

Multi-scale habitat selection by a cryptic, critically endangered grassland bird—The Plains-wanderer (*Pedionomus torquatus*): Implications for habitat management and conservation

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Abstract Our understanding of the habitat needs of grassland fauna is often incomplete because of their cryptic behaviour. This presents a barrier to identifying important habitat attributes, whether these change at different spatial scales, and how this informs management decisions. Here, we use a critically endangered bird, the Plains-wanderer (*Pedionomus torquatus*, Pedionomidae), as an exemplar of the challenge of managing grasslands for cryptic species. Until now, almost all ecological knowledge of Plains-wanderers has come from the detection of nocturnally roosting individuals and habitat assessments at fine-scales that indicate open swards are preferred habitat. We GPS-tracked 13 adult Plains-wanderers to better understand diurnal habitat utilization in native grasslands of south-eastern Australia. Using these data, we assessed whether Plains-wanderers select for different habitat attributes during the day and night, and whether this varied according to spatial scale. At the fine-scale (< 1 ha), daytime foraging occurred in denser swards than those of nocturnal roosting sites. At the patch-scale (1–50 ha), Plains-wanderers selected for denser vegetation, with higher grass and lichen cover, whilst avoiding areas where structure was impacted by a high exotic plant cover. Plains-wanderers did not select habitat based on grassland type at the landscape-scale (>100 ha). We demonstrate that Plains-wanderers require grasslands with both open and denser swards to support foraging and roosting. In doing so, we address the biases associated with habitat assessments based on roost-only locations and extend known habitat associations critical to the successful management of the species. Our findings highlight that a precautionary approach to the classification of habitat requirements is warranted when uncertainty around habitat use of cryptic grassland fauna exists.

Key words: cryptic species, grasslands, habitat selection, movement ecology, Plains-wanderer.

INTRODUCTION

Managing habitat for obligate grassland fauna can be challenging; grasslands are typically dynamic habitats that can undergo rapid changes in structure in response to abiotic (e.g. rainfall; Baker-Gabb *et al.* 2016) and biotic factors (e.g. grazing; Williams *et al.* 2015). Because of this dynamic, frequent and targeted management of biomass is often necessary to provide the diversity of habitat able to support grassland fauna species with opposing vegetation structural preferences in landscapes (Bailey *et al.* 2019; Hovick *et al.* 2015a). However, as grassland fauna are typically cryptic, management recommendations are often guided by

incomplete ecological knowledge of species requiring management. This presents the potential for misalignments between habitat attributes that form the focus of management and those that are actually important to the species of concern.

The typical traits of grassland fauna (e.g. small, camouflaged), coupled with the featureless landscape they inhabit, often impede the reliable detection and observation of individuals *in situ* (Gibson & New 2007; McGrath *et al.* 2015; Nielsen *et al.* 2016). Furthermore, the cryptic behaviour of many grassland species makes it difficult to identify which habitat attributes are important, and how to best manage habitats at finer scales. The Grassland Earless Dragon (*Tympnocryptis pinguicolla*), for example, is an endangered obligate grassland reptile that is difficult to detect (McGrath *et al.* 2015) and thought extinct until

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fortuitous discovery after not being recorded for 30 years (Osborne *et al.* 1993). Grassland earless dragons were assumed to be restricted to basalt-derived soils with rocks until an investigation of alternate survey methods improved detectability and extended known habitat associations of the species (McGrath *et al.* 2015). Similarly, the habitat needs of the Night Parrot (*Pezoporus occidentalis*), which occupies hummock grasslands, have only become known in the past decade because of extreme crypsis utilized by the species (Murphy *et al.* 2017a). Intensive fieldwork, coupled with novel technologies, has identified that the habitat characteristics of diurnal roost sites and nocturnal foraging sites differ markedly for the species (Murphy *et al.* 2017b). Together, these examples underscore the challenge of managing habitat for cryptic fauna.

Grassland fauna are often highly responsive to differing vegetation structures and may express strong preference for specific structural attributes, in particular, specific spatiotemporal habitat configurations. This type of habitat selectivity typically relates to the need to balance predator avoidance with shelter, food availability and intraspecific interactions (Brennan & Kuvlesky Jr 2005; Winter *et al.* 2005). Owing to the dynamic of vegetation structure in grasslands, species often select habitat based on decisions made at multiple spatial scales. Habitat requirements of Prairie-chickens (*Tympanuchus* spp.), for example, encompass a broad range of vegetation structures at different spatial scales to meet their behavioural needs (Marks & Marks 1988; Derner *et al.* 2009). Some species require landscapes with high shrub cover, as well as open patches for leks within home ranges (Woodward *et al.* 2001). Historically, disturbance regimes such as indigenous land management practices, small animal digging and large herbivore grazing created resource heterogeneity across spatiotemporal scales that benefited fauna. However, many of these processes have been lost from grassland biomes, and now careful management is required to maintain the optimal spatial configuration of resources to meet the needs of faunal communities (Hovick *et al.* 2015a). In instances where the importance of vegetation structure differs with life histories, this added complexity means it can be difficult to identify targets for management of habitat attributes at different spatial scales.

The Plains-wanderer *Pedionomus torquatus* (Pedionomidae) is a small, ground-dwelling bird of tussock-forming native grasslands across eastern Australia. The species is listed as Critically Endangered under federal legislation and the IUCN Red List (Commonwealth of Australia 2016). Habitat loss and degradation are key threats to the Plains-wanderer and have led to a major range contraction and population decline over the last 100 years (D'Ombra 1926;

Commonwealth of Australia 2016). Plains-wanderers have an appearance that resemble the quail, but they are more closely related to shorebirds, and comprise the monotypic family Pedionomidae (Olson and Steadman 1981). Owing to their taxonomic uniqueness and high level of extinction risk, the Plains-wanderer is considered to be of outstanding global conservation importance (Jetz *et al.* 2014) and regarded by some as *the* bird species of highest priority for conservation action globally (EDGE 2021). Plains-wanderers occupy grasslands that are characterized by a mosaic of soil types which give rise to floristically and structurally distinct grassland communities at patch-scales (Foreman 2010).

Plains-wanderers are thought to prefer sparse tussock grassland on red clay soils (Baker-Gabb *et al.* 1990), but this is based almost exclusively on nocturnal observations when birds are roosting and easiest to detect (Antos & Schultz 2020; Baker-Gabb *et al.* 2016). Assessments of roost site characteristics have been used to define habitat suitability for the species and guide management targets. Grassland that supports a cover of 50% bare-ground, 10% litter, with the remaining 40% consisting of grasses and herbs is categorized as 'ideal' Plains-wanderer habitat (DPIE 2020, Baker-Gabb 2016). Combined, these habitat characteristics have been thought to provide a structure that is preferred as it facilitates efficient foraging as well as concealment from predators. During the day, the Plains-wanderer is highly cryptic and remarkably few daytime observations have ever been recorded (Baker-Gabb 1988; D'Ombra 1926). Consequently, information on fine-scale movements and habitat uses, as well as longer-distance dispersal, is lacking for the species. There is potential for different types of grassland habitat to be selected and used for foraging or other diurnal activities, but such habitat occupancy remains unquantified.

Major change in grassland structure is a key threat to the Plains-wanderer and has been implicated in significant population declines (Baker-Gabb *et al.* 2016). Management of biomass is therefore an important concern of land managers tasked with conserving the species. Grazing by livestock is the primary tool used to manage vegetation structure and achieve desired grassland states. At present, habitat management for the Plains-wanderer is guided by the premise that open vegetation, which is preferred for nocturnal roosting, is indicative of the habitat utilized for daytime foraging. Consequently, most management prescriptions guide land managers to replicate the definition of 'ideal' habitat (short and sparse vegetation), with little or no emphasis on the need to promote structural heterogeneity at specific spatial scales for different behavioural activities (Baker-Gabb *et al.* 2016; Baker-Gabb 2016; Commonwealth of Australia 2016; DPIE 2020; Parker & Oliver 2006).

In practice, this can mean management units are judged ‘too dense’ if patches of vegetation (*i.e.* >10 hectares) remain tall and closed within a matrix of short, open vegetation. Additionally, the protection and biomass management of red soil grassland is prioritized over other grassland types (Baker-Gabb 2016). Because our understanding of the habitat needs of Plains-wanderers is biased towards micro-habitat scales where birds sleep, there is significant risk that current management strategies are not delivering optimal habitat for all behavioural requirements (*i.e.* foraging, roosting and courtship) at appropriate spatial scales. This would particularly be the case if different vegetation structures are required for foraging as there are no management targets for structural heterogeneity at patch-scales (*i.e.* home range scales).

Here, we use the Plains-wanderer as an exemplar of the challenge of identifying habitat requirements for cryptic grassland fauna. We examine whether understanding of habitat use derived from one part of the Plains-wanderer’s behaviour (roost site characteristics) can be used to infer the full complement of habitat needs of the species. We also investigate the spatial scales at which Plains-wanderers select habitat. We used miniaturized GPS trackers to quantify habitat use by Plains-wanderers during the day, the time of greatest crypticity, and to establish a more complete understanding of their habitat needs. Movement data also provided an opportunity to identify the influence of vegetation structure on habitat selection at fine-, patch- and landscape-scales. Furthermore, it allowed us to test the accuracy of assumption that relatively homogenous, open grassland is optimal habitat for the Plains-wanderer.

METHODS

Study region

The study took place in the Northern Plains Grasslands of south-eastern Australia, a community listed as Critically Endangered under Australian federal legislation (TSSC, 2012). Study sites were located on the Patho Plains, north-central Victoria, Australia (36.12 S, 144.35 E). In this region, less than 1% of pre-European extent of native grasslands remain due to conversion for cropping (Foreman 2010). Native grassland occurring on private land is typically used as pasture for production of sheep and cattle. Some areas of grassland on private land are protected and managed under conservation agreements. The largest conservation reserve is Terrick Terrick National Park (3491 ha), a park comprising multiple fragmented grassland blocks, ranging in size from 60 to 300 ha, situated in an agricultural matrix.

Climate is a key driver of dynamics in vegetation structure, food resources and bird populations in grasslands (Yang *et al.* 2008). The climate of the region is semi-arid

with average annual rainfall of 414 mm and high inter-annual variability (range 163–871 mm; BOM 2021). The region experienced mostly dry to average conditions across the study period (2018 = 67% of average rainfall; 2019 = 62% of average rainfall; 2020 = 107% of average rainfall).

Soil type plays an important role in shaping vegetation structure and composition in grasslands (Morgan and Williams 2015). Soils of Northern Plains Grasslands are poorly drained red clay-loams and grey clays derived from the deposition of Quaternary alluvial sediments (Skene and Harford 1964). They typically vary spatially at scales of tens of metres. Red clays are generally located on gentle rises adjacent to drainage channels and depressions of grey clays. In some areas, soils are mix of red and grey clays or ‘Gilgais’—small mounds of friable red and grey clays that contract and expand in response to moisture (hereafter classified as ‘mosaic’ soil type).

The three dominant soil types of Northern Plains Grasslands (red, grey and mosaic) support distinct vegetation (Fig. 1) (Foreman 1996). Red soils typically support short-statured (<0.3 m) tussock grasses (*e.g.* *Rytidosperma setacea*, *R. caespitosa*, *Austrostipa scabra* and *Enteropogon acicularis*) and a rich diversity of biocrusts, ground cover and sub-shrubs, particularly *Maireana* spp. Grey soil supports tall (> 0.5 m), robust tussock-forming grass species (*e.g.* *Austrostipa gibbosa*, *A. aristiglumis* and *Walwhalleya prolata*) and a generally high cover of non-native annual grasses (*e.g.* *Avena* spp., *Lolium* spp. and *Hordeum* spp.). Mosaic soils tend to support a mix of species characteristic of both red and grey soils, with an intermediate structure.

Study species

The Plains-wanderer is a native grassland specialist and not known to use non-native pastures, crops, or areas with scattered trees (Baker-Gabb *et al.* 1990). They are resident year-round and have a generalist diet, feeding on seed and invertebrates (Baker-Gabb 1988). It remains unclear what role food availability plays in habitat selection. Most aspects of Plains-wanderer dispersal patterns remain unknown, and it is unclear if they undertake regular short (< 100 km) or long-distance (>100 km) movements when seeking to establish territories and find mates. However, population genetic and mark-recapture studies have demonstrated they are capable of long-distance movements (≥ 150 km) (Antos & Schultz 2020).

The Plains-wanderer is unusual among birds because it is the female that is larger and more brightly plumaged than the male (Baker-Gabb *et al.* 1990). Females also defend a territory and attract mates with deep, booming vocalizations. Plains-wanderers can breed in every month of the year, responding to increases in grassland productivity and food availability driven by large rainfall events, more so than season (D. Baker-Gabb *pers. obs.*). Radio telemetry studies have suggested territories range between 10 and 15 ha (Baker-Gabb *et al.* 1990). Most other aspects of the Plains-wanderer’s mating system are poorly understood because there has been no direct observation of male–female interactions or courtship behaviour in the wild.

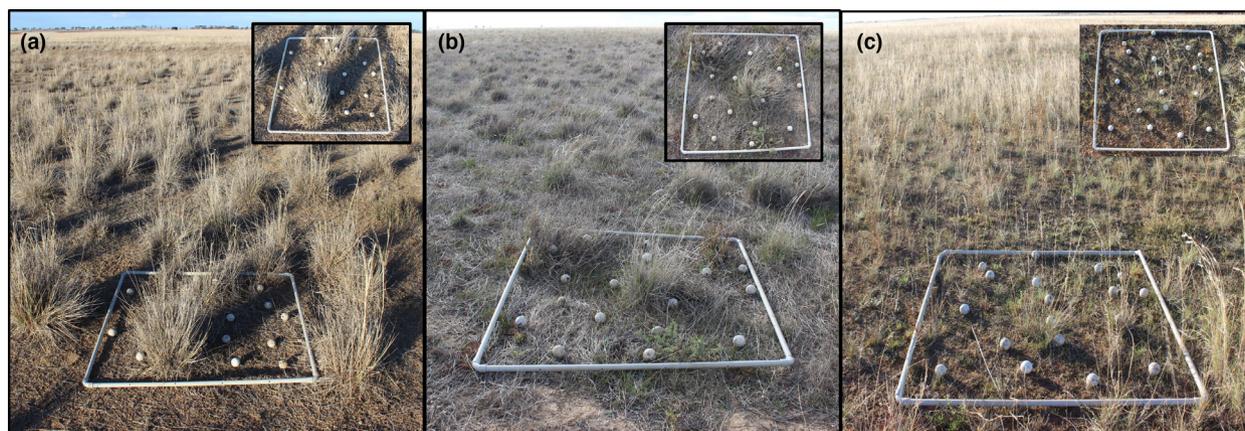


Fig. 1. Vegetation structure typical of a) grey soil (quadrat scored a golf ball value of 11), b) mosaic soil (quadrat scored a golf ball value of 13.5) and c) red soil (quadrat scored a golf ball value of 16) in autumn in native grasslands of the Northern Plains of Victoria, south-eastern Australia.

Although not conclusive, evidence arising from newly established captive breeding settings suggests that lekking may form part of their biology (Pauligk 2020).

Despite its distinctive, far-carrying call and colourful female plumage, Plains-wanderers are nearly impossible to detect during daylight hours when the species is active. They are typically very reluctant to flush at any time (Keartland 1901). At night, birds are typically unwilling to run or fly away when approached and, instead, will often stand erect, making them comparatively easier to detect during vehicle-based surveys. Plains-wanderers do not appear to modify vegetation to create a roost.

Radio and GPS tracking of Plains-wanderers

We searched at night for wild Plains-wanderers using spotlights and thermal scanners in areas of known habitat. Searches were principally undertaken by vehicle, with a total of 126 km travelled. Birds were captured using a hand net. Each bird was fitted with a 1.2 g GPS receiver (Pinpoint 10, SWIFT fix strategy, Lotek, UK) bundled with a 0.6 g VHF transmitter (PicoPip Ag317, Lotek, UK) as a single tag. Only adult birds were fitted with tags, as juveniles were typically too small to meet the >60 g tag: body mass threshold (<3% of body mass) to carry trackers. GPS receivers captured satellite fixes of bird locations at scheduled times, while VHF transmitters facilitated relocation of birds and recovery of tags and GPS data at the end of tracking. Tags were attached using a glue-mount to trimmed feathers on the back or a backpack harness constructed with fitted elastic bands. Birds were released at point of capture.

Between 2018 and 2020, 15 adult Plains-wanderers were fitted with a tracker; of these, 13 were relocated and recaptured and tags were removed at the end of the tracking period (Appendix S1, Table S1). The remaining two individuals likely dispersed from the area as no VHF signal could be detected within a 5 km radius of the release site. In total, Plains-wanderers were successfully tracked at nine sites which represented distinct management units

(paddocks). These sites ranged in size from 60 to 150 ha and were at least 800 m apart. Most sites were surrounded by non-irrigated crops or non-native pasture.

We used two GPS fix scheduling programs during the study. For the first, GPS tags were programmed to capture fixes every 15 mins between dawn and dusk for 4 days. This short-duration program was only used for two birds (F1, M1) before a longer-duration setting was adopted (Appendix S1). The second program involved fixes captured every 3 h for 8 days from dawn to dusk. The first and last diurnal fix was programmed for 1 h after sunrise and 1 h before sunset (or as near as possible), respectively, to distinguish areas used for foraging *versus* roosting. At night, two fixes were obtained to confirm roost location: 2 h after dusk, and 2 h before dawn. Of the 11 birds sampled with the longer program, the shortest tracking period was 5 days, owing to battery failure. As the short-duration program did not collect information on roosting sites, movement data of these birds are only used in patch-scale analyses.

Tracking data cleaning

We assumed bird movements would be compromised by the disturbance of initial capture and tracker attachment; thus, fixes recorded from time of release through until mid-day the following day (*i.e.* ~15-h post-capture) were excluded. All fixes were accompanied with a 'degree-of-precision' value (DOP) that estimates the accuracy of coordinates based on the number of satellites a tag communicated with at the time of a fix. Field tests and manufacturer recommendations identified that DOP values >3 were unsuitable for our study objectives (>10 m error), and these were omitted. On average, 13% of all fixes were removed from the dataset with this filtering process. There were five obvious outliers also manually excluded (*e.g.* a single fix >1 km from home range cluster) as they were not consistent with known Plains-wanderer behaviour. Cleaned movement data were primarily visualized in QGIS (QGIS Development Team 2021), with initial exploratory analyses

conducted in ZoaTrack (<https://zoatrack.org/>), an online platform for the spatial analysis of animal tracking (Dwyer *et al.* 2015).

Fine-scale soil map development

We used soil type as a proxy for grassland vegetation types to facilitate mapping over large spatial scales. The strong association of different vegetation communities with soil types in grasslands of the Northern Plains has been used to map vegetation and habitat features at a similar scale (Foreman 1996). Similarly, soil maps play a key role in management decision-making at reserve-scales in this ecosystem (TAG 2010). We used multiple resources to develop a fine-scale map (~10 m resolution) of soil type (red soil, grey soil and mosaic soil) for all land with native grassland across the study region (Fig. 2). Mapping resources included 1) existing soil maps (TAG 2010), 2) satellite imagery, 3) on-ground knowledge and 4) on-ground field surveys. The extent of native grassland on private and public land was identified through consultation with local land holders and land managers, non-government organizations involved in grassland conservation, and spatial layers of

vegetation classes available from government databases (ARI 2021). For most grasslands in the conservation network, soil maps with adequate resolution already existed (TAG 2010). In cases where existing mapping was at a finer resolution than required for our purposes, categories of soil types were amalgamated (*e.g.* red soil types 1 to 5 categorized in TAG (2010) were combined to 'red soil' for this study). Areas within 200 m of tall trees and farm infrastructure, and water storage dams and channels within grassland, were deemed unsuitable for Plains-wanderers and were excluded.

Fine-scale (< 1 ha)

GPS fixes captured at different times of day were used to test for birds selecting different habitat for distinct behaviours (*i.e.* where to sleep or forage) at the fine-scale (< 1 ha). We categorized each fix as either 'day' or 'night', based on their time of capture. Roosting sites were identified from locations where night fixes were captured. In cases where multiple night fixes were located within 10 m of each other (within the margin of error for tags) over different nights, they were considered the same roost. The

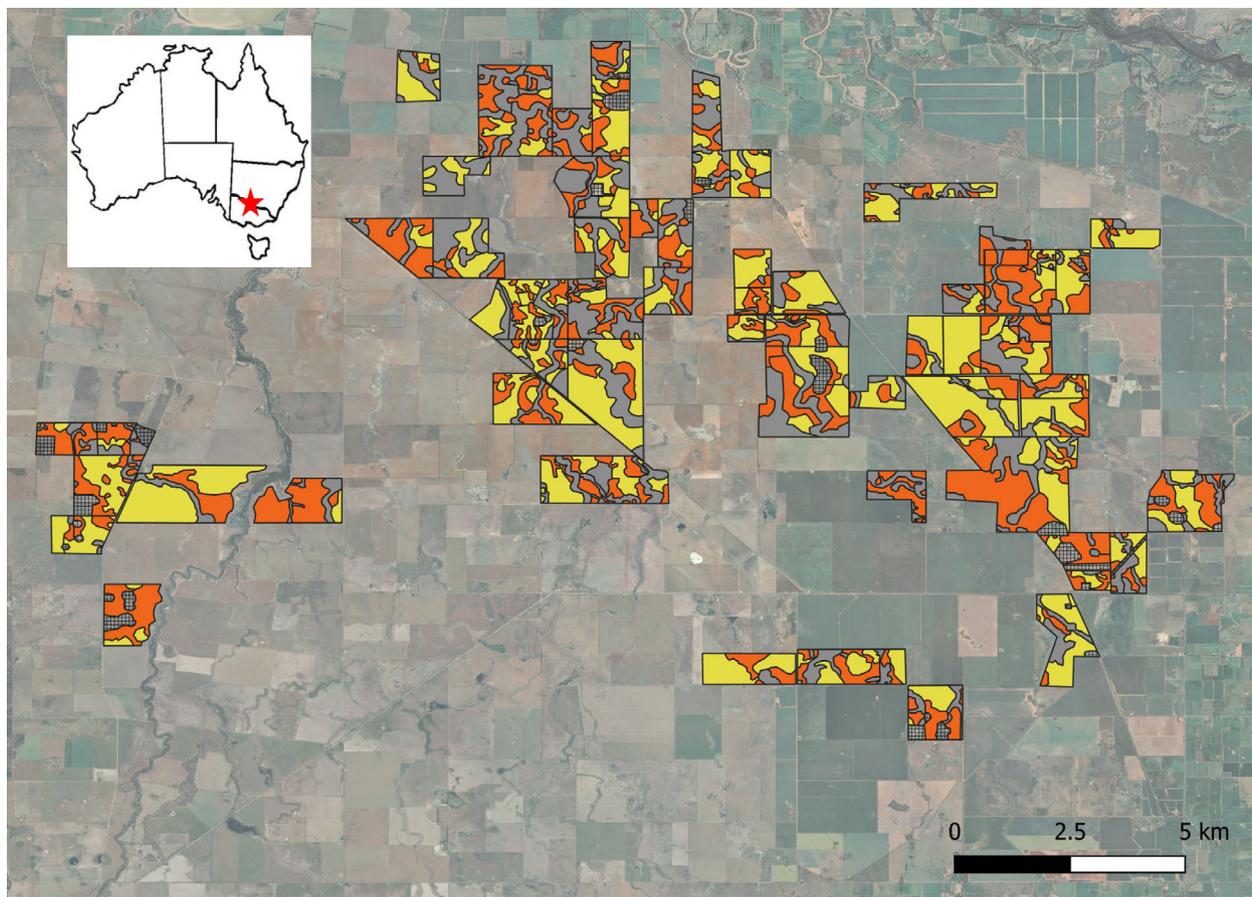


Fig. 2. Distribution of native grasslands and associated soil types (orange = grasslands on red soil; yellow = grasslands on mosaic soil; grey = on grey soil) in the agricultural matrix on the Northern Plains of Victoria, Australia. The areas of mapped native grassland were considered available habitat in landscape-scale analyses.

dominant soil type at each location (soil type with highest proportion within a 30 m radius) was identified by overlaying fixes and fine-scale soil map layers. To test whether Plains-wanderer select for a particular soil type when roosting, we first calculated the proportion of each soil type available in individual 95% kernel home ranges and the corresponding proportion of roosts recorded in each soil type. Next, we calculated Manly Selectivity Measures for each soil type and tested overall selection using a type III log-likelihood test statistic (K_{hi2L}) based on pooled data (Manly *et al.* 2007) in the R package *adehabitatHR* (Calenge 2006).

To facilitate on-ground surveys of habitat within a home range, a minimum convex polygon (MCP) was created encompassing all fixes for an individual bird. Each MCP was categorized as the 'used' patch and, within it, a grid of plots was positioned at least 60 m apart, at a density of 1–3 plots/ha to support habitat assessment (Fig. 3). In three cases where multiple birds were tracked at the same site, MCPs strongly overlapped. We avoided pseudo-replication of sampling plots by treating overlapped MCPs as a single 'used' polygon. Our primary aim was to understand what habitat features Plains-wanderers are utilizing and avoiding, irrespective of interactions amongst individuals, and so this approach was deemed appropriate for analyses. In total, nine MCPs were produced (Appendix S2). Field surveys of plots were conducted 1–3 weeks after tracking. At each plot, a 1 m² quadrat was placed in vegetation representative of the surrounding 10 m radius. The openness of vegetation (*i.e.* 3-dimensional plant-gap dynamics) was assessed within a quadrat using the 'golf ball' method (Schultz *et al.* 2017), a technique regularly used to quantify suitability of habitat for the Plains-wanderer and other grassland-dependent fauna species (Baker-Gabb *et al.* 2016). The method relies on 18 golf balls (*i.e.* standardized objects) that are dropped, one at a time, at different points around the 1 m² area being obscured from a bird's-eye view, to varying degrees, depending on the quantity and structure of vegetation. Each of the balls is scored one of three possible values: a ball is scored as 1 if more than 90% of the ball is visible; a ball is scored as 0 if less than 33% is visible; and all other balls are scored as 0.5. Hence, a low total score in a frame suggests a closed grassland structure, and high vegetation cover, whereas an open structure and low vegetation cover will give a high golf ball score. Maximum vegetation height was measured at each corner of the quadrat to generate a mean value. The cover of bare-ground, litter, bryophyte, lichen, native grass, exotic grass, native herb and exotic herb was estimated using the Braun-Blanquet cover-abundance method within each quadrat (Braun-Blanquet 1932). The same method was also used to estimate the percent cover of plant species. To allow visualization and further analysis of structural and species cover data, Braun-Blanquet values were converted to the midpoint of the relevant cover-abundance range.

The distribution of fixes in relation to plots in the MCP was used to test whether vegetation attributes differed between areas where Plains-wanderer forage and roost. First, all fixes within a 30 m radius of each habitat survey point were identified. Points were then categorized as either 'day', 'night', 'none' or 'day and night' (D + N) based on the type of fixes recorded in the radius.

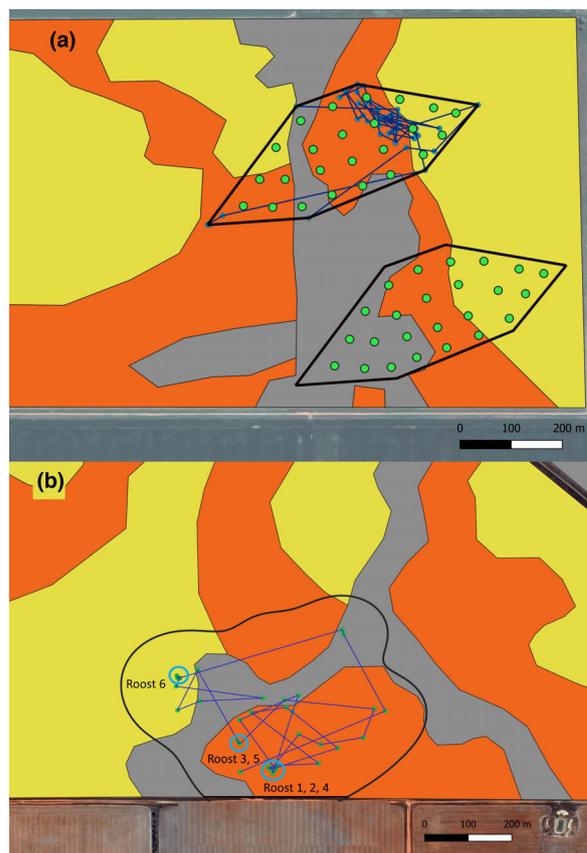


Fig. 3. Home range estimates of GPS-tracked Plains-wanderers overlaid on a fine-scale soil map (orange = grasslands on red soil; yellow = grasslands on mosaic soil; grey = on grey soil). (a) Paired habitat survey design showing 'used' and 'unused' survey areas generated as a minimum convex polygon and the movement path of the focal bird (blue line). The minimum convex polygon was then replicated and randomly positioned at a distance of ~500 m to provide a 'paired' comparable area of habitat that was not known to be used by Plains-wanderers. The distribution of survey plots is shown as green circles. (b) 95% kernel home range of a male Plains-wanderer that displayed random selection of soil diversity at the landscape-scale. Locations where the bird roosted are indicated by light blue circles with each roost night numbered.

Patch-scale (1–50 ha)

To test whether Plains-wanderers selected for particular vegetation structural attributes at a patch-scale (*i.e.* home range size; ~1–50 ha), we used a paired survey design. Using GIS, we randomly placed a paired 'random' polygon matching the configuration of the 'used' patch ~500 m away in an area of similar soil type not visited by tracked birds (Fig. 3, A). Within the random polygon, an identical grid of plots was positioned and surveyed using the same methods as described above. Paired polygons were situated in the same management unit. In total, nine paired polygons were surveyed (Appendix S2). Whilst the entire management unit was intensively surveyed at night for

Plains-wanderers at the start and end of the tracking period, it is possible an undetected Plains-wanderer used the 'random' patch. However, we deem this unlikely with so few Plains-wanderers present in the landscape during the study period (population monitoring activities undertaken concurrently reported encounter rates of 0.26 Plains-wanderer per km of survey effort (PW/km) in 2018, and 0.06 PW/km in 2019 and 2020, D. Nugent & D. Baker-Gabb *unpublished data*). For our purposes, we hereinafter refer to the 'random' polygon as the 'unused' polygon.

Patch-scale multivariate analyses

We used a permutational multivariate analysis to test whether Plains-wanderers select for vegetation communities at the patch-scale, with patch pair (used and unused) fitted as the predictor. The mean cover of each plant species at a site was calculated, and values were square-root transformed. Differences in plant community composition between used and unused patches were visualized with non-metric multi-dimensional scaling (NMDS) implemented with the *ggplot2* package (Wickham *et al.* 2016). We used principal component analysis (PCA) based on Euclidean distances of scaled data to observe how the measured habitat variables combine to explain structural differences between patches used and not used by Plains-wanderers. Analyses were undertaken using the *vegan* package (Oksanen *et al.* 2007).

Fine- and patch-scale models

We developed generalized linear mixed models to test hypotheses of habitat selection at fine- and patch-scales. To identify vegetation structural attributes influencing habitat selection at a fine-scale, we constructed five models using habitat data collected from 'used' habitat patches ($n = 9$). Each model was fitted with one habitat attribute (vegetation openness (golf ball score), bare-ground cover, native grass cover, exotic grass cover or native herb cover) as a response variable and *time-of-day* (three classes: day = foraging; night = roosting; day and night = both) as a predictor variable. We selected these five habitat attributes because we considered them to be most ecologically relevant to describing habitat preference of the species. To identify habitat attributes influencing habitat selection at a patch-scale ($n = 9$), we constructed nine models; each model was fitted with one habitat attribute (vegetation openness, bare-ground cover, lichen cover, bryophyte cover, litter cover, native grass cover, exotic grass cover, native herb cover or exotic herb cover) and patch pair (two levels: used or unused) as a predictor variable. Vegetation height was excluded from models because it was correlated with vegetation openness ($r = -0.62$). For vegetation openness and vegetation cover attributes, a weighted binomial distribution and logit link were assumed. In all models, site was fitted as a random effect to account for spatial correlation of survey plots. As the predictor variable in all models was a categorical variable, we interpreted directions of coefficient estimates as evidence of selection for or against the habitat attribute in question. A significant P -value (<0.05) was interpreted as evidence of

habitat selection. We developed models using LME4 package (Bates *et al.* 2015) and checked model assumptions and diagnostics using DHARMA package (Hartig 2017) in R (R Core Team 2021).

Landscape-scale (>100 ha)

We used a Monte Carlo simulation approach to investigate whether Plains-wanderers select for specific soil types or combinations of soils (as a proxy for vegetation types), by comparing the frequency of soil types in actual home ranges ('observed') against the 'expected' frequency of soil types if these same home ranges were randomly situated anywhere in the study region across thousands of hectares. To do this, we overlaid our fine-scale soil map with the 50% and 95% kernel home range polygons of 11 Plains-wanderers and then calculated proportions of each soil type for each polygon in R. For each tracked bird, 1000 polygons matching the shape of that home range (both 50% and 95% kernel) were randomly placed across the landscape, by randomizing both centroid position and polygon orientation (Appendix S3). The proportions of soil types and the diversity of soils (Shannon index) of each random polygon were then calculated. Finally, the 0.025 and 0.975 percentiles of the randomized values for each soil type were calculated. We concluded that individual birds showed 'choice' in their selection of home range if the observed values for the proportions or diversity of soil types fell below the 0.025 or above the 0.975 percentiles of the randomized values. We selected this approach in place of a test between available and used proportions of soil type because we considered the shape of a home range to be of ecological relevance when birds select a home range within a landscape.

RESULTS

Movement summary

The mean home range size of Plains-wanderers was 32.05 ha (SD 25.99 ha) as calculated by 95% kernel density polygon (Appendix S1). Home ranges of males ($n = 5$, mean = 28.6 ha, SD = 24.06 ha) were generally smaller than females ($n = 8$, mean = 41.5 ha, SD = 27.04 ha). Maximum home range size was found to peak for most birds after four days of tracking and then remain stable or decline until the end of the tracking period (Appendix S4).

Fine-scale (<1 ha)

From a total of 81 tracking nights, Plains-wanderers ($n = 11$) returned to a previously used roost on 50% of occasions. All birds were found to have a roost they returned to at least twice or more. Roosts were mostly revisited over consecutive nights. When multiple birds were tracked at single site, individuals

roosted alone (>30 m apart). Plains-wanderers selected roost sites correlated with soil type ($Khi2L = 384.24$, $df = 9$, $P < 0.001$), favouring areas of red soil that typically support open vegetation structure (66% of individual roosts identified) over grey (5%) and mosaic soils (29%) that typically support relatively denser structure. Plains-wanderers favoured more structurally dense habitats that supported a higher cover of native grass during daylight hours when foraging (Fig. 4; Appendix S5). There were no significant differences in other habitat attributes between day, night or day and night fix locations (Appendix S5). Diurnal Plains-wanderer activity (*i.e.* foraging) was not correlated with a specific soil type, based on available soil types within home ranges ($Khi2L = 14.36$, $df = 18$, $P = 0.71$).

Patch-scale (1–50 ha)

Habitat of Plains-wanderer home ranges ($n = 9$) was characterized by a relatively open structure, with a moderate cover of native tussocks and herbs, and a

low cover of exotic species and ground litter. Across home ranges, 50% and 95% of golf ball scores were between 13.5 to 16 and 11 to 17, respectively (Appendix S6).

There was strong evidence that Plains-wanderers selected for particular habitat attributes at the patch-scale (Appendix S7). Areas of grassland used by Plains-wanderers had a lower cover of exotic herbs and litter compared with areas not used (Fig. 5). Furthermore, areas used by Plains-wanderers had a denser cover of predominately native vegetation and had higher cover of lichen, bryophyte and native grass.

Used and unused patches differed slightly in structural characteristics, as indicated by separation of ellipses along the PC2 axis (19.5% of variance; Appendix S8). Along this axis, cover of bryophyte and lichen was longest vectors in the direction of ‘used’ ellipse, while exotic herb and litter were longest vectors in the direction of the ‘unused’ ellipse. Along the PC1 axis (24.2% of variance), ellipses were mostly overlapping, with golf ball score and bare-

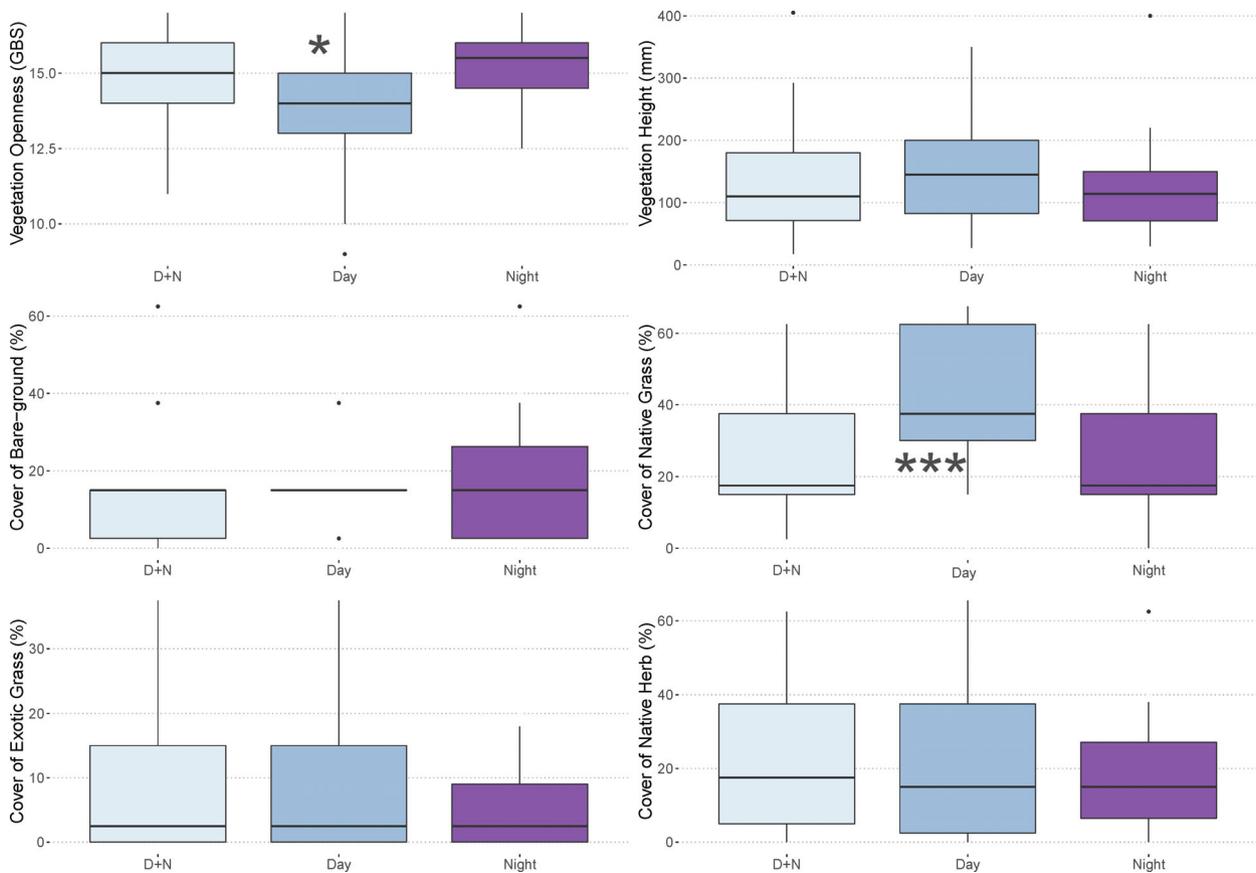


Fig. 4. Comparison of habitat attributes used for roosting (purple), foraging (dark blue) and both foraging and roosting (‘both’, light blue) by Plains-wanderers ($n = 11$). Generalized linear mixed models were used to indicate selection for or against a habitat variable when ‘foraging’ (day) or ‘roosting’ (night). The models included a fixed effect of time-of-day (three classes: day, night, day + night) and random effect of site. P values < 0.05 and < 0.001 are indicated by ‘*’ and ‘***’, respectively.

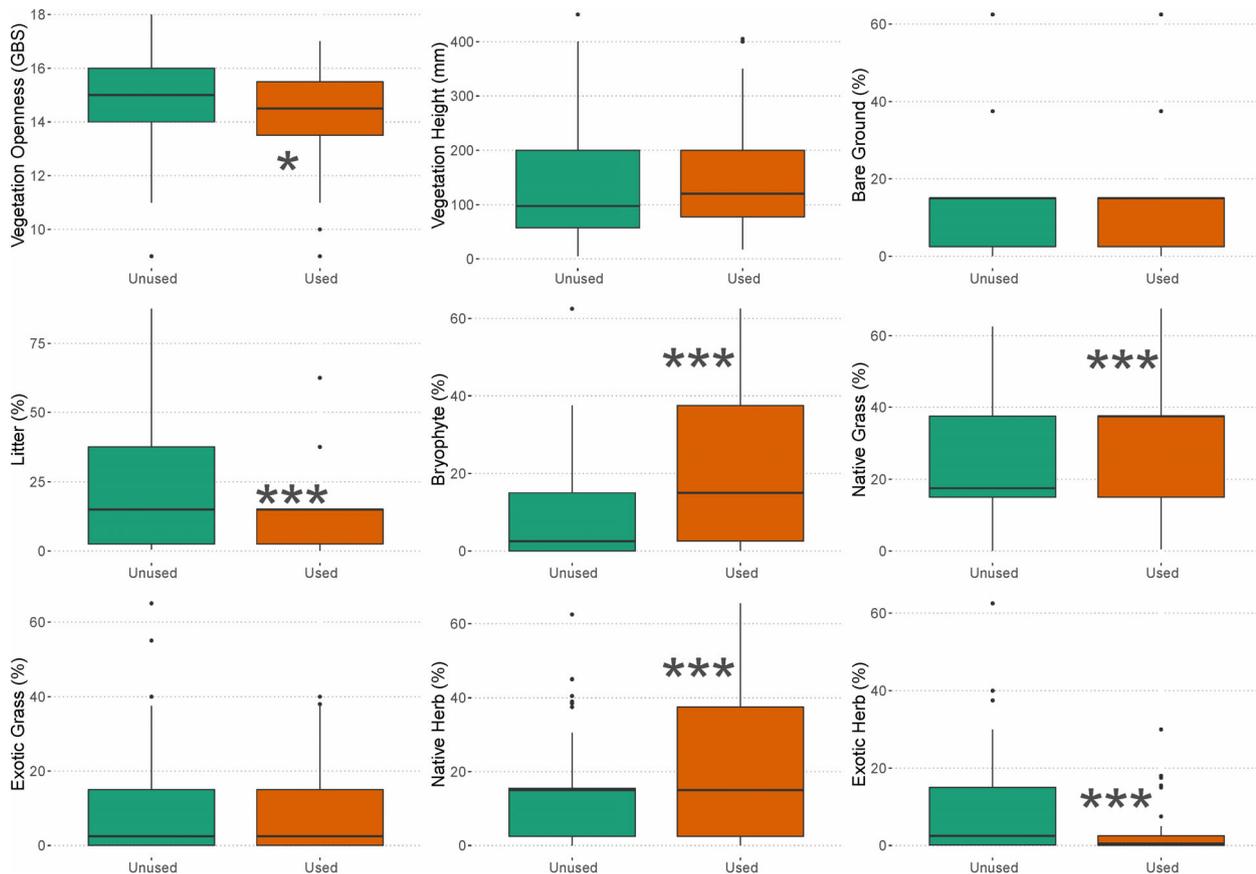


Fig. 5. Comparison of habitat attributes in patches used (orange) or unused (green) by Plains-wanderers ($n = 9$). Generalized linear mixed models were used to indicate selection for or against a habitat variable at the patch-scale. The models included a fixed effect of patch pair (two levels: used and unused) and random effect of site. GBS indicates golf ball score. P values < 0.05 and < 0.001 are indicated by ‘*’ and ‘***’, respectively.

ground longest vectors in the direction of negative values, and exotic grass the longest vector in direction of positive values. Plant communities did not differ between patches of habitat used and not used by Plains-wanderers (pseudo- $F = 0.87$, $P = 0.53$).

Landscape-scale (>100 ha)

Plains-wanderers ($n = 11$) did not show preference for any specific soil-derived grassland type based on what was available at a landscape-scale. Furthermore, the proportion of each grassland type was highly variable across home ranges. The mean proportion of red soil, mosaic soil and grey soil vegetation within a home range (95% kernel polygon) was 0.41 (CV% 68.35), 0.45 (CV% 39.19) and 0.14 (CV% 67.46), respectively (Appendix S9). The most consistent feature of home ranges, based on coefficient of variation, was a high proportion of combined red and mosaic grassland types.

We did find weak evidence that birds select home ranges with a higher diversity of grassland types than

would be expected by chance (Appendix S10). This type of non-random selection was observed in five out of eleven birds, mostly at the 95% home range kernel size (Appendix S11).

DISCUSSION

Plains-wanderers selected habitats based on attributes that vary with spatial scales. Furthermore, grassland type and structure used at roosts, which underpins most management decisions, did not capture the full habitat needs of the species. We did not find conclusive evidence of Plains-wanderers selecting for habitat attributes at the landscape-scale. However, at patch- and fine-scales, structural attributes did influence what habitat was selected. More broadly, our results highlight how cryptic behaviour can limit a basic understanding of an animal’s ecology. Based on the new insights into Plains-wanderer ecology provided here, we suggest that management targets should shift from maintaining a uniform, open-structured grassland to a more structurally heterogenous sward,

with areas of both denser and sparser vegetation (range = 13 to 16 golf balls) at a patch-scale (1–50 ha).

Our results demonstrate that Plains-wanderers use grassland types previously considered largely unsuitable for the species (*e.g.* Baker-Gabb *et al.* 1990, DPIE 2020). Importantly, however, the species does not appear to be necessarily selecting unique configurations of grassland types in the landscape. Rather, most home ranges supported a mix of all three soil-derived grassland types, with composition typically including a high proportion of combined red soil and mosaic soil grassland types, with less representation of grey soil vegetation. Although this composition of grassland types does not appear rare in the landscape, this finding is of management significance as previous work has failed to allocate sufficient priority to mosaic or grey soils, both of which support denser grass for foraging (Parker & Oliver 2006; Baker-Gabb *et al.* 2016; Baker-Gabb 2016). Management actions such as strategic stock fencing should aim to protect mosaic and grey soil areas of grassland, as well as red soil areas, from overgrazing during years of low rainfall. Other ground-dwelling grassland bird species, such as Burrowing Owls (*Athene cunicularia*) and Little Bustard (*Tetrax tetrax*), also select specific parts of the landscape that support the different vegetation types needed for different activities (*i.e.* nesting, foraging and courtship displays; Wolff *et al.* 2002, Stevens *et al.* 2011). That Plains-wanderers also use the range of resources available throughout the grasslands aligns with responses elsewhere. In recognition of the likely importance of structural diversity to Plains-wanderer at the home range scale, we recommend a review of current landscape habitat management goals such that they incorporate the value of different grassland types for Plains-wanderers.

At patch-scales, we found a range of vegetation structural attributes influence habitat selection by Plains-wanderers. Specifically, the cover of native grasses and native herbs, as well as bryophyte and lichen cover, was higher in areas used by Plains-wanderers. Biocrusts comprising lichens have previously been identified as a key feature of habitat for the Plains-wanderer—presumably because the open, unobstructed surface it supports improves their foraging efficiency (Antos & Schultz 2020). Our research supports this conclusion. Plains-wanderers also appear to avoid areas of high exotic herb and litter cover. The most abundant exotic herb species in this system support rosette growth forms (*i.e.* *Erodium botrys*, *Hypochaeris* spp.) and occupy space between tussocks. Invasion of grasslands by weeds can alter vegetation structure (Sanderson *et al.* 2017) and impact the balance birds try to achieve between predator avoidance and foraging efficiency (Maron &

Lill 2005). We speculate that Plains-wanderers avoid areas of high weed and litter cover because these attributes occupy inter-tussock space, impacting foraging efficiency by reducing ease of movement. Weed invasion has been found to have similar impacts in other grassland systems. For example, the invasion of European meadows by a broad-leaf weed led to a reduction in the richness of endangered grassland bird species (Skórka *et al.* 2010). Exotic herb invasion and/or litter accumulation has not previously been identified as a threat to the Plains-wanderer. This may reflect an oversight that stems from a focus on habitat use at a micro-scale, as opposed to that used at larger spatial scales. Based on our findings, we suggest land managers target localized areas of weed invasion and limit excessive biomass accumulation to improve the availability of suitable habitat.

We found that at fine-scales Plains-wanderers select specific vegetation attributes to meet the needs of different behavioural requirements, suggesting structural heterogeneity of home ranges is important to the species. Roost site characteristics are one of the best understood elements of Plains-wanderer ecology, and our results support previous research that open areas of grassland typically found on red soils are favoured (Baker-Gabb *et al.* 1990; Baker-Gabb *et al.* 2016). In contrast, foraging ecology is poorly understood (Baker-Gabb 1988). Our research provides an important insight into this cryptic activity, identifying that Plains-wanderer use vegetation structure previously considered largely unsuitable for the species (Baker-Gabb *et al.* 1990; Baker-Gabb *et al.* 2016). Specifically, areas of denser vegetation (*i.e.* 11–13.5 golf ball score) with higher native grass cover, as well as more open vegetation (*i.e.* 14–17 golf ball score), are selected for foraging. This finding partly supports the hypothesis of Antos & Schultz (2020) that Plains-wanderers select grasslands with denser patches of perennial grass for nesting and shelter. We agree that denser patches are likely to be important for these activities but suggest that denser patches are also important for foraging. Based on our findings, and those by Antos & Schultz (2020), incorporating patch-scale structural heterogeneity targets into management plans should be a priority for land managers.

The precise mechanisms of differences in habitat use over a diel period can only be speculated from the data, but we hypothesize that these differences partly relate to their mating system, predator avoidance strategy and food availability. Areas of open vegetation may act as performance arenas for lekking and denser areas for foraging and nesting. Female Plains-wanderers most frequently call at dusk and dawn (K.Rowe, *pers.comm*), a time-of-day when our results indicate they occupy more open vegetation. It is possible this pattern of vocalization relates to

lekking behaviour. By contrast, of the very few nests that have been found, most are located in denser vegetation (Antos & Schultz 2020; DPIE 2020; D.Baker-Gabb *pers.obs*). Indeed, two Plains-wanderers tracked during our study showed movement patterns consistent with nesting (high fidelity to a central home range position) in denser grey soil vegetation. In the absence of finding nests or chicks, it is difficult to determine whether birds were breeding during our study period and conclude what affect breeding behaviour may have on habitat selection. Furthermore, it remains unclear what role food availability may play in selection of different vegetational structures by the Plains-wanderer and what effect it had on our results. Food availability has been found to influence habitat selection of Greater Prairie-Chickens (*Tympanuchus cupido*) at micro-scales, with individuals selecting areas of grassland supporting more food (Londe *et al.* 2021). However, the habitat use of some grassland species is not affected by food resources. Preference for different structures by short-snouted elephant shrew (*Elephantulus brachyrhynchus*) in grasslands, for example, was speculated to relate to predator avoidance more so than food availability (Yarnell *et al.* 2008). Further research is needed to identify the factors that determine fine-scale habitat selection by the Plains-wanderer, particularly the role of food availability and breeding.

The inherent heterogeneity of resources across scales—ranging from tens of square meters (fine-scale) to thousands of hectares (landscapes)—in grasslands is an important driver of multi-scale habitat selection by grassland fauna. Grassland heterogeneity also likely enables species to adapt to using distinct vegetation structures for different activities (Fuhlendorf *et al.* 2006, 2017). Prairie-chicken's (*Tympanuchus* sp.), for example, select home ranges within landscapes based on factors including elevation and land use type which influence the configuration of critical resources (Matthews *et al.* 2013). Within home ranges, Prairie-chickens select areas with short vegetation for their lekking sites and dense vegetation in some proximity within which to build nests (Hovick *et al.* 2014). Management strategies that mimic historical fire and grazing regimes, enhancing grassland heterogeneity, have been found to be important in the conservation of Prairie-chickens (McNew *et al.* 2015), and other threatened grassland species and communities (Fuhlendorf *et al.* 2006; Scroggie *et al.* 2019). It may also be the case that Plains-wanderers require a matching level of home range structural heterogeneity for similar reasons.

Studies of cryptic, rare and threatened species are often challenged by drawing conclusive findings from small sample sizes (Thaxter *et al.* 2017). Although our study utilizes data from a small number of birds, results show strong patterns of habitat use and what

likely constitute real habitat associations. We are confident that critical areas of habitat were identified as home range size for most birds had reached a point of stability during periods of tracking. Our knowledge of Plains-wanderer habitat requirements would benefit from future studies that investigate habitat use in other parts of the species' range with a different suite of biotic and abiotic factors (*i.e.* New South Wales Riverina, more arid grasslands of South Australia and Queensland) and periods when breeding is confirmed on the Northern Plains of Victoria.

Our study has improved the understanding of what constitutes optimal grassland structure for the Plains-wanderer. Until now, management of habitat for the Plains-wanderer has principally focused on maintaining a uniform, open-structured grassland across multiple spatial scales (Parker & Oliver, 2006; Baker-Gabb *et al.* 2016; Baker-Gabb 2016). Our results indicate management goals should shift to promote a structurally heterogeneous sward, with areas of slightly closed and open vegetation, at the home range scale (1–50 ha). Success in achieving structural heterogeneity goals could be measured by quantifying variation or spread of golf ball scores recorded from across a site at different points in time. There are multiple tools available to land managers to achieve structural heterogeneity including targeted livestock grazing using temporary electric fencing and crash grazing (Dorrough *et al.* 2004, Derner *et al.* 2009). The efficacy of patch-burning, pyro-herbivory and fine-scale slashing (cut and bailing, mowing) to create structurally variable grasslands should also be investigated as they are tools frequently used in other systems, but remain unstudied in Australian grasslands (McCoy *et al.* 2001, Zuckerman and Vickery 2006, Churchwell *et al.* 2008, Davis *et al.* 2016). In addition to creating heterogeneity through top-down processes, the mosaic of different soil-derived vegetation communities characteristic of Northern Plains Grasslands should be used to guide management activities. Frequent and targeted management of vegetation structure will likely be essential in most grasslands to maintain suitable habitat condition as overriding climate conditions influence biomass dynamics—particularly during wet climate phases. It will be critical to accompany any changes in grassland management strategies with targeted monitoring to further understand the optimal spatial configuration of habitat resources across sites and landscapes.

CONCLUSIONS

Our understanding of the basic ecology of grassland fauna may evolve with time because of cryptic behaviours—as we have demonstrated here for the critically endangered Plains-wanderer. For cryptic grassland fauna, it is important that management

targets account for uncertainty of optimal habitat requirements and be reviewed as new ecological knowledge is acquired. We have highlighted the difficulty of identifying optimal habitat management targets for a cryptic grassland bird, as well as the benefits of research that aims to address knowledge gaps surrounding cryptic behaviour. Furthermore, we demonstrate that even for a species of outstanding global significance, our understanding of basic ecology, fundamental to conservation management, can be incomplete. Our findings demonstrate that a precautionary approach to the classification of habitat requirements is warranted when uncertainty around habitat use of cryptic grassland fauna exists. Research that seeks to improve understanding of habitat use during cryptic life phases of threatened grassland fauna should be given a high priority.

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AUTHOR CONTRIBUTIONS

Daniel T. Nugent: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (equal); project administration (lead); writing – original draft (lead); writing – review and editing (lead). **David J. Baker-Gabb:** Conceptualization (equal); investigation (supporting); methodology (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting). **Peter Green:** Conceptualization (equal); formal analysis (supporting); investigation (supporting); methodology (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting). **Bertram Ostendorf:** Formal analysis (supporting); investigation (supporting); methodology (supporting); visualization (supporting); writing –

review and editing (supporting). **Finella Dawlings:** Data curation (supporting); investigation (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Rohan H. Clarke:** Data curation (supporting); investigation (supporting); writing – original draft (supporting); writing – review and editing (supporting). **John W. Morgan:** Conceptualization (equal); funding acquisition (supporting); investigation (supporting); methodology (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from Figshare (Nugent *et al.* 2021: Habitat selection by Plains-wanderers); DOI: 10.6084/m9.figshare.16545627

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. GPS tracking parameters and home range sizes for Plains-wanderers. For Bird ID, ‘M’ = male and ‘F’ = female. ‘Paired with’ represents individuals that shared overlapping home ranges. ‘MCP’ = minimum convex polygon.

Appendix S2. Description of paired patch polygon design. Multiple birds are listed at a site where home ranges were highly overlapped. Note: birds at site ‘Murray’ were only included in patch-scale analyses as their fixes were captured under a shortened GPS program.

Appendix S3. Snapshot of the study region showing a portion of the 1000 polygons (green polygons) matching the shape of the 50% home range of Plains-wanderer ‘M5’ randomly placed across a fine-scale soil map of the landscape (orange = grasslands on red soil; yellow = grasslands on mosaic soil; grey = on grey soil) by randomizing both the centroid and orientation.

Appendix S4. Plains-wanderer home range size (hectares) across tracking periods as calculated by 95% kernel density polygon. Note: area of seven of the ten home ranges is presented after day 0 as a minimum of five fixes are required to calculate a kernel polygon and successful GPS fix acquisitions differed between birds.

Appendix S5. Coefficient estimates for generalized linear mixed models relating to habitat selection by Plains-wanderers ($n = 9$) at a fine-habitat scale (<1 ha) in semi-arid grasslands of south-eastern Australia. The models included a fixed effect of time-of-day (three classes: day, night and day + night) and

random effect of site. Positive coefficients indicate selection for a habitat variable when ‘foraging’ (day) or ‘roosting’ (night) and negative coefficients indicate selection against. GBS indicate golf ball score. *P* values <0.05 are indicated in bold type and represent selection for or against an attribute.

Appendix S6. Mean and standard deviation (SD) percentage of different golf ball scores across Plains-wanderer home ranges ($n = 9$). Note: increasing golf ball values equal increasing vegetation openness.

Appendix S7. Coefficient estimates for generalized linear mixed models relating habitat selection for vegetation structure at a patch-scale (1–50 ha). The models included a fixed effect of patch pair (two levels: used and unused) and random effect of site. Positive coefficients indicate selection for a habitat variable at the patch used by Plains-wanderers ($n = 9$), and negative coefficients indicate selection against. *P* values <0.05 are indicated in bold type and represent selection for or against an attribute.

Appendix S8. Principal component analysis of habitat variables in patches used (orange dots and ellipse) and not used (green dots and ellipse) by Plains-wanderers ($n = 9$) based on Euclidean distance.

Appendix S9. Proportion of grassland types in Plains-wanderer home ranges ($n = 11$). The 95% kernel polygons represent all habitat predicted to have been used, while 50% kernel polygon represents predicted core habitat used. CV% indicates coefficient of variation. ‘G + R’ indicates proportions of grey and red soil combined. ‘G + M’ indicates proportions of grey and mosaic soil combined. ‘R + M’ indicates proportions of red and mosaic soil combined.

Appendix S10. Ternary plots of soil composition of randomized home range polygons and actual home range polygon (red triangle) of a Plains-wanderer. Darker blue indicates higher frequency of random polygons with the same soil composition. (A) Example of an individual bird (M5) showing non-random selection or ‘choice’ of home range supporting a ‘rare’ mix of all three soil types. (B) Example of a home range (M2) with soil composition that could be expected by chance, and therefore, not evidence of ‘choice’. To aid in interpretation, randomized polygons that fall on the exact apices of the triangle contain a single soil type, polygons falling on the edges have two soil types, and polygons falling in the interior of the triangle have three soil types.

Appendix S11. Summary of Monte Carlo randomizations to determine whether particular characteristics of observed home ranges (95% or 50% kernel) show evidence of non-random selection by Plains-wanderers ($n = 11$). ‘Prop observed’ is the proportion of either grey, red or mosaic soils found in each home range kernel. ‘Lower 5th’ and ‘Upper 95th’ are the lower and upper percentiles of the range of values derived from the random placement and orientation of 1000 polygons of the same size shape and shape placed at random through the landscape (see text). ‘Verdict’ compares the observed value to the percentiles—if the observed value falls within the percentiles, there is no evidence of non-random placement of the home range by the birds (R = Random). Values lying outside the percentiles indicate non-random placement (NR = non-random)—values below the lower percentile indicate avoidance, and values above the upper percentile indicate preference.