

Importance of woody vegetation for foraging site selection in the Southern Pied Babbler (*Turdoides bicolor*) under two different land use regimes

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Abstract

Intensified land use practices have changed savannas worldwide. Both, heavy grazing-induced shrub encroachment and the decrease in tree density due to woodcutting are assumed to reduce animal diversity. However, most studies in animal ecology have focused on the effects of one of these two land use practices. In our study we analyzed the importance of both shrubs and trees, for foraging site selection of the Southern Pied Babbler (*Turdoides bicolor*) in the Southern Kalahari, South Africa for two different grazing regimes: endemic wildlife at Molopo Nature Reserve versus domestic livestock at neighboring farms. We compared vegetation structure at babbler foraging sites with random sites at the microhabitat scale (5 × 5 m) and the mesohabitat scale (50 × 50 m), and recorded babbler group size and the amount of leaf litter. Our results show for both scales that mean density of shrubs and trees was higher at foraging sites compared to random sites. We found no differences in foraging site characteristics (i.e. vegetation cover at microhabitat scale and composition and density of woody plant species at both scales) and group size between the two grazing regimes. We conclude that shrub encroachment affects the Southern Pied Babbler positively whereas woodcutting has negative effects.

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1. Introduction

During the last century, the intensification of land use practices has led to strong changes and degradation of arid and semiarid ecosystems (e.g. Archer et al., 1995; Cabral et al., 2003; Louw and Seely, 1982; Sankaran et al., 2005; Sharp and Whittaker, 2003). Land use induced changes in landscape structure are particularly strong in the Southern Kalahari where heavy grazing has led to shrub encroachment (Jeltsch et al., 1997; Skarpe, 1991; Weber and Jeltsch, 2000) and the increase of woodcutting for firewood production to a significant decline of savanna tree density (Anderson and Anderson, 2001; Liversidge, 2001).

In most studies both shrub encroachment and the decline of trees are assumed to reduce species diversity (Blaum et al., 2007a, c, in press; Dean et al., 1999; Tews et al., 2004; Wichmann et al., 2003). Nevertheless,

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large and solitary shrubs and trees are important habitat structures for animals and are used as nesting, perching and foraging sites and provide shelter against predators and extreme climatic conditions (Blaum et al., 2007b; Cooper and Whiting, 2000; Dean et al., 1999; Milton and Dean, 1995). Consequently, the increase of shrubs and the decrease in trees changes inter-patch distances between habitat structures and affects habitat connectivity, particularly for arboreal species (Eccard et al., 2004; Huey and Pianka, 1977).

However, most studies of land use induced habitat changes in animal ecology have focused on species that are affected either by shrub encroachment or by woodcutting (Tews et al., 2004). Nevertheless, many species, particularly birds, are likely to depend on both shrubs and trees as habitat structures.

For example, the Southern Pied Babbler (*Turdoides bicolor*), a territorial and cooperatively breeding bird which is endemic to the savannas of the Southern African Subregion (Fry et al., 2000; Hockey et al., 2005), uses large thorn trees, particularly *Acacia*-trees for nesting and perching (Fry et al., 2000; Hockey et al., 2005) but forages on insects in leaf and twig litter on the ground where vegetation cover is low (Fry et al., 2000; Hockey et al., 2005). Shrubs and trees produce leaf litter but their role as foraging sites for this bird species remains unclear. First, shrub encroachment increases the amount of leaf litter so that prey availability increases (Cousin, 2004) but as shrubs become the dominant vegetation, the accessibility of foraging sites with low vegetation cover decreases. Second, for a group-living bird that forages on the ground such as the Southern Pied Babbler (Fry et al., 2000; Hockey et al., 2005), predator avoidance is particularly important at foraging sites (Elchuk and Wiebe, 2002; Suhonen, 1993) where shrubs and trees can be used as hiding places. These characteristics likely mean the Southern Pied Babbler is particularly sensitive to changes in savanna landscape structure and may therefore be a suitable indicator species for rangeland management.

The aim of our study was to investigate the importance of woody vegetation on foraging site selection for Southern Pied Bblers to assess the role of shrub encroachment and woodcutting for this bird species. We focused on the foraging habitat exclusively because foraging sites are among the most important habitat structures for birds (Cody, 1985). We analyzed habitat preferences of Southern Pied Bblers by comparing vegetation structure at foraging sites with random sites. To assess the effects of different land use practices i.e. grazing by indigenous wildlife versus domestic livestock grazing on foraging site selection of Southern Pied Bblers we compared foraging sites and random sites between the Molopo Nature Reserve (MNR) and neighboring cattle farms. In the MNR grazing pressure was low (16 ha/large stock unit in 2003, 1 large stock unit (LSU) = 420 kg body mass (Dean and Macdonald, 1994)) and woodcutting was prohibited for 15 years. On the farms grazing pressure was similar but woodcutting took place in some areas. Vegetation structure of foraging sites was assessed at two different scales: (i) microhabitat scale (5 m × 5 m) and (ii) mesohabitat scale (50 m × 50 m). At microhabitat scale we recorded number and height of shrubs and trees, amount of leaf litter, and ground cover percentages of shrubs, grasses and bare ground. At mesohabitat scale we recorded number and height of trees, and group size and reproductive success of Southern Pied Bblers over one breeding season.

2. Methods

2.1. Study site

Southern Pied Bblers were studied in the Molopo Nature Reserve (MNR) and two neighboring commercial cattle farms in the North West Province, South Africa (25°50'S, 22°55'E). The distance between the MNR and the two farms is 10 km. The MNR was established in 1987 in an area formerly used for commercial game hunting and cattle farming. Since that time it has been stocked with game (mainly Gemsbok (*Oryx gazella*), Red Hartebeest (*Alcephalus buselaphus*), Eland (*Taurotragus oryx*), Blue Wildebeest (*Connochaetes taurinus*), Zebra (*Equus burchelli*), Kudu (*Tragelaphus strepsiceros*) and Impala (*Aepyceros melampus*)). On both cattle farms game, in particular Gemsbok and Impala, were present in low numbers. Farms were divided in camps and cattle were managed in a rotating system. In some camps, farmers have removed woody vegetation to increase grazing capacity. Stocking rates were similar to those of the MNR (16 ha/LSU in 2003).

The study area was characteristic of the Kalahari Thornveld (Leistner, 1967; van Rooyen and Van Rooyen, 1998). Mean annual precipitation is 332 mm but highly erratic (CV = 38%). Most precipitation falls in summer (October–April) with a peak from January to March.

2.2. Survey of Southern Pied Babbler groups

Groups of Southern Pied Babblers were surveyed from November 2002 to February 2003. For each study site, we established several random subplots (2.5 × 2.5 km): four subplots in the MNR and three subplots on the farms. We located bird groups by calls and sight and collected data for the first 3 babbler groups for each subplot except for one farm's subplot where 4 babbler groups were recorded (Table 1).

For each babbler group, number of adults and young was recorded. If at least one group member was observed foraging, the site was considered a foraging site and GPS-position was recorded. For each group we mapped 3 foraging sites.

2.3. Habitat survey at microhabitat scale

Foraging sites: At each foraging site several habitat parameters were mapped according to bird-centered vegetation sampling (Larson and Bock, 1986). Habitat parameters were recorded at microhabitat (5 m × 5 m around the GPS-position) and mesohabitat (50 m × 50 m around the GPS-position) scale. At microhabitat scale, number of trees and shrubs higher than 1 m and larger than 1.5 m in diameter were recorded. Woody vegetation below this height plays a minor role for this bird species as we never observed babblers using small woody vegetation. Trees were further divided into three height classes (class 1: > 1–3 m; class 2: > 3–5 m; class 3: > 5 m) and species recorded. In addition, we estimated ground cover percentages of shrubs, grasses (and herbs), bare ground and leaf litter. The sum of ground cover of shrubs, grasses and bare ground always summed to 100%. To determine babbler habitat preferences, we established random sites in each subplot. The number of random sites established corresponded to the number of foraging sites in the respective subplot (Table 1). At random sites we recorded the same habitat parameters as at foraging sites.

Foraging trees: To obtain more detailed information about foraging sites at microhabitat scale, we made additional measures at 23 foraging trees. For this purpose, two birds of one group were caught and radio-tagged. The group was traced on 10 consecutive days at different times of day, 2–3 times daily. After locating the group, we followed the birds to their next foraging site, a perching site where at least one group member was observed foraging. There, we recorded foraging time at each radio-located foraging site for 30 min.

For each foraging tree we recorded the same habitat parameters as for foraging sites and also estimated distance from ground to shelter and nearest neighbor distance of the foraging tree. Distance from ground to shelter was height of the foraging tree where foliage was dense enough to provide shelter for the babblers. It was estimated in intervals of 1 m (0–1 m; > 1–2 m; > 2–3 m; > 3 m) from ground level. Nearest neighbor distance was the distance to the nearest tree which was potentially suitable as a foraging site (all *Acacia*

Table 1
Overview of sampling design (for further details see text in Sections 2.2 and 2.3)

	Molopo Nature Reserve	Farms
# Subplots	4	3
# Babbler groups	12 (3 per subplot)	10 (2 subplots a 3 groups, 1 a 4 groups)
# Foraging sites	36 (3 per group → 9 per subplot)	30 (3 per group → 2 subplots a 9 foraging sites, 1 a 12 foraging sites)
# Random sites	36 (9 per subplot)	30 (2 subplots a 9 random sites, 1 a 12 random sites)
# Foraging trees	23 (trees at foraging sites of radio-tagged group)	–
# Random trees	23 (trees potentially suitable as foraging sites in same territory as foraging trees)	–

species, *Ziziphus mucronata* and *Boscia albitrunca* higher than 1 m and with a diameter of at least 1.5 m; personal observations) and was measured in intervals of 5 m. Finally, the same parameters as for the foraging trees were measured at 23 randomly chosen, potentially suitable trees inside the home-range of the same group (Table 1).

2.4. Habitat survey at mesohabitat scale

At mesohabitat scale, total number of trees, height class and species of individual trees were recorded for each foraging site and random site respectively. Again, only trees higher than 1 m and with a diameter of at least 1.5 m were recorded.

2.5. Statistical analysis

First, data of the respective 3 foraging sites of one group were pooled because independence of data could not be confirmed. We did the same for each 3 random sites of one subplot to allow a proportionate sampling design. After this, data of foraging sites and random sites were checked for normal distribution using a Kolmogorov–Smirnov test. If the data followed a normal distribution, a comparison of habitat parameters of foraging sites and random sites were conducted using a Student's *t*-test; otherwise we used Mann–Whitney U-test. We did the same for the comparison of habitat parameters of foraging trees and random trees. For the comparison of the two grazing regimes (MNR and the farms) data of the foraging sites and random sites were analyzed separately.

Foraging tree preferences for both height class and species were analyzed using data of availability (tree distributions of random sites at mesohabitat scale) versus used resources (tree distributions of foraging sites at microhabitat scale). To verify whether the distributions of used trees differed significantly to their availability we used a chi-square test (Zar, 1999). Subsequently, we calculated the selection index w_i (Savage, 1931) to assess for a tree specific preference or avoidance at foraging sites:

$$w_i = \frac{o_i}{p_i},$$

where o_i is the proportion of used tree species and p_i the proportion of available tree species.

We regarded w_i as statistically significant at the 95% confidence level. Finally, w_i was converted into the standardized selection index B_i (Manly et al., 1993). Index values of (1/number of resource categories) indicate no preference; higher values indicate a preference and lower values indicate a relative avoidance of a resource category (here tree species (number of resource categories = 8) and height class (number of resource categories = 3), respectively). B_i was calculated according to the following equation:

$$B_i = \frac{\hat{w}_i}{\sum_{i=1}^n \hat{w}_i},$$

where \hat{w}_i is the selection index.

Both index values were calculated using Niche Measure–Resource Selection 2.0, part of the “Ecological Methodology” software (Krebs, 2002; see also Krebs, 1999).

We analyzed preferences of babblers for certain tree densities by comparing number of trees at mesohabitat scale between foraging sites and random sites (unpooled data, $n = 66$). Therefore, we classified 9 different categories of tree densities (1: 0–25 trees/ha; 2: > 25–50 trees/ha; 3: > 50–75 trees/ha; 4: > 75–100 trees/ha; 5: > 100–125 trees/ha; 6: > 125–150 trees/ha; 7: > 150–175 trees/ha; 8: > 175–200 trees/ha; 9: > 200 trees/ha). Differences in tree densities were analyzed by a Student's *t*-test.

The impact of the particular habitat parameters of the foraging trees and leaf litter on the foraging time of a group, group size and number of young was analyzed by multiple regression analysis under stepwise inclusion of all variables. Further, the impact of the tree species on the independent variables included in the final model was analyzed by an analysis of variance (ANOVA).

3. Results

The Southern Pied Babbler favored foraging sites situated close to woody vegetation structures, i.e. trees or tall shrubs. Despite the different grazing history of the Molopo Nature Reserve and the neighboring commercial farms, the recorded habitat parameters (i.e. vegetation cover, tree species composition, tree density) of foraging sites and random sites, respectively, did not differ significantly between the two study sites. We also found no differences in mean babbler group size (MNR: 5.33 ± 0.38 SE; $n = 12$; Farm: 4.5 ± 0.31 SE; $n = 10$) and the number of young (MNR: 1.0 ± 0.30 SE; $n = 12$; Farm: 1.0 ± 0.26 SE; $n = 10$) between the two grazing regimes. Therefore, we pooled data of the two study sites.

3.1. Microhabitat preferences

At microhabitat scale (5 m × 5 m), Southern Pied Babblers favored sites for foraging where the number of trees and shrubs was higher ($U = 11.5$; $p < 0.001$; $n = 22$) and grass cover was lower ($t = -13.564$; $p < 0.001$; $n = 22$) compared to random sites in the area. Trees and shrubs used by Southern Pied Babblers as foraging sites differed significantly from available woody vegetation structures, in both height class ($\chi^2 = 119.884$; $p < 0.001$) and species ($\chi^2 = 107.776$; $p < 0.001$). The babblers favored high trees (> 3 m; $w_i > 1$; $p < 0.05$; Table 2) and the species *Acacia mellifera* ($w_i > 1$; $p < 0.01$; Table 3) but avoided *Grewia flava* ($w_i < 1$; $p < 0.01$; Table 3). *Terminalia sericea* and *Acacia haematoxylon* were not used as foraging sites.

The comparison of the vegetation parameters at foraging trees with those of random trees highlighted some significant differences (Fig. 1). Ground cover percentage of herbs and grasses was lower at foraging trees ($U = 160.5$; $p < 0.01$; $n = 23$, Fig. 1a) while ground cover percentage of leaf litter was higher at these sites ($t = 3.573$; $p < 0.001$; $n = 23$, Fig. 1a). Tree structure, i.e. height class, distance from ground to shelter and nearest neighbor distance did not differ significantly (Fig. 1b).

Foraging time of a babbler group per site was explained by only one parameter: it increased with decreasing distance from ground to shelter (Multiple linear regression: R^2 -adjusted = 0.135; $F = 4.437$; $d.f. = 1$; $p < 0.05$). All other variables were not included by the stepwise selection procedure.

An analysis of variance showed that the five most used tree species (*Acacia mellifera*, *A. luederitzii*, *A. erioloba*, *Boscia albitrunca* and *Ziziphus mucronata*) differed significantly in leaf litter production ($F = 14.111$; $d.f. = 4$; $p < 0.001$) and distance from ground to shelter ($F = 16.102$; $d.f. = 4$; $p < 0.001$). In both cases tree species could be divided into two homogenous subgroups. Leaf litter production was higher in *A. mellifera*, *Z. mucronata* and *B. albitrunca* compared to *A. luederitzii* and *A. erioloba* ($p < 0.05$; Table 4). Distance from ground to shelter was higher in *A. erioloba* compared to all other tree species ($p < 0.05$; Table 4). Ground cover percentages of shrub, grass and bareground did not differ between tree species (Table 4).

3.2. Mesohabitat preferences

At mesohabitat scale (50 m × 50 m), foraging sites had significantly more trees ($\bar{x} = 41.29 \pm 4.73$ SE; $n = 22$) than random sites ($\bar{x} = 25.53 \pm 2.94$ SE; $n = 22$; $t = 2.831$; $p < 0.01$; Fig. 2). These differences were recorded

Table 2
Preferences for tree height classes by babbler groups at microhabitat scale

Height class	Proportion of trees available (p_i)	Proportion of trees used (o_i)	Selection index (w_i)	95%-confidence limits (CL) ^a		Standardized selection index (B_i) ^b
				Lower	Upper	
1 (1–3 m)	0.7616	0.3455	0.4537 ^c	0.3438	0.5636	0.0756
2 (3–5 m)	0.1847	0.5026	2.7209 ^c	2.0781	3.3637	0.4532
3 (>5 m)	0.0537	0.1518	2.8293 ^c	1.3537	4.3050	0.4712
Total	1.000	1.000	–	–	–	1.000

^aConfidence limits with Bonferroni correction ($\alpha_{\text{corrected}} = \alpha/n_{\text{height classes}}$); α corrected to 0.0167.

^bStandardized selection indices more than 0.33 (1/number of resource categories) indicate preferences.

^cSignificantly different from random selectivity.

Table 3
Preferences for tree species by babbler groups at microhabitat scale

Tree species	Proportion of trees available (p_i)	Proportion of trees used (o_i)	Selection index (w_i)	95%-confidence limits (CL) ^a		Standardized selection index (B_i) ^b
				Lower	Upper	
<i>A. mellifera</i>	0.2651	0.5266	1.9860 ^c	1.5601	2.4118	0.2393
<i>A. luederitzii</i>	0.1349	0.1546	1.1464	0.5980	1.6947	0.1382
<i>A. erioloba</i>	0.1700	0.1304	0.7671	0.3725	1.1617	0.0925
<i>Z. mucronata</i>	0.0599	0.0676	1.1284	0.2732	1.9837	0.1360
<i>B. albitrunca</i>	0.0143	0.0435	3.0336	0.0000	6.2582	0.3656
<i>G. flava</i>	0.3277	0.0773	0.2359 ^c	0.0792	0.3926	0.0284
<i>A. haematoxylon</i>	0.0150	0.0000	0.0000	0.0000	0.0000	0.0000
<i>T. sericea</i>	0.0130	0.0000	0.0000	0.0000	0.0000	0.0000
Total	1.000	1.000	–	–	–	1.000

^aConfidence limits with Bonferroni correction ($\alpha_{\text{corrected}} = \alpha/n_{\text{height classes}}$); α corrected to 0.0063.

^bStandardized selection indices more than 0.125 (1/number of resource categories) indicate preferences.

^cSignificantly different from random selectivity.

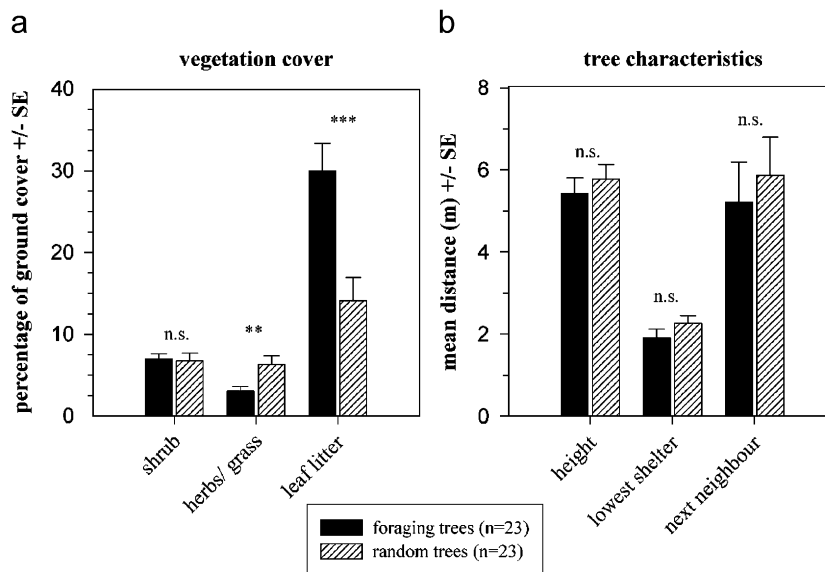


Fig. 1. Ground vegetation cover (a) and tree characteristics (b) of foraging trees compared to random trees at microhabitat scale.

for each height class (class 1 (>1–3 m): $t = 2.067$; $p < 0.05$; class 2 (>3–5 m): $t = 4.09$; $p < 0.001$; class 3 (>5 m): $t = 4.354$; $p < 0.001$). Although only the number of *A. mellifera* trees ($t = 3.546$; $p < 0.001$; Fig. 2) was higher at foraging sites, we found clear trends also for the other *Acacia* species (Fig. 2). By excluding small trees (<3 m; height class 1) from this analysis numbers of tall (>3 m) *A. erioloba* ($t = 3.03$; $p < 0.01$) and *A. luederitzii* trees ($u = 143.5$; $p < 0.05$) were significantly higher at foraging sites than at random sites. In contrast, mean number of *Boscia albitrunca* and *Ziziphus mucronata* trees did not differ.

The proportion of sites with high tree densities (>175 trees/ha) used by Southern Pied Babbler was significantly higher than the proportion of available sites ($p < 0.05$; Fig. 3). Sites with medium tree densities (75–150 trees/ha) did not differ in use and availability while sites with low densities (50–75 trees/ha) were less frequently used by the babbler ($p < 0.001$). Availability of sites with even lower tree densities was in fact

Table 4
Characteristics of foraging trees of Southern Pied Babblers at microhabitat scale

Tree species	Ground cover percentage (mean ± SE)				Distance (m) from ground to shelter (mean ± SE)
	Shrub	Grass	Bareground	Leaf litter	
<i>A. mellifera</i> (n = 42)	7.45 ± 0.79 ^a	9.40 ± 1.34 ^a	84.05 ± 1.28 ^a	25.00 ± 2.11 ^a	1.36 ± 0.15 ^a
<i>A. luederitzii</i> (n = 28)	6.25 ± 0.49 ^a	8.57 ± 1.43 ^a	85.18 ± 1.53 ^a	9.64 ± 1.33 ^b	1.79 ± 0.13 ^a
<i>A. erioloba</i> (n = 25)	7.20 ± 0.77 ^a	10.20 ± 1.21 ^a	82.60 ± 1.26 ^a	7.80 ± 2.35 ^a	3.24 ± 0.12 ^b
<i>Z. mucronata</i> (n = 4)	8.75 ± 2.39 ^a	7.50 ± 1.44 ^a	83.75 ± 3.75 ^a	20.00 ± 7.91 ^a	1.25 ± 0.25 ^a
<i>B. albitrunca</i> (n = 16)	6.88 ± 0.63 ^a	8.44 ± 2.88 ^a	84.69 ± 2.79 ^a	20.94 ± 5.15 ^a	2.31 ± 0.15 ^a

^{a,b}Different letters indicate different subgroups (Student–Newman–Keuls–test; $p < 0.05$).

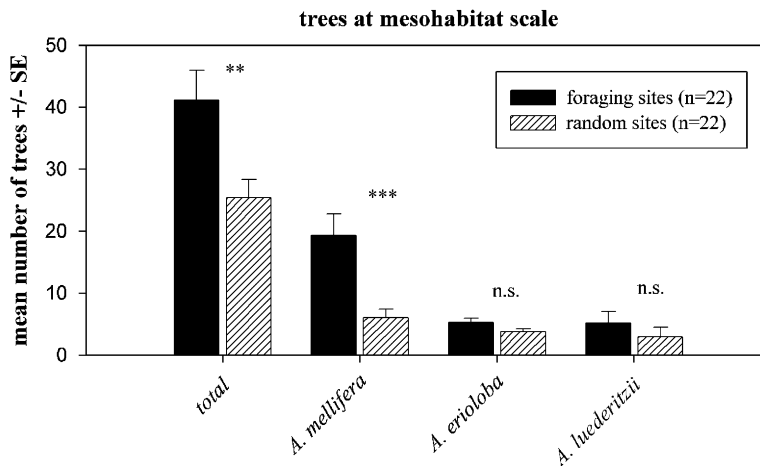


Fig. 2. Mean number of trees in total and of the *Acacia*-species alone at the foraging sites of Southern Pied Babblers compared to random sites at mesohabitat scale.

higher than their use, but differences were not significant. Although sites with less than 25 trees per hectare were available, birds did not use those sites for foraging.

3.3. Group size and number of young

Mean group size was 4.95 adults (± 1.21 SE; $n = 22$) ranging from 3 to 8 individuals. On average, each group fledged 1.0 young (± 0.93 SE; $n = 22$; range: 0–2). However, 9 of the 22 groups did not reproduce. None of the observed groups had a second brood during the observation period. Although there was no correlation between number of young and number of adults in a group, large groups (≥ 6 adults) fledged significantly more young ($\bar{x} = 1.57 \pm 0.33$ SE; $n = 7$) than smaller groups ($\bar{x} = 0.73 \pm 0.37$ SE; $n = 15$; $t = -2.139$; $p < 0.05$).

None of the recorded habitat parameters was correlated with group size or the number of young. Habitat parameters did not differ between large and small groups at the microhabitat and mesohabitat scale.

4. Discussion

In our study we analyzed the foraging site selection of the Southern Pied Babbler in terms of density of woody vegetation, leaf litter and distance to shelter under two grazing regimes in the Southern Kalahari.

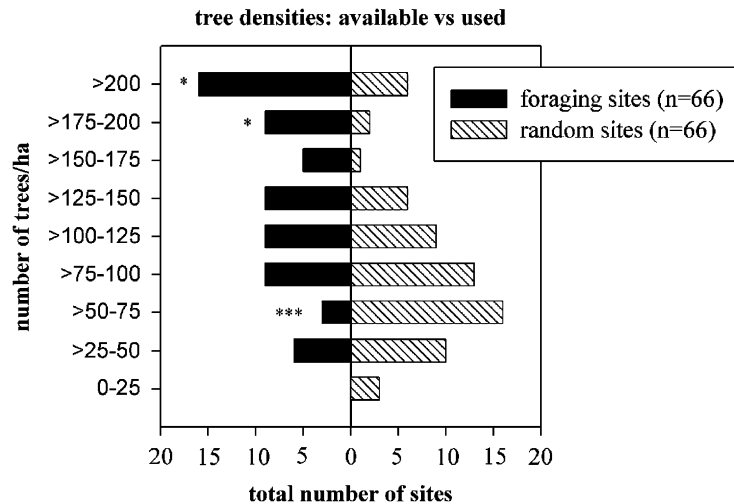


Fig. 3. Distribution of tree densities at foraging sites of Southern Pied Babblers compared to random sites at mesohabitat scale.

Despite the different grazing impact we found no differences in vegetation cover and structure of foraging sites and random sites respectively between the Molopo Nature Reserve and adjacent commercial cattle farms. Our results show clearly that this bird favors sites for foraging in dense woody vegetation i.e. trees or tall shrubs at both the microhabitat (5 m × 5 m) and mesohabitat scale (50 m × 50 m).

4.1. Habitat preferences at microhabitat scale

At the microhabitat scale Southern Pied Babblers favored foraging in the leaf litter under thorny *Acacia*-species. In general, the selection for foraging sites in birds depends on food availability, foraging efficiency and predation risk (Elchuk and Wiebe, 2002).

Food availability: Southern Pied Babblers mainly feed on arthropods that they search for in the leaf litter of trees and shrubs (Fry et al., 2000). As leaf litter favors higher abundance of ground invertebrates (Cousin, 2004; Thiele, unpublished data), the amount of leaf litter is directly proportional to food availability. Indeed, leaf litter was higher at foraging sites compared to random sites. Moreover, the birds favored leaf litter rich microhabitats under *A. mellifera* shrubs for foraging compared to *A. erioloba* trees where the amount of leaf litter was 70% lower.

Foraging efficiency: One measure of foraging efficiency is the ratio of harvest rate to foraging costs (e.g. Brown, 1988; Fierer and Kotler, 2000). Thus, the longer the birds forage at one site (harvest rate) and the less energy they will spend for searching new foraging sites (foraging costs), increases foraging efficiency. Hence, the time birds forage at one site can be related to foraging efficiency. Foraging time of babblers increased with the ability of shrubs and trees to provide shelter close to the ground. Therefore, we assume that foraging efficiency of babblers in the open savanna of the Southern Kalahari strongly depends on predation risk.

Predation risk: Foraging under the shelter of trees and shrubs reduces predation risk of Southern Pied Babblers because long and sharp thorns of *Acacia*-species effectively protect babblers against raptors such as the Gabar Goshawk (*Melierax gabar*). Trees were used as foraging sites when their height was more than 3 m. Below this height crowns are not large enough to effectively shelter babblers from avian predators. Nevertheless, increasing tree height leads also to an increase in predation risk at the ground because of the growing distance of the protective crown. This may explain the preference of Southern Pied Babblers to forage under *A. mellifera*-shrubs which provide shelter close to the ground. Ground cover of herbs and grasses was lower at foraging trees compared to random trees. Elchuk and Wiebe (2002) found similar patterns for the Northern Flicker (*Colpates auratus*) in grasslands in British Columbia. In Kalahari savanna microhabitats where vegetation cover is low, ground-dwelling predators such as snakes can be detected earlier (Blaum et al.,

2007b). The importance of reducing predation risk at ground level in this bird species is further supported by the presence of a sentry in most of our observations. Second, although leaf litter production in *Grewia flava* was high (Thiele et al., unpublished data), Southern Pied Babblers did not use this shrub as foraging sites. It does not provide sufficient shelter against ground-dwelling and avian predators as it has no thorns and no dense crown.

4.2. Habitat preferences at mesohabitat scale

The importance of woody vegetation for the babblers is further supported at the mesohabitat scale. Mean number of trees at foraging sites was nearly twice as high compared to random sites.

Southern Pied Babblers used only sites for foraging where tree density was higher than 25 trees per hectare. This was also the case when sites of lower quality i.e. lower tree density were close to a high quality site. Although *A. mellifera* is one of the main shrub encroachers in Southern Africa (Richter et al., 2001; Skarpe, 1980, 1990; van Vegten, 1983), babblers favored sites for foraging where the density of this shrub species was high. In contrast to other studies (Blaum et al., 2007a, b, c, in press; Meik et al., 2002), we assume therefore that heavy grazing induced shrub encroachment can also affect animal populations positively as for the Southern Pied Babbler. Our results are in line with the recent study of Seymour (2006) on avian assemblages in the Kimberley region, South Africa, where bird diversity increased with shrub cover, particularly if large trees remained in the habitat.

Nevertheless, in shrub dominated Kalahari savanna areas arthropod abundance and diversity are low (Blaum et al., in press) and result in a low food availability for babblers. Moreover, direct impacts of livestock on food availability of babblers were not measured in this study but other studies found that the diversity of arthropods decreases with hoof trampling frequency (Rivers-Moore and Samways, 1996) and that overall arthropod abundance decreases at high stocking levels (Hutchinson and King, 1980). These trends suggest that babbler abundance is expected to be low in highly overstocked and shrub encroached savanna habitats.

4.3. Group size and number of young

Foraging group size of babblers was 4.95 ± 1.21 adults. Similar group sizes were found in the Southern Kalahari Desert (4.6 ± 0.8 , Ridley and Raihani, 2007). Despite the high importance of woody vegetation at foraging sites, group size was not correlated to tree or shrub cover across both spatial scales. Our results on the Southern Pied Babbler are in contrast to a study on Hall's Babbler (*Pomatostomus halli*), where group size was positively correlated with crucial habitat parameters, i.e. the amount of herbaceous cover and the amount of tree cover (Brown and Balda, 1977).

Reproductive success in the Southern Pied Babbler was significantly higher in large groups (≥ 6 adults) than in small groups. A higher reproductive success with increasing group size was also found in the Arabian Babbler (*Turdoides squamiceps*) (Wright, 1998). In the Grey-crowned Babbler (*Pomatostomus temporalis*), the feeding rates of parents declined as the number of helpers increased up to four (Brown et al., 1978). The reproductive advantage in large groups can be explained by the social behavior of Southern Pied Babblers. In Southern Pied Babblers, all group members feed the young (Hockey et al., 2005; Radford and Ridley, 2006). This suggests a threshold group size above which a successful reproduction is easier. This is further supported by another study of Southern Pied Babblers where the amount of time group members acted as a sentry was higher in smaller groups and so the individual foraging time decreased (Ridley and Raihani, 2007). Nevertheless, despite the higher investment in sentries in small babbler groups predation risk was still higher compared to large babbler groups (Ridley and Raihani, 2007). Especially in years where food availability is low the advantage to breed in a large group may be even higher. In fact, rainfall was below average during our study and only in the end of the study period (end of February) there was good precipitation. Second broods may have been produced, after our study period.

In contrast, group size is not related to reproductive success in other babbler species (Arrow-marked Babbler, *Turdoides jardineii*, Monadjem et al., 1995; Bare-cheeked Babbler, *Turdoides gymnogenys*, Shaw and Shewry, 2000). Nevertheless, although additional group members in the Arrow-marked Babbler did not increase the reproductive success, they helped to defend and to enlarge the territories (Monadjem et al., 1995).

A positive relationship between territory size and habitat quality is also documented for other bird species (Brooker and Rowley, 1995; Luck, 2002). High habitat quality can otherwise allow groups to occupy smaller territories (Cody and Cody, 1972; Ford, 1981; Miller and Watson, 1978; review in Cody, 1985; Stenger, 1958) or increase the reproductive success as in the Jungle Babbler (*Turdoides striatus*) (Gaston, 1978). However, in our study habitat parameters of foraging sites did not differ between groups of different sizes so that there is no evidence that large groups of Southern Pied Babblers can defend higher quality territories.

4.4. Impact of land use

We found no differences in mean babbler group size and foraging site characteristics between the Molopo Nature Reserve (endemic wildlife) and the two commercial cattle farms. Although foraging habits of endemic wildlife (grazers and browsers) differ largely from cattle grazing, the overall stocking rates of 16 ha/LSU were similar in the study sites and have led to similar habitat characteristics.

Grazing-induced shrub encroachment improved foraging site quality of the Southern Pied Babbler. In contrast, other studies showed that shrub encroachment affected animal abundance and diversity negatively, e.g. ground-dwelling mammals (Blaum et al., 2007a, b, c, in press). For the Southern Pied Babbler, in savanna habitats with low shrub cover, the distances between suitable foraging sites are large. Thus, while searching for food-rich shrub patches predation risk is high and foraging efficiency low. The increase of shrubs therefore theoretically enriches the availability of high quality foraging sites. As a consequence, inter-foraging-patch distance decreases which leads to a reduction of predation risk and an increase of foraging efficiency. Therefore, our study suggests that Southern Pied Babblers benefit from grazing induced shrub encroachment. Nevertheless, we assume an upper threshold for shrub cover above which babblers will be negatively affected by shrub encroachment. That is, when shrubs become the dominant vegetation form and cover larger areas (Skarpe, 1990). For babblers in such shrub dominated savanna habitats food availability is likely to be low as a consequence of low arthropod abundance and diversity (Blaum et al., in press).

Woodcutting for firewood production has a strong negative impact on habitat use by Southern Pied Babblers. Although large *Acacia*-trees played a minor role for foraging site selection, a systematic and area wide tree removal reduces suitable perching and nesting sites for the Southern Pied Babbler. This negative effect is supported by our observation that babblers were absent in wood cleared sites (Thiele et al., unpublished data). The importance of large trees for the babbler is in line with the keystone structure concept (Milton and Dean, 1995; Tews et al., 2004). Keystone vegetation structures such as *A. erioloba* in the Southern Kalahari provide important services e.g. nesting/perching sites for birds (Dean et al., 1999), arboreal mammals (Eccard et al., 2006) and reptiles (Huey and Pianka, 1977), and improved microclimatic conditions for germination of many plant species (Tews et al., 2004).

We conclude that an optimal habitat for Southern Pied Babblers requires the presence of both shrubs and trees as important vegetation structures: shrub patches for food-rich foraging resources and large thorn trees (> 3 m) for perching and nesting. Moderate land use (grazing and wood cutting) of savanna habitats positively affects Southern Pied Babblers, but over utilization may go beyond the range of optimal habitat used by Southern Pied Babblers and lead to their decline in both highly shrub encroached and cleared areas.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.jaridenv.2007.06.011](https://doi.org/10.1016/j.jaridenv.2007.06.011).

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