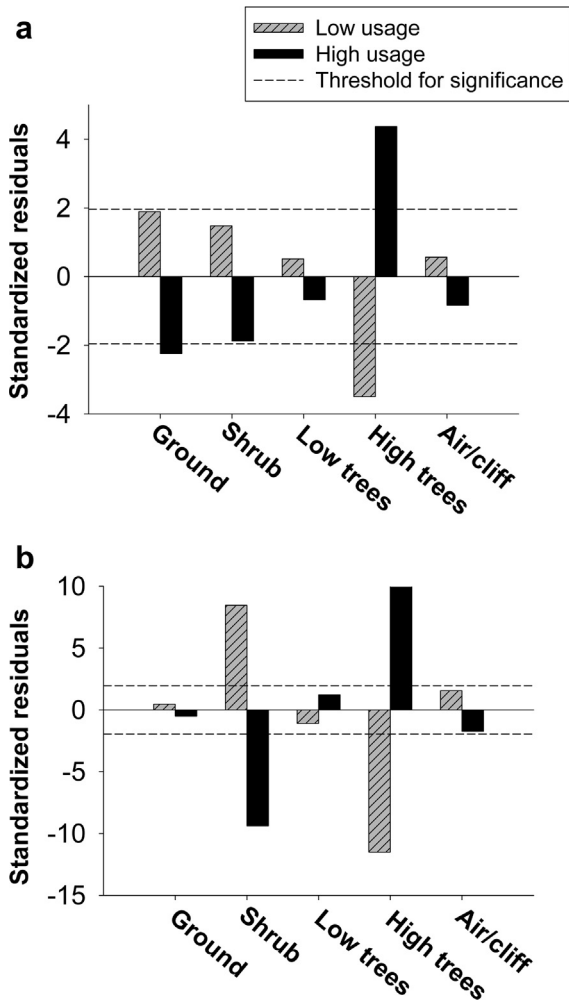


Fig. 3. Standardized residuals for the chi-square analysis of the interaction effect between intensity of tourist usage and vertical strata chosen by birds observed next to (a) roads or (b) hiking trails ($\chi^2_{(4)} = 463.49, P < 0.001$) in arid-lands gorges. As the triple interaction between usage intensity of roads \times gorge \times strata choice was statistically significant (hiloglinear analysis: $\chi^2_{(8)} = 46.12, P < 0.001$), separate chi-square analyses were conducted for each vehicle gorge ($\chi^2_{(4)}$, Brachina Gorge = 15.49, $P < 0.004$; $\chi^2_{(4)}$, Chambers Gorge = 130.75, $P < 0.001$; $\chi^2_{(4)}$, Parachilna Gorge = 51.95, $P < 0.001$) and an average value of the standardized residuals is presented. Bold reference lines indicate the threshold for significance, indicating that a particular stratum was used considerably more or less frequently than expected depending on the usage intensity.

In contrast, species that tended to avoid more disturbed sites included many smaller-bodied passerines. High usage may create a transition (ecotone) between vegetated areas suitable for perching and detection of prey, and open space for prey capture. This was the

case where adjacent campsites had greatly increased open space providing niches for open-country foragers. We frequently observed birds perching in the vegetation within our census plots from where they foraged into the cleared space of abutting campgrounds to forage, matching similar observations elsewhere (Arnold and Weeldenburg, 1990; Piper and Catterall, 2006).

The attraction to this ecotone may also be a richer foraging habitat, due to supplementation directly or indirectly by tourists or tourism infrastructure. We witnessed incidents of intentional and unintentional feeding, birds drinking water from rain collecting systems or sewage, and birds sheltering or perching in tourism infrastructure. Such benefits do not accrue equally to all species, so community changes may reflect modified species interactions. For example, the more competitive or predatory nature of several of our high usage indicator species such as the Noisy Miner or Grey Butcherbird may have eliminated smaller, less competitive species from otherwise suitable habitat (Grey et al., 1997).

Furthermore, species (and individuals) differ in their reactivity to aversive stimuli (Webb and Blumstein, 2005). Differences in the sensitivity of species within the same community have been attributed to food preferences (Canaday, 1995), geographic distribution, size (Cooke, 1980) and microhabitat specialization (Blakesley and Reese, 1988). Many of our high-usage indicator species are known to habituate readily to human disturbance. For example, birds associated with Australian recreation areas did not actively avoid peak visitor times suggesting habituation to, rather than avoidance of, disturbance (Densmore and French, 2005).

However, we did find avoidance expressed in the differential use of vegetation strata, in that more birds were counted in lower habitat strata compared to higher strata in low relative to high-usage sites. This was not a function of differential habitat availability but rather suggests that birds using lower vegetation strata were more affected by tourism activities such as exposure to direct disturbance or the likelihood of colliding with vehicles. Consistent with differential habitat use was our finding that the majority of high tourist-usage indicator species were viewed in trees whereas the low-usage ones were mostly viewed in ground or shrub layers. This suggests that high-usage was not associated with a shift of birds from lower to higher strata (Gutzwiller et al., 1998), independent of species, but rather that species with a preference for lower habitat strata were repelled (Blakesley and Reese, 1988). This is consistent with Martínez-Abraín et al. (2010) who found that raptors breeding in lower strata were more impacted on by human presence than raptors breeding on cliffs. Similarly, Smith-Castro and Rodewald (2010) noted that female Northern Cardinals (*Cardinalis cardinalis*) on higher nests were less likely to flush from human disturbance. Sewell and Catterall (1998) found that native Australian birds attracted to urbanized areas preferred heights above 8 m in natural open forest or woodland whereas those absent from urban areas used habitat below 3 m.

Table 4

Step-wise multiple regression models including all main terms and interactions which significantly (bold values) explained variation in (a) number of birds and (b) bird species richness of arid-lands gorges.

| (1) Next to roads | | | | | | (2) Next to trails | | | | | |
|----------------------------------|--------------|--------|------|---------|------------------|----------------------------------|--------------|--------|------|---------|------------------|
| | ΔR^2 | B | SE B | β | P | | ΔR^2 | B | SE B | β | P |
| (a) Number of birds | | | | | | (a) Number of birds | | | | | |
| (Constant) | | 177.94 | 4.68 | | <0.001 | (Constant) | | 149.55 | 3.21 | | <0.001 |
| PCA axis 1 | 0.56 | 1.42 | 0.22 | 0.57 | <0.001 | PCA axis 1 | 0.45 | 0.92 | 0.15 | 0.72 | <0.001 |
| High usage | 0.19 | -41.24 | 6.80 | -0.43 | <0.001 | PCA axis 2 | 0.08 | -0.41 | 0.17 | -0.28 | 0.020 |
| PCA axis 1 \times high usage | 0.07 | 1.33 | 0.37 | 0.31 | 0.001 | | | | | | |
| (b) Bird species richness | | | | | | (b) Bird species richness | | | | | |
| (Constant) | | 19.18 | 0.52 | | <0.001 | (Constant) | | 21.17 | 0.44 | | <0.001 |
| PCA axis 1 | 0.47 | 0.14 | 0.02 | 0.69 | <0.001 | PCA axis 1 | 0.61 | 0.11 | 0.01 | 0.72 | <0.001 |
| High usage | 0.17 | -3.16 | 0.75 | -0.41 | <0.001 | High usage | 0.09 | -2.16 | 0.66 | -0.30 | 0.002 |

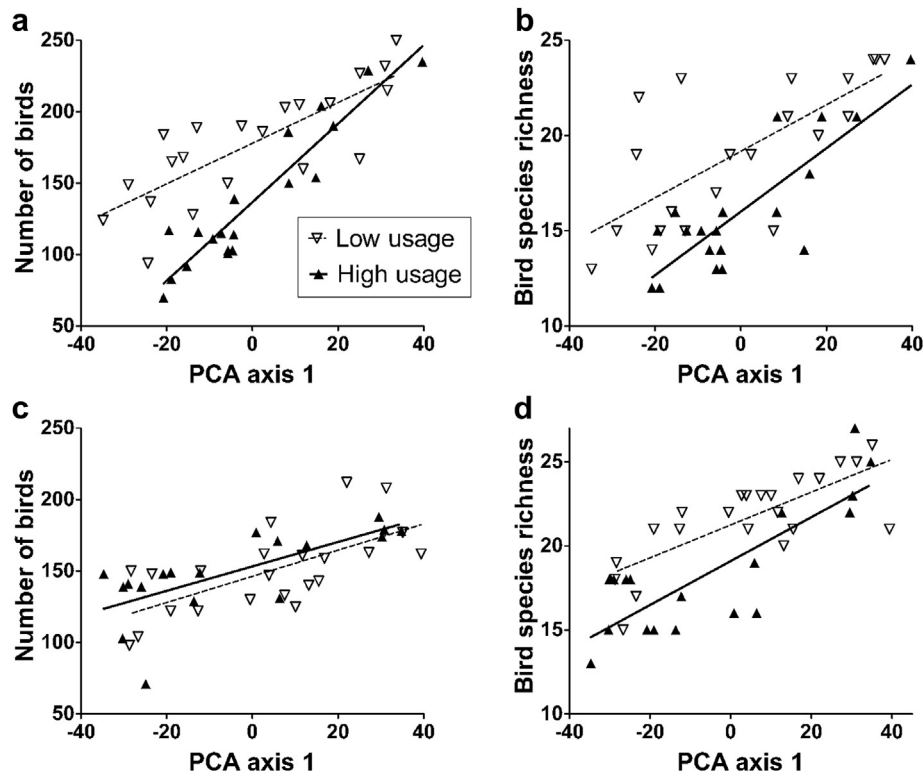


Fig. 4. Total number and species richness of birds in relation to high (\blacktriangle) or low (∇) tourist usage intensity and PCA axis 1. Birds were censused on 50 m \times 50 m plots during 20-min counts on 10 independent occasions next to (a, b) roads or (c, d) hiking trails in arid-lands gorges. Cover, height and diversity of shrub and tree cover and height increase along PCA axis 1 for roads (Table 1.1). Cover and height of shrubs as well as tree cover and vertical structure of the vegetation increase along PCA axis 1 for trails (Table 1.2).

Species richness and community composition were more sensitive indicators of tourist disturbance than was bird abundance. Despite sporadic camping activity and few campgrounds, tourist usage along hiking trails affected species richness and community composition similarly to the usage of roads. Tourists taking breaks at high-usage sites along trails were likely responsible for repelling some birds and attracting others. For instance, people at picnic areas flushed sensitive birds and fed more tolerant birds. Even seemingly unobtrusive activities such as the passing of hikers seem to multiply with increased usage and suggests that some species have low thresholds to disturbance (Madsen, 1985).

5. Conclusions

The severity of the effects and thus the risk to the conservation of bird species depends on whether the changes are temporary or long-term and whether they affect certain individuals, populations, the species as a whole or an entire bird community (Knight and Gutzwiller, 1995; Sekercioglu, 2002). We focussed on the more severe end of the scale where tourism impacts manifest as long-term changes in the abundance and/or distribution of numerous bird species. This is important in that behavioural responses by birds, especially if short-term and occasional, may not necessarily translate into population and ultimately community consequences (Gill et al., 2001). Conversely, a lack of an obvious behavioural response may not preclude important eventual effects such as nesting failure (Bouton et al., 2005). The ecosystem that we studied provides a small, often moist, habitat refuge from surroundings that are typically dry and arid. Many of our focal species are not adapted to the latter and so displacement from suitable habitat through visitor disturbance is prone to have long-term aversive effects.

Tourist activity may be beneficial such as a 'scare crow' effect on mammals preying on birds and thereby reducing nest predation (Leighton et al., 2010). However, our comparisons of high- and low-usage tourist sites suggested that this phenomenon, if at all relevant, was out-weighted by the primary negative consequences of human activity on birds. Similarly, while habituation to human disturbance in high-usage sites may have had a positive influence on some of our less sensitive species, as observed by others (Martínez-Abraín et al., 2008), there was no positive overall net effect on the bird community.

Our findings have direct implications for the management of impacts of tourism on avifauna along roads or trails: (1) Our observations reinforce the idea that recreational access should be controlled to conserve avifauna. Often in recreation areas access to hiking trails is restricted from a few access points. In our case, visitors aggregated in the sections that were closer to the favoured access point(s) although some visitor traffic was still noted at the alternate access points. Hence closing off the farther and less popular sections and alternate access points creates spatial refuges from any tourist usage (Pearce-Higgins et al., 2007; Pearce-Higgins and Yalden, 1997). This would likely find support by the public as fewer people are impacted by the restriction than if this measure was enforced along roads. This will also benefit cryptic bird species whose conservation is a particular challenge because a reduction in their abundance may evade notice. A temporal closure during breeding periods may be another effective measure to protect some bird species. However, this may require more enforcement to ensure compliance because of the temporary nature of such restrictions. Road networks traversing recreation areas are unlikely to be closed off but some closures may be beneficial given that the effects of roads on avifauna were substantial in our study.

- (2) The abundance of tourist-sensitive species rather than the total number of individuals should be monitored as simply quantifying the numbers can mask the changes in composition: for instance, the total number of birds recorded at high-usage sites along trails was not markedly lower than at low-usage sites, despite considerable and meaningful differences in species composition.
- (3) Our findings support the idea that avian communities are highly sensitive to changes in habitat characteristics, but impacts may be buffered by conserving well-vegetated areas. We found numerous unregulated campsites along roads to be particularly problematic. They should be closed and revegetated whilst a few, official campsites, preferably at the beginning of the natural recreation areas, should be maintained. This would especially benefit more sensitive bird species that preferably utilize ground and shrub layers in undisturbed parts of the study area.

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