Persistence of the threatened Knysna warbler *Bradypterus sylvaticus* in an urban landscape: do gardens substitute for fire?

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Abstract

Food resources can limit populations of insectivorous birds. Previous studies have shown strong correlations between bird population densities and their invertebrate food, with declining populations being attributed to loss of prey. This might also be the case for the threatened Knysna warbler (*Bradypterus sylvaticus*), which in the last 20 years has declined precipitously on the Cape Peninsula, South Africa. The bird is abandoning natural, protected forests, retreating to narrow belts of suburban, riverine woodland with dense, tangled understoreys. The potential invertebrate food availability in natural forests and suburban woodland was assessed against what is known of the bird's preferred prey. The invertebrate food resource spectrum and abundance were determined using three sampling techniques in both natural forest and suburban woodland. Despite greater overall abundance of invertebrates in suburban woodland, the warbler's preferred prey items were equally abundant in both habitats. This suggests that reduced food supply does not explain abandonment of natural forests by the warbler. Rather, it is concluded that the availability of suitable nesting substrata, which are more abundant in suburban woodland, has driven the biotope shift. This is an unusual case of a localized and threatened bird species faring better under transformed conditions than in natural habitats.

Key words: arthropods, fire, food availability, Knysna warbler, urban conservation

Résumé

Les ressources alimentaires peuvent limiter les populations d'oiseaux insectivores. Des études antérieures ont montré de fortes corrélations entre la densité de populations d'oiseaux et les invertébrés qui leur servent de nourriture, le déclin des populations étant attribué à la perte de la nourriture. Ceci pourrait aussi être le cas de la fauvette de Knysna (*Bradypterus sylvaticus*) qui a décliné très rapidement sur la Péninsule de Cap, en Afrique du Sud, au cours des 20 dernières années. L'oiseau abandonne des forêts naturelles protégées et se retire vers des ceintures de forêts riveraines suburbaines, dont les étages inférieurs sont denses et touffus. La disponibilité potentielle des invertébrés dont ces oiseaux se nourrissent fut évaluée dans des forêts naturelles et dans des forêts suburbaines en fonction de ce que l'on connaît des préférences des oiseaux. On a déterminé le spectre et l'abondance des ressources en invertébrés consommés en recourant à trois techniques d'échantillonnage dans les deux types de forêt. Malgré une plus grande abondance générale d'invertébrés dans la forêt suburbaine, les proies préférées de la fauvette étaient aussi abondantes dans les deux habitats. Ceci laisse supposer que ce n'est pas un apport de nourriture réduit qui explique l'abandon de la forêt naturelle par la fauvette. On en conclut plutôt que c'est la disponibilité en substrats propices pour la nidification, qui sont plus abondants dans la forêt suburbaine, qui a entraîné le changement vers l'autre biotope. Ceci est un exemple inhabituel d'espèce d'oiseau locale et menacée qui prospère mieux dans des conditions modifiées que dans des habitats naturels.

Introduction

For insectivorous birds, food is often seasonal in availability (Eeva, Lehikoinen & Pohjalainen, 1997; Johnson & Sherry, 2001) and can limit populations (Zanette, Clinchy & Smith, 2006; Dennis *et al.*, 2008). The dependence of

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such birds on the availability of invertebrate prey predisposes them to stochastic fluctuations in their local populations along with that of the invertebrates. Invertebrate loss in European agricultural lands is believed to be a major contributor to reductions in avian diversity (Wilson *et al.*, 1999; Benton *et al.*, 2002).

It has been well established that avian diversity decreases as a result of urbanization (Beissinger & Osbourne, 1982), particularly the diversity of ground-nesting, insectivorous birds (Chace & Walsh, 2006). The insectivorous Knysna warbler (*Bradypterus sylvaticus*) presents an interesting exception to this general rule: it is a threatened bird which nests close to the ground and forages on the ground for invertebrates (favouring arachnids and amphipods), yet it fares better in a transformed urban landscape than in an adjacent protected area (Visser & Hockey, 2002).

The Knysna warbler is endemic to southern South Africa and is globally threatened (Vulnerable on IUCN Red List) because of its restricted and decreasing geographical range, patchy distribution and small population size (estimated at 2500 birds – BirdLife International, 2004). These warblers occur on the fringes of Afro-temperate forests and in associated streamside thickets (Hockey, Dean & Ryan, 2005), where they breed in spring and early summer between August and December (Pringle, 1977; Hockey, Dean & Ryan, 2005). This is the time of year at which local invertebrates, particularly the surface-active invertebrates (Pryke & Samways, 2010), are at their most abundant (Pryke & Samways, 2008).

The most westerly population of Knysna warblers occurs on the Cape Peninsula, Western Cape Province (33°58 S, 18°24 E). This small population is isolated from populations farther east by extensive urbanization. Much of the species' original habitat on the Peninsula has been lost to agriculture, urbanization and exotic tree plantations (pines and eucalypts – Pryke & Samways, 2009a). These birds now occur mostly in suburban woodland on the lower eastern slopes of Table Mountain. These suburban woodlands have previously been invaded by alien trees, many of which have now been removed, creating a habitat which is structurally similar to the natural forest, although more light is able to penetrate the canopy promoting the development of a structurally diverse understorey. They have become increasingly rare in protected natural forests at higher elevations, where they occurred historically (P.A.R. Hockey, unpubl. data), suggesting changes to the protected forests that have reduced habitat quality for the warbler. In the 1970s, there were estimated to be fewer than 100 pairs of Knysna warblers on the Peninsula (Pringle, 1977); this number has at least halved since the late 1980s (Hockey, Dean & Ryan, 2005) and the population may now be as small as 25–30 pairs (P.A.R. Hockey, unpubl. data).

The natural forests of Table Mountain are important refuges for invertebrates (Ratsirarson *et al.*, 2002; Pryke & Samways, 2010), supporting many species endemic to the Cape Peninsula (Picker & Samways, 1996; Pryke & Samways, 2009b). Surface-active invertebrates are small, hyper-diverse and sensitive to environmental changes (Colwell & Coddington, 1994; Weaver, 1995; McGeoch, 1998; Kotze & Samways, 1999). They rely almost entirely upon resources provided within leaf litter (Stork & Eggleton, 1992; Giller, 1996), and their low mobility affords them little potential to avoid disturbance (Lawes *et al.*, 2005).

The suburban woodland within which the Knysna warbler occurs has higher species richness and abundance of surface-active invertebrates than do protected forests on Table Mountain, although many of those invertebrates occur more commonly in pine plantations than natural forests (Pryke & Samways, 2010). Afro-temperate forests on the Cape Peninsula typically exist as narrow belts in riverine ravines, where they are largely protected from the fires that drive the ecology of the adjacent fynbos vegetation (Campbell & Moll, 1977). Protecting forests from fire thickens the canopy, reducing light penetration to the forest floor and thus reducing understorey cover. Fire management in peri-urban areas is problematic, and fire has been excluded for over 38 years (in an area with natural burn cycles of 12–15 years) from extensive areas in the core of the warbler's range, most notably in the National Botanical Gardens at Kirstenbosch (Forsyth & van Wilgen, 2008).

In view of the links between invertebrate loss and declining bird populations elsewhere, we hypothesized that food availability was the factor driving the decrease in Knysna warbler numbers. The aim of this study was thus to compare prey availability between warbler-occupied and unoccupied habitats. Specifically, we ask whether the higher abundance of invertebrates in suburban woodland necessarily translates into high food availability for the Knysna warbler, and whether natural forest and suburban woodland experience different seasonal bottlenecks in terms of prey availability. Finally, management recommendations are made as to how it may be possible to encourage the Knysna warbler to return to the Cape Peninsula's natural forests.

Methods

Sampling area and layout

Table Mountain (33°58 S; 18°24 E) lies within the Table Mountain National Park (TMNP). Both undisturbed and disturbed, natural, southern Afro-temperate forests on the eastern and southern slopes of the mountain were sampled in this study (Table 1, Fig. 1). All sampling of the natural protected forests was performed within the TMNP, where the forests have been protected from fire for more than 38 years (Forsyth & van Wilgen, 2008) and, as a result, now have closed canopies and little understorey vegetation. Suburban woodland sampling was carried out on land managed by the City of Cape Town. These sites have been highly disturbed and are currently regenerating, with much more open canopies – and hence more understorey vegetation – than the protected, montane forests. The main disturbance factors in these suburban woodlands are the presence of alien trees and their removal (Pryke & Samways, 2009a).

Thirty sites were selected to represent six types of natural forest on Table Mountain that were formerly occupied by Knysna warblers and within which the warblers are now either very rare or absent (Table 1, Fig. 1). There were five replicates within each forest type. An additional five study sites were selected within suburban woodland, the habitat which now supports the majority of the remaining warblers (Fig. 1).

To sample a representative cross-section of invertebrates, pitfall trapping, quadrat searches and Berlese-Tullgren funnel litter extractions were used (Olson, 1991; Jimenez-Valverde & Lobo, 2005; Snyder, Draney &

Sierwald, 2006). Sampling was carried out four times from July 2005 to April 2006 (January, April, July, and October) at each of the 35 sites, giving a total of 140 sampling events.

Invertebrate sampling

Each site had four pitfalls traps. Each trap was 70 mm in diameter, effective for ants (Abensperg-Traun & Steven, 1995) and arachnids (Brennan, Majer & Moir, 2005), but small enough to prevent vertebrate bycatch. Traps were half-filled with a 50% ethylene glycol solution which, when compared to most nonevaporative killing agents, is less toxic to most vertebrates and does not attract invertebrates (Woodcock, 2005). Traps were left open for 1 week to sample local invertebrate assemblages (Borgelt & New, 2006), after which all contents were sieved out, washed and placed in 75% ethyl alcohol.

Quadrat sampling consisted of an intensive ground search of an area of 1 m^2, searching for all arthropod types known to be eaten by Knysna warblers: these were collected and preserved for later identification. The litter extraction consisted of 725 ml of litter collected and then placed in a Berlese-Tullgren funnel for 72 h. The size range of invertebrates analysed in this study was 4–20 mm, representing the range of prey sizes eaten by Knysna warblers (Visser & Hockey, 2002).

For all sampling methods, the collected arthropods were sorted, and those belonging to the Classes Arachnida (except mites), Malacostraca, Chilopoda, Diplopoda and the Insecta orders Blattodea, Coleoptera, Hymenoptera and Orthoptera were counted and, where possible, identified to species. In the case of isopods and centipedes, individuals

Table 1 Forest habitats sampled, with their codes and elevations. Riverine forest is natural forest less than 10 m from a stream, while nonriverine forest is forest more than 10 m from a stream

| Code	Elevation (m a.s.l.)	Description
EaRF	320–380	Natural riverine Southern Afro-temperate forest on the east side of Table Mountain.
EaNR	320–380	Natural nonriverine Southern Afro-temperate forest on the east side of Table Mountain.
SoHRF	320–340	Natural riverine Southern Afro-temperate forest on the south side of Table Mountain.
SoHNF	320–340	Natural nonriverine Southern Afro-temperate forest on the south side of Table Mountain.
SoLRF	100–160	Natural riverine Southern Afro-temperate forest on the south side of Table Mountain.
SoLNR	100–160	Natural nonriverine Southern Afro-temperate forest on the south side of Table Mountain.
SubWood (suburban woodland)	100–140	Southern Afro-temperate forests that have been highly disturbed by alien vegetation and its removal. Like the natural forests, they have a thick layer of leaf litter, but unlike natural forests, they also have extensive understorey vegetation.
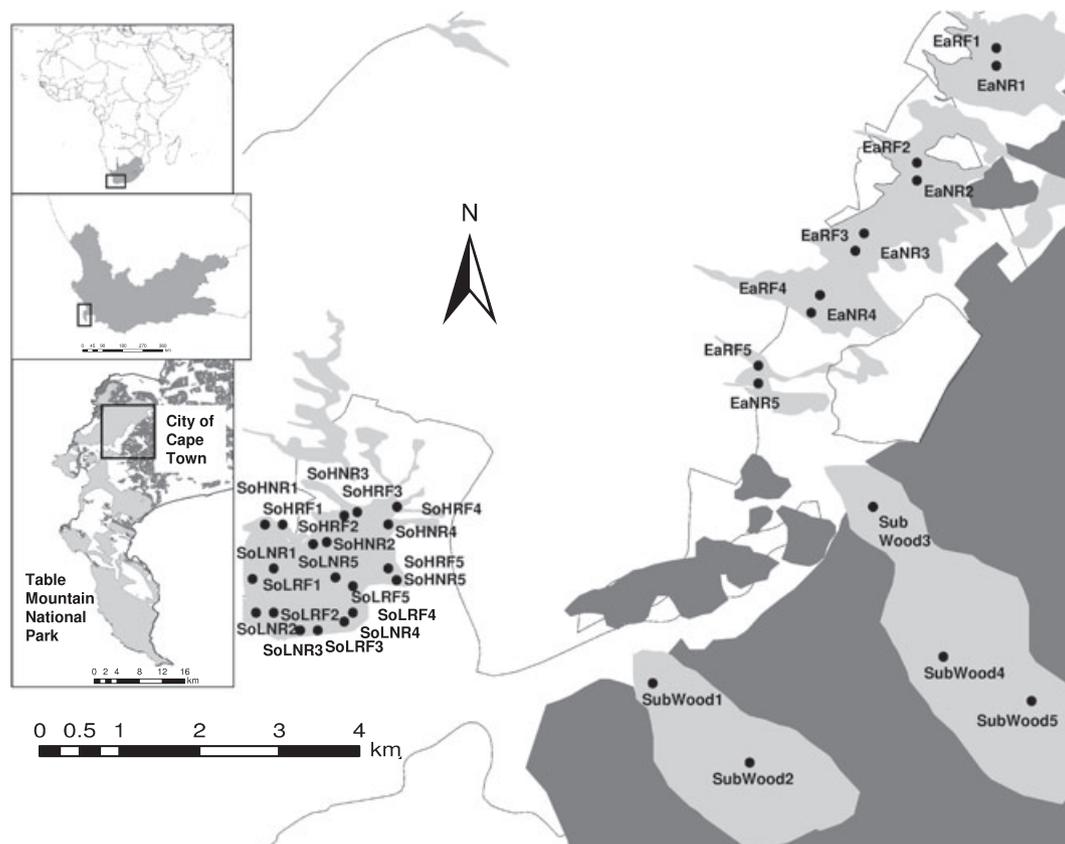
Fig 1 Map showing the 35 sites used in this study on the southern and eastern slopes of Table Mountain. Light grey areas show the extent of the woodlands, while the dark grey areas show the extent of the urban areas and pine plantations. Ea = east, So = south, H = higher, L = lower, NR = nonriverine, RF = riverine forest and SubWood = suburban woodland

were allocated to morphospecies. Specimens were dried and weighed using a 0.0001 g scale.

Data analyses

All invertebrate abundance and biomass data had non-normal distributions, and their variances were heterogeneous (Shapiro and Wilk's W-statistic), even after log-transformation (Underwood, 1997; Legendre & Legendre, 1998). To estimate the relative availability of prey for warblers across sites, the average biomass of each species caught was multiplied by the numerical percentage that its taxonomic group contributed to the diet of Knysna warbler chicks (data from Visser & Hockey, 2002). These data were also non-normal with heterogeneous variances. For habitat comparisons, repeated-measure analysis of variances (ANOVA) was calculated on the bootstrap means (Efron &

Tibshirani, 1993), with post-hoc uncorrected pair-wise comparisons. Repeated-measure analyses were used to reduce the effect of season on site data (Legendre & Legendre, 1998). The means were bootstrapped 9999 times to overcome non-normality of the data. Seasonal variation was analysed using pair-wise Kruskal–Wallis nonparametric ANOVAs (Legendre & Legendre, 1998).

Results

Invertebrate species richness and abundance

A total of 4634 invertebrates representing at least 95 species (including morphospecies) were sampled from all habitats combined. Of these, only 36 species (36.8%) and 3048 individuals (66.0%) were considered potential prey for warblers (based on the 4–20 mm prey size constraints

and they types of prey know to be eaten by warblers – Visser & Hockey, 2002).

The two most abundant invertebrate groups potentially available to warblers were amphipods and isopods, both of which were fed to chicks. However, the next four most abundant groups (beetles, millipedes, grasshoppers and ants) were not delivered to chicks (Fig. 2). Arachnids, the group most frequently delivered to chicks, ranked only seventh in abundance. A small percentage (8.2%) of Knysna warbler prey types (Visser & Hockey, 2002) was not recorded in this study.

Across all sites, there were no significant differences in the numerical abundance of invertebrates known to be eaten by Knysna warblers ($F_{6,28} = 0.48$, $P = 0.82$; Fig. 3a). Among these invertebrate groups, only the cockroaches showed significant differences in their abundances across sites ($F_{6,28} = 3.14$, $P = 0.02$; Fig. 3d), with densities in suburban woodland being significantly higher than in forests. Abundances of amphipods ($F_{6,28} = 0.75$, $P = 0.62$), arachnids ($F_{6,28} = 2.33$, $P = 0.06$) and isopods ($F_{6,28} = 1.10$, $P = 0.39$) did not differ significantly between sites (Figs 3b,c,e).

Invertebrate biomass

When seasonal effects are suppressed in the repeated measures ANOVA and all prey types known to be eaten by warblers are combined, there were no significant differ-ences in overall invertebrate sampled biomass between sites ($F_{6,28} = 0.95$, $P = 0.48$; Fig. 3f). When comparing invertebrate groups sampled biomasses per site, there were significant differences in the biomasses of arachnids ($F_{6,28} = 5.36$, $P < 0.01$), with the eastern nonriverine forests and southern lower riverine forests supporting sig-nificantly higher biomasses than other forests sites and suburban woodlands (Fig. 3h). The biomass density of cockroaches in suburban woodlands was significantly higher than elsewhere ($F_{6,28} = 3.88$, $P < 0.01$; Fig. 3i), but amphipod ($F_{6,28} = 0.75$, $P = 0.62$; Fig. 3g) and isopod biomass density ($F_{6,28} = 0.96$, $P = 0.47$; Fig 3j) did not differ across sites.

The corrected biomass (sampled biomass per site multi-plied by the numerical percentage of each prey type delivered to chicks) showed significant pair-wise differences between natural forests sites ($F_{6,28} = 3.09$, $P = 0.02$), al-though there were no significant differences between the suburban woodland and any of the other forest types (Fig. 4).
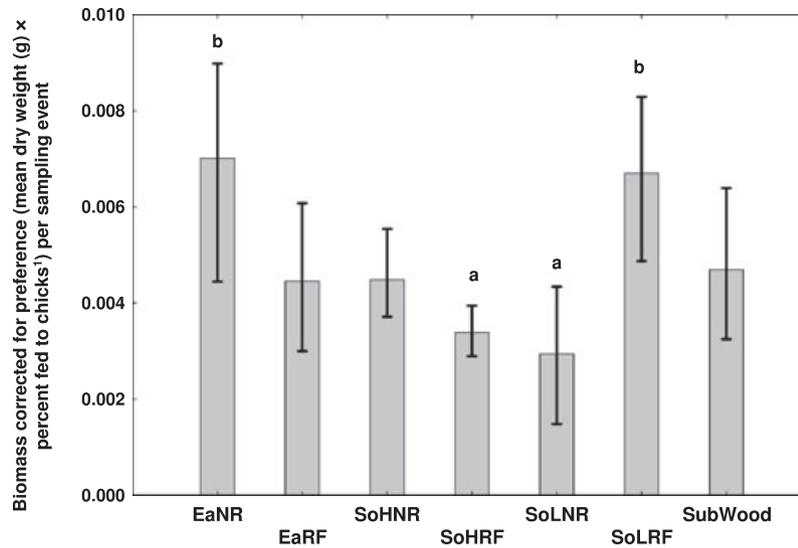
Seasonal variations in the invertebrate food source

There were no significant seasonal differences in the cor-rected biomass of the invertebrate groups preyed on by warblers, either between seasons ($H_{3,138} = 2.74$, $P = 0.43$) or between habitat types within seasons ($H_{7,138} = 8.05$, $P = 0.33$; Fig. 5). However, during spring
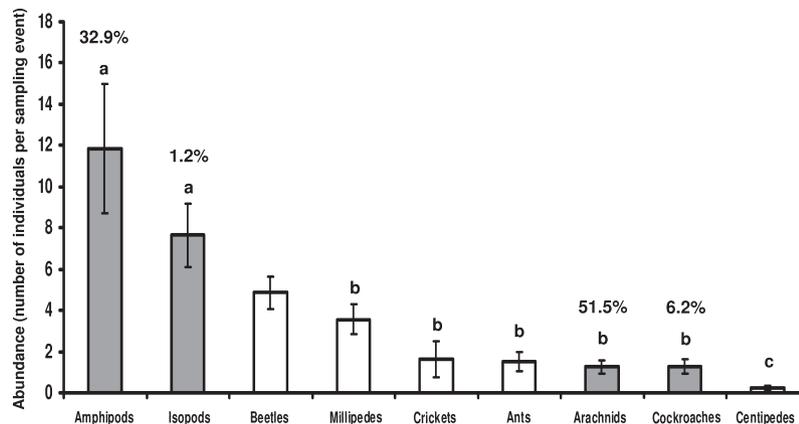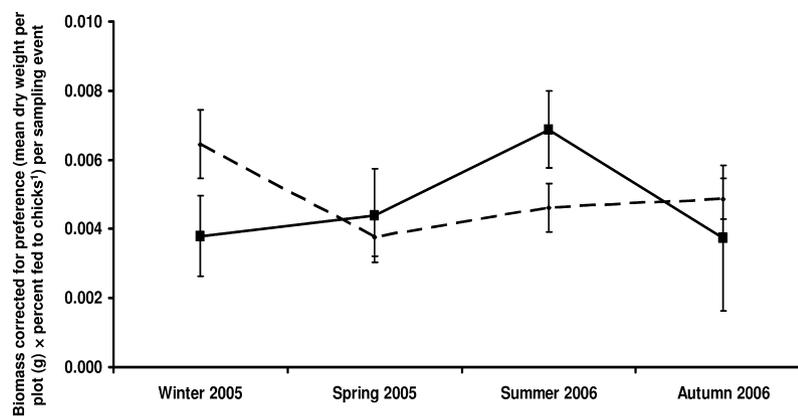

Fig 2 Mean (±1 SE) abundance per sampling event (site per season) of invertebrate groups sampled in natural forests on Table Mountain. These results are for all the sampling techniques data pooled. Grey bars represent groups which Knysna warblers are known to eat, while the percentage values above the bars is the proportion of these prey types that were fed to chicks: 8.2% of invertebrates fed to chicks (Visser & Hockey, 2002) were not recorded in this study. Groups of invertebrates with the same letter above the respective bars did not differ significantly in their mean abundances (5% significance level)

Mean abundance (number of individuals per sampling event) / **Mean biomass (weight per sampling event (g))**
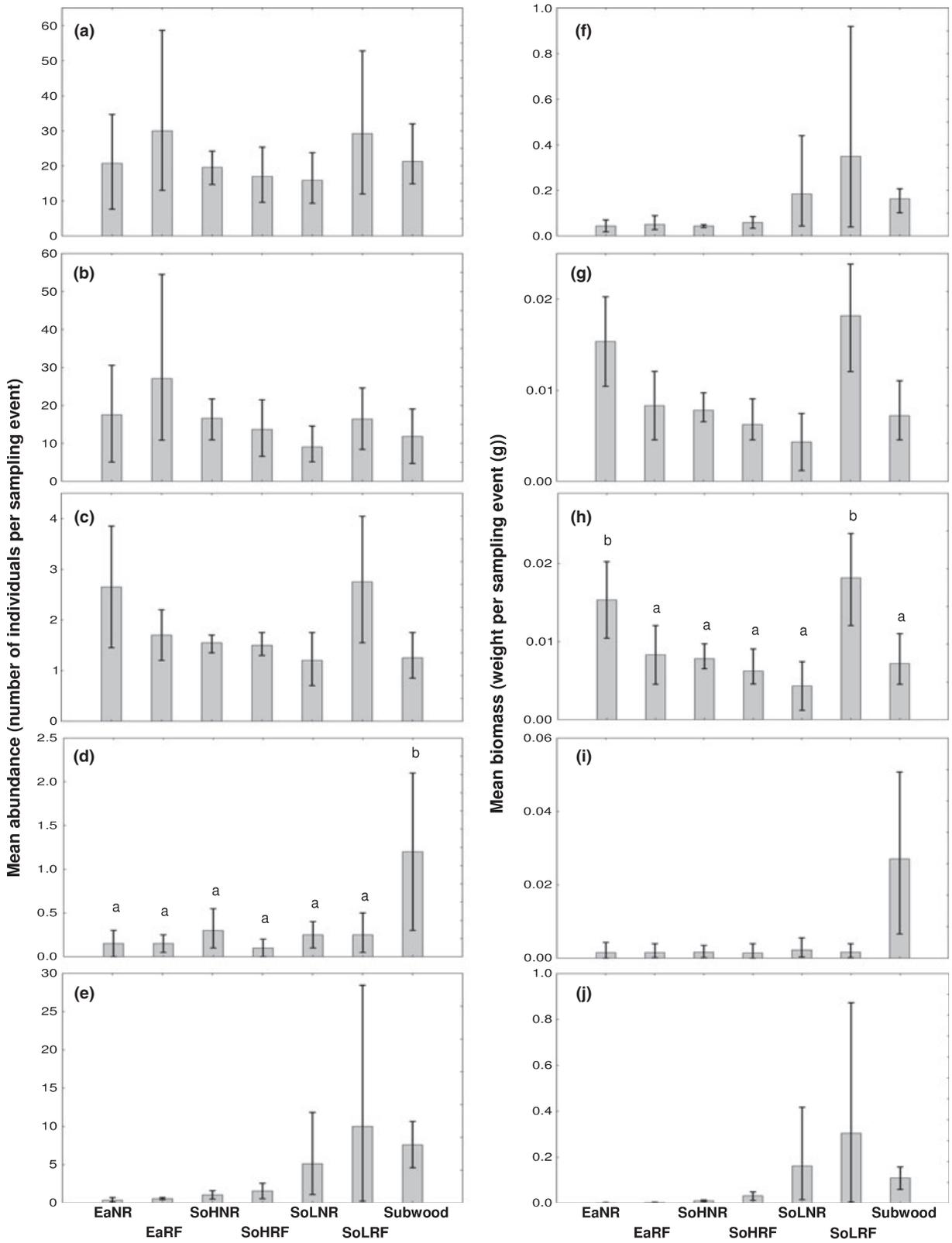
Fig 4 Bootstrapped means with 95% confidence intervals for the available biomass sampled per sampling event (site per season) of invertebrates corrected for the Knysna warbler's preferred prey type. These results are for all the sampling techniques data pooled. [1]Percentage of individual groups of invertebrates fed to chicks (from Visser & Hockey, 2002). Ea = east, So = south, H = higher, L = lower, NR = nonriverine, RF = riverine forest and SubWood = suburban woodland. Different letters above bars represent significantly different means (5% significance level)

Fig 5 Mean (±1 SE) seasonal invertebrate biomass sampled per sampling event (site per season) corrected for the Knysna warbler's preferred prey types. These results are for all the sampling techniques data pooled. [1]Percentage of particular groups of invertebrates fed to chicks (from Visser & Hockey, 2002), in suburban woodlands where Knysna warblers are present (solid line) and forests where they are rare or absent (dashed line)

and early summer – the breeding season of Knysna warblers – invertebrate biomass in suburban woodland was increasing.

Discussion

Food availability

There appears to be an abundance of invertebrates available to the Knysna warblers in all the forests of Table Mountain. The warbler is, however, selective in its choice of prey. The favoured prey (at least when feeding chicks) are arachnids (Visser & Hockey, 2002), but these are certainly not the most abundant prey in the landscape. Arachnids and amphipods accounted for 84.4% of the prey items fed to chicks (Visser & Hockey, 2002), yet in suburban woodland they made up only 38.9% of invertebrate numbers (amphipods 35.2%, arachnids 3.7%) compared to 56.2% (amphipods 51.2%, arachnids 5.0%) in natural forests. Amphipods alone account for about 32% of the birds' diet by numbers and are common in all forest types. Interestingly, the abundance of the two invertebrate groups least preferred by the warbler (cockroaches and isopods, together making up less than 8% of items fed to chicks) were high in the suburban woodland. Based on the above, differences in prey abundance between forests and woodlands cannot be invoked to explain why the Knysna warbler is disappearing from natural forests on the Peninsula.

In contrast to prey abundance, which varies little across forest types, prey biomass density is higher in the suburban woodland (Fig. 3), but much of this difference is accounted for by relatively high biomasses of (least-preferred) cockroaches (Fig 3i). Thus, although there are differences in prey biomass between sites, these too are unlikely to explain the birds' changing habitat preference.

Seasonal availability of food

Changes in the seasonal availability of food could be a factor precipitating the decline of the Knysna warbler in protected forests on the slopes of Table Mountain. Although sampling was restricted to a single year, during spring and summer (the breeding season) corrected biomass of invertebrate prey was highest in suburban woodland. Autumn (post-breeding) was the season of lowest invertebrate biomass in the suburban woodland. Interestingly, pairs that fledge chicks successfully leave the territory with their broods soon after fledging, with males returning fairly soon thereafter, and females only at the start of the next breeding season (Visser & Hockey, 2002). Although it is unknown where dispersing birds go, such dispersal behaviour would minimize pressure on food supplies within their breeding habitats at the time of the year when food availability is at its lowest.

Conclusions

This is an unusual case of a threatened, locally endemic forest/forest edge bird species faring better under transformed conditions than in ostensibly natural habitats. Based on our comparison of the food resources in forest and suburban woodland, it would be very difficult to invoke food supply to explain the abandonment of natural forests by Knysna warblers, despite the fact that loss of invertebrate food resources has proven to be a major causal factor for insectivorous bird declines elsewhere (Wilson *et al.*, 1999; Benton *et al.*, 2002).

Areas currently favoured by the warbler are narrow, suburban belts of fairly tall, riverine woodland with a dense, tangled and highly heterogeneous understorey. The presence of this dense understory vegetation appears critical for the bird's nesting (Visser & Hockey, 2002) but not for their prey. In much of the bird's natural (forest) range on the Cape Peninsula, the adjacent fynbos areas have been protected from fire since the 1970s (Forsyth & van Wilgen, 2008) despite the fact that the natural fire regime for the area is 12- to 15-year burns (van Wilgen, Bond & Richardson, 1992). Fynbos protected from fire becomes invaded by, and eventually replaced by forest (Luger & Moll, 1993). As such forest spreads laterally from riverine ravines into the adjacent (unburnt) fynbos, lateral light penetration is reduced. As a consequence, the understorey vegetation becomes progressively more sparse.

The birds' retreat into suburban, riverine woodland seemingly is better explained by vegetation structure than by food availability or floristics (many of the plants in these areas are aliens). We propose that suburban gardens adjacent to these woodlands, with their extensive open areas, are creating conditions in the woodlands comparable to those that were present in riverine forest when the adjacent fynbos was allowed to burn. Gardens allow substantial lateral penetration of light into the woodlands, promoting the dense understorey that the birds need for nest sites (Visser & Hockey, 2002). In this way,

anthropogenic disturbance (open areas) unintentionally mimics natural disturbance (fire). Whether the montane, riverine forest habitat can be returned to its natural state by controlled burning is equivocal, with lateral forest expansion now being extensive. Manual removal of the nonflammable forest component of the invaded fynbos vegetation may be a prerequisite.

Acknowledgements

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