

# Camera-trapping successfully and non-invasively reveals the presence, activity and habitat choice of the Critically Endangered White-winged Flufftail *Sarothrura ayresi* in a South African high-altitude wetland

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## Summary

The ‘Critically Endangered’ White-winged Flufftail *Sarothrura ayresi* is regarded as one of the rarest and most threatened rallids in Africa. Due to the species’ low density, habitat preference, cryptic colouration, elusive behaviour and lack of auditory cues has resulted in it being one of the most challenging species to survey using traditional methods such as auditory surveys and rope dragging. Numerous data deficiencies exist regarding facets of the species’ ecology, distribution, habitat-use and population status. A stratified array of nine camera localities was used within high-altitude palustrine wetland habitat to ascertain if this non-invasive technique could successfully document the first estimate of site occupancy, fine scale habitat use and activity patterns of this very rare species. Our study accumulated a total of 626 camera days and eight independent sightings of White-winged Flufftail across the respective austral summer season. Furthermore, our study confirms the applicability of camera trapping to other rare and elusive rallid species. Our results confirm that White-winged Flufftail is a low-density habitat specialist species, with site occupancy influenced positively by basal and canopy vegetation cover and detection probability influenced negatively by water depth within associated wetland habitats. Activity pattern analyses displayed that peak activity occurred at dawn and dusk, which yielded the highest degree of activity overlap with the only other migratory rallid recorded, Spotted Crake *Porzana prozana*. Our study also recorded the first apparent territorial display behaviour noted for the species. Our study supports the need for conservation initiatives focused on securing contiguous sections of suitable wetland habitat in order to accommodate the persistence of this globally threatened species.

## Introduction

The White-winged Flufftail is regarded as the rarest and most threatened rallid species in Africa (Taylor 1994, BirdLife International 2018, Evans *et al.* 2015). It is currently listed as ‘Critically Endangered’ (CR) (BirdLife International 2018), with an estimated global population size of 700 mature individuals. However, due to data deficiency, confidence in the population estimate is low and it is believed that the population could be significantly smaller (Evans *et al.* 2015). A study describing the Toll-like receptor genetic diversity in White-winged Flufftail confirms low genetic diversity in the innate immune regions similar to that observed in other bird species that have undergone population bottlenecks (Dalton *et al.* 2016). This species is largely known from the

Ethiopian Highlands and eastern South Africa, with isolated historical sightings also noted in Zambia and Zimbabwe (Taylor 2005). Records across the two primary regions display significant temporal separation, with Ethiopian and South African records being largely confined to June–September and October–March respectively (Taylor 1994, Taylor and van Perlo 1998). Furthermore, despite numerous surveys, all breeding records have been exclusively confined to the Ethiopian Highlands (Mendelsohn *et al.* 1983, Taylor 1994, Taylor and van Perlo 1998, Taylor 2005, Allan *et al.* 2006, Davies *et al.* 2015). These two factors, together with the lack of subspeciation between the two regional populations (Dalton *et al.* 2018), has suggested that the species is migratory between the northern breeding range in the Ethiopian highlands and non-breeding austral summer range in South Africa (Taylor 2005, Sande *et al.* 2008).

In the context of southern African rallids, the White-winged Flufftail is one of the smallest species occurring in the region (length 13.5–14.5 cm, mass 32 g; Taylor 2005). It is noted as a habitat specialist, inhabiting palustrine wetland habitats at typically higher elevations (1,100–1,900 m asl), but three vetted records have been noted at lower elevations in the South Africa (e.g. 150 m) (Taylor and van Perlo 1998). South African records have generally originated from dense and short (50 cm) sedge *Carex* spp. dominant vegetation, but have also been noted in mixed stands of sedge and taller species (*Phragmites* and *Typha* spp.) (Taylor 2005, Evans *et al.* 2015). Furthermore, one commonality across studies suggests a strong preference for shallow water within wetland habitats, with an increase in water level through flooding (natural or anthropogenic) generally leading to the abandonment of the respective site (Taylor 1994, 2005). Unlike other African rallid species, White-winged Flufftail has a noted lack of vocalisation across its range (Allan *et al.* 2006, Davies *et al.* 2015). Although auditory surveys have been used previously for this species (Taylor 1995), recent surveys (Allan *et al.* 2006, Davies *et al.* 2015) suggest discrepancies exist. Until clarified, the implications thereof impede the use of auditory surveys as a suitable/reliable monitoring method. Therefore, the exact vocalisation and use by White-winged Flufftail remain relatively ambiguous.

The low density, localised distribution, small body size, cryptic colouration, aquatic and densely vegetated habitat preference, extremely elusive behaviour and lack of auditory cues have made this species notoriously difficult to study (Mendelsohn *et al.* 1983, Taylor 1994, 2005, Allan *et al.* 2006, Davies *et al.* 2015). Subsequently, there are significant data deficiencies with regard to facets of the species' population status, biology, distribution, habitat use, activity patterns, migratory status and dispersal behaviour (Evans *et al.* 2015). A recent study based on the sequencing of mitochondrial (COI, Cytb, 12S/Val/16S) and nuclear (ADH-5, GPD3-5 and bfb7) markers affirms that South African and Ethiopian birds are genetically similar (Dalton *et al.* 2018), supporting the hypothesis that these two regions do not host different species or subspecies but rather one migrating population, having separate ranges during the different seasons in Ethiopia and South Africa. Given the current conservation status of the species, it is of utmost importance that fundamental gaps in our understanding of this species be addressed in order to better direct conservation efforts.

Until recently, the most common method utilised to confirm the presence of this species was an invasive form of sampling that elicits a flushing response of individuals inhabiting the target habitat type through walked transects and/or rope dragging (Green 1985, Bibby *et al.* 1998). However, the elusive and skulking nature of many rallid species, particularly those of the *Sarothrura* (flufftail) genus, combined with their reluctance to take flight, has been noted as a potentially significant limitation to the efficiency of rope dragging for these species (Davies *et al.* 2015). In addition to the detection bias and limited efficacy associated with rope dragging for some rallid species, the potential impact of rope dragging (e.g. trampling and disturbance) on both the target species and associated habitat has elicited concern (Davies *et al.* 2015, Colyn *et al.* 2017). However, a recent study utilising a non-invasive array of camera traps proved efficient at registering the presence and activity of multiple cryptic and elusive rallid species (including one flufftail species) within palustrine wetland habitat in South Africa (Colyn *et al.* 2017). The primary aim of our study was to ascertain if a non-invasive array of camera traps could be used to document the first estimate of site occupancy, fine scale habitat use, and activity patterns of White-winged Flufftail across an austral summer season. Furthermore, we aimed to assess the site

occupancy, habitat use and activity patterns of other rallid species recorded and determine if inter-species influences were noted.

## Methods

### Study site

Our study area is located between the Dullstroom (25°25′6.18″S 30° 6′14.66″E) and Belfast (25°40′28.67″S 30° 4′47.71″E) areas of Mpumalanga, South Africa. This area has yielded the most frequent and consistent number of White-winged Flufftail records in South Africa (Taylor 1994) and has been the focal area for a recent species-specific study (Davies *et al.* 2015). A particular palustrine wetland system within the given region, namely Middelpunt Wetland (MW), has been actively surveyed for White-winged Flufftail presence and activity using rope dragging in 2005, 2006, 2011, 2014 and 2015 (Davies *et al.* 2015). Given the existing survey history of MW and recorded presence of the species across some of the respective years surveyed (e.g. Davies *et al.* 2015), occasioned MW as being an ideal study site.

The broader study site is largely comprised of high-altitude palustrine wetland and adjacent highland grassland. MW is part of the Lakenvlei wetland system, which is currently listed as an the Steenkampsberg Important Bird and Biodiversity Area (IBA; SA 016) (Marnewick *et al.* 2015) and forms part of the recently declared Greater Lakenvlei Protected Area. The palustrine wetland vegetation communities present at MW include three dominant habitat types, namely sedge meadows (Cyperaceae spp.), and *Phragmites* and *Typha* beds (Davies *et al.* 2015). Additionally, six notable habitat patches incorporating mixed vegetation (sedges, forb, reed spp., etc.) have been documented (Davies *et al.* 2015). Apart from White-winged Flufftail, MW is known to host six other rallid species across the respective years surveyed (Davies *et al.* 2015).

### Survey design

The survey design in terms of camera placement was tailored as per Colyn *et al.* (2017). However, given the primarily species-specific focus and aim to estimate site occupancy, the survey design had to be altered to maintain occupancy assumptions (MacKenzie *et al.* 2006). Given the absence of data related to territory size of White-winged Flufftail, the territory size of a sympatric species known to co-occur in similar habitats, namely Red-chested Flufftail *Sarothrura rufa* (Mendelsohn *et al.* 1983, Taylor 1994), was used to inform camera spacing. Red-chested Flufftail territory size in continuous habitat such as MW is noted as 0.10–0.45 ha, resulting in a potential average territory diameter of 10–50 m (Taylor 1994). Therefore, in order to maintain independence and prevent spatial auto-correlation, camera spacing was larger than the diameter of the average territory size (Rovero *et al.* 2013).

A further consideration incorporated into our survey design was the noted efficiency of surveying extensively when studying rare species (MacKenzie and Royle 2005). Extensive surveying incorporates surveying at as many sites as feasible to increase spatial coverage (MacKenzie and Royle 2005). Similarly, MacKenzie *et al.* (2002) note that increasing the number of sampling occasions (temporal coverage), increases both the precision and accuracy of derived occupancy estimates. Although the majority of sightings have been documented in sedge-dominant vegetation at MW (Mendelsohn *et al.* 1983, Taylor 1994, Davies *et al.* 2015), Taylor (1994) includes records obtained in South Africa from *Phragmites*, *Typha* and mixed vegetation habitats. Additionally, MacKenzie and Royle (2005) recommend that sites are not exclusively selected based on historical or pre-existing knowledge of occurrence alone, as this can produce inflated occupancy estimates. Therefore, the resulting survey design incorporated a stratified grid of nine Ltl Acorn 6540MC camera traps spaced at a minimum distance of 50 m across the core wetland habitats at MW (Figure 1). The grid allowed for camera placement across all dominant vegetation communities present at MW. These included sedge-dominant, *Phragmites*-dominant,

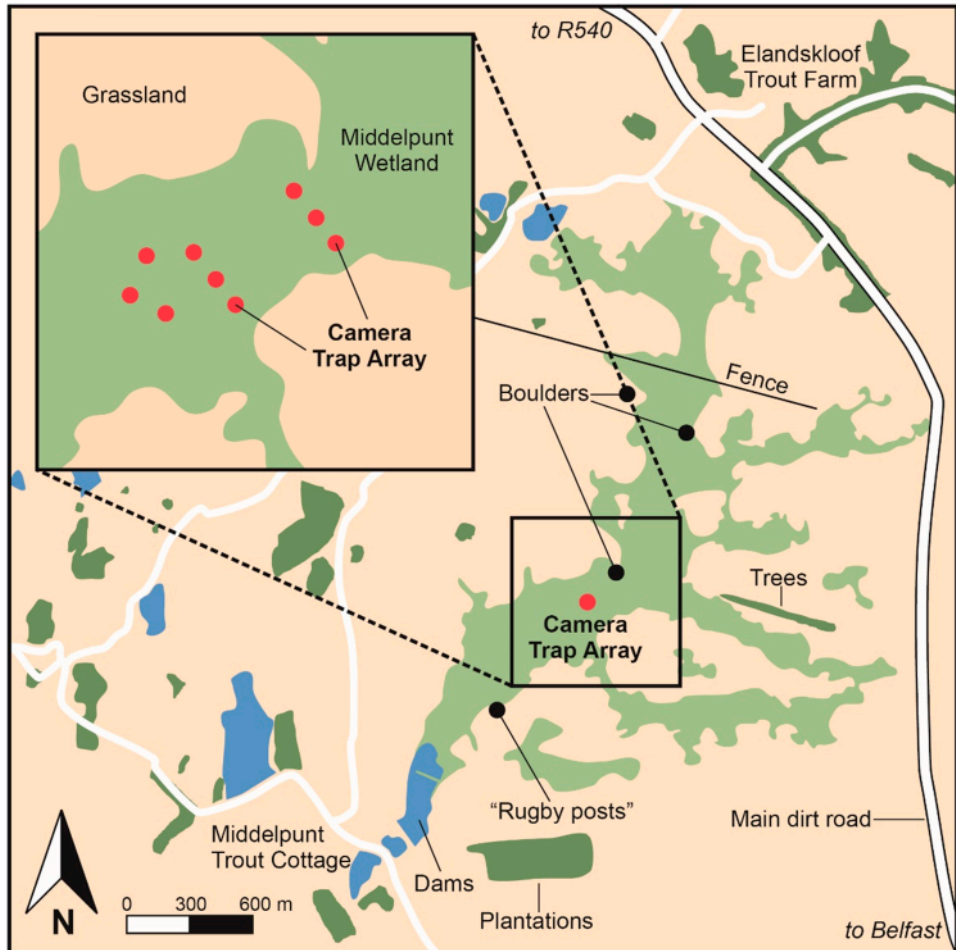


Figure 1. The survey design layout of camera traps across core wetland habitat at the study site, Middelpunt Wetland.

*Typha*-sedge and sedge-forb mixed vegetation communities (Table S1 in the online supplementary material). Due to the unreliability and stochasticity of White-winged Flufftail presence, survey duration was maximised to include a consecutive 72-day survey across the entire peak temporal period known to host records in South Africa, namely December to February (Taylor 2005).

#### *Camera trap site characteristics*

Rainfall and fire history are two drivers known to influence the state of wetland microhabitats (Rogers *et al.* 1989). Microhabitat characteristics known to influence White-winged Flufftail presence includes water depth, vegetation structure and vegetation community (Davies *et al.* 2015). Broad vegetation communities were mapped out by recording coordinates of community boundaries whilst walking through the wetland (Davies *et al.* 2015), which was further supplemented by high resolution aerial (drone) photographs. Water depth was logged using a yardstick within each camera trap detection arc (i.e. photo boundary) and recorded as a categorical variable: 1 (< 3 cm), 2 (3–10 cm) and 3 (> 10 cm).

The period surveyed (December 2016–February 2017) produced 690.4 mm of rainfall, which was higher than the average (585 mm) for the area (South African Weather Services 2017). As part of management practices by landowners, MW was burnt during the dry wintering months preceding the survey. Additional data related to rainfall, water depth and fire history across the respective study site are provided in Table S1 and Figure S1.

### Data analyses

In addition to the assumption of independence addressed through our survey design above, closure is another assumption requiring consideration with regard to occupancy modelling (MacKenzie *et al.* 2002, 2006). Closure assumes that all sites sampled remain closed to changes in occupancy state over the course of sampling (MacKenzie *et al.* 2002, 2006, O'Connell and Bailey 2011, Rovero *et al.* 2013). Closure can be impacted on by immigration, emigration, births and deaths and is particularly relevant to studies focusing on wide ranging and/or migratory species (MacKenzie *et al.* 2006). Due to the unpredictable nature of White-winged Flufftail presence across its range and therefore at MW, closure across the entire peak season (December to February) could not be assumed. Immigration into and emigration out of the site could occur at any given period and the average length of use/stay within an occupied wetland is unknown. Kendall (1999) addresses the immigration or emigration of a species during the study period by pooling datasets, but if both movements are expected, the associated bias will remain (MacKenzie *et al.* 2006). Therefore, in order to maintain closure for White-winged Flufftail or any other migratory rallid recorded during the respective survey, data were truncated to include samples from the first and last detection only (MacKenzie *et al.* 2002). Furthermore, for any resident/non-migratory rallid species assessed, truncation was not utilised and closure was assumed as per single-season occupancy models (MacKenzie *et al.* 2002, O'Connell and Bailey 2011, Hamel *et al.* 2013, Rovero *et al.* 2013).

Data were collated into binary (presence/absence) detection history matrices for the consecutive 72 days surveyed. Data collation included all ground-dwelling avian species and medium-to-large (> 0.2 kg) mammal species. Key identification characteristics of White-winged Flufftail during data collation included primarily white secondaries and chestnut-barred tail, as well as hind neck, mantle and breast colouration (Taylor 1994). In order to increase the detection probability of each individual survey period, every three consecutive days were further collated and synthesised to represent one survey (Ramesh and Downs 2013). If camera trap malfunction, interference and/or theft prevented data collection at a given site and over a given sample/s, these were included into the detection history matrix as missing observations (MacKenzie *et al.* 2002). However, given the increase in standard error associated with data loss and associated missing observations (MacKenzie *et al.* 2002), if missing samples for a given site exceeded 20% of the total expected samples to be collected, the site was removed from the dataset utilised for analyses. Furthermore, given the low capture rate of the focal species and resultant low naïve occupancy estimate (< 0.2), site localities were grouped to represent habitat patches (Ehlers Smith *et al.* 2017). The software package Presence was utilised to run occupancy models for respective species and included both site and sample specific covariate data. Categorical covariates were translated into multiple series of binary indicator variables depicted as 0 or 1 (MacKenzie 2012). All continuous covariate data were standardised using the *z-transformation* equation (MacKenzie 2012). Covariate data collected and/or collated per camera trap site included average vegetation height, basal cover, canopy cover, dominant fine-scale vegetation community, water depth, trail presence/absence, trail width and trail type (Colyn *et al.* 2017). Model fit was assessed and ranked using the Akaike Information Criterion (AIC) model selection criteria, which included AIC, delta AIC, AIC weight and Model Likelihood values (Anderson and Burnham 2002). Additionally, the Pearson's chi-square statistic and parametric bootstrapping (1,000 runs) as per MacKenzie and Bailey (2004) were used to further test model fit.

Activity pattern analysis was conducted to estimate activity peaks and overlap between associated species of interest across two temporal periods, namely a conventional 24-hour cycle and a seasonal cycle (December to February) (Meredith and Rideout 2017). Consecutive sightings of the same

species at the same camera trap site were deemed independent when separated by a 30 min interval (Rovero *et al.* 2005). Furthermore, capture frequency was defined as the number of independent sightings per 100 camera days (Kelly and Holub 2008). Kernel density estimation (KDE), a non-parametric method of evaluating the density function (Rideout and Linkie 2009), was utilised to assess activity patterns in software R (R Development Core Team 2008). Furthermore, the R package “overlap” was used to assess the measure of overlap between peak activity periods of species assessed (Meredith and Rideout 2017). Due to the influence of sample size on the performance of estimators of coefficient of overlapping, sample sizes smaller than 50 were allocated formula “Dhat1” (Linkie and Rideout 2011, Meredith and Rideout 2017). Furthermore, 95% confidence intervals were obtained from 10 000 bootstrap samples per overlap interaction assessed (Linkie and Rideout 2011, Meredith and Rideout 2017). Due to detection bias, very small avian species (< 20 g) and species utilising an alternative foraging strategy to that of rallids (e.g. foliage gleaners), were listed as non-target avian species and excluded from all analyses (Colyn *et al.* 2017).

## Results

### Capture frequency and occupancy estimation

Our study was effective in confirming the presence of White-winged Flufftail at MW, with eight independent sightings and an associated capture frequency (cf) of 1.28 (Table 1, Figure 2). The study accumulated a survey effort of 626 camera days from nine camera traps over the survey period, December 2016–February 2017. White-winged Flufftail were exclusively recorded at one of the nine survey locations, a *Typha*-sedge mixed vegetation community. Furthermore, out of the total survey duration, seven (88%) of the independent sightings were recorded across a consecutive 10-day period from late December to early January, whilst the remaining one independent sighting was recorded 18 days later (late January). Mean occupancy ( $\psi$ ) and detection probability (P) estimates over the truncated period were  $0.20 \pm 0.18$  and  $0.22 \pm 0.07$  (Table 2). Results indicated that basal and canopy cover both had strong positive influences on site occupancy ( $\beta = 27.28$  and  $\beta = 29.51$ ), whilst water depth negatively influenced detection probability ( $\beta = -96.95$ ). The resultant SE of occupancy estimates ( $0.20 \pm 0.18$ ) and the goodness-of-fit value ( $\hat{c} = 1.5$ ) for the global model, highlight the influence of the short temporal period during which the species was present and narrow resultant detection-history data obtained.

The vegetation community surrounding the presence locality was comprised of c.30% sedge (mean height = 30 cm), 60% *Typha* (mean height = 170 cm) and 10% forbs (mean height = 20 cm). During the core period at which 88% of independent sightings were made (i.e.

Table 1. All target (rallid) and non-target (non-rallid) avian species recorded during the camera trap survey at Middelpunt Wetland. Species classified as regionally threatened (Taylor *et al.* 2015) are highlighted in bold, whilst all non-rallid species are highlighted in grey below the dotted line.

Common Name	Scientific Name	Family	No. of independent Sightings	Capture Frequency	Regional Conservation Status
Spotted Crake	<i>Porzana porzana</i>	Rallidae	12	1.92	Least Concern
Red-chested Flufftail	<i>Sarothrura rufa</i>	Rallidae	14	2.24	Least Concern
<b>White-winged Flufftail</b>	<b><i>Sarothrura ayresi</i></b>	<b>Rallidae</b>	<b>8</b>	<b>1.28</b>	<b>Critically Endangered</b>
African Rail	<i>Rallus caerulescens</i>	Rallidae	303	48.40	Least Concern
Yellow-billed Duck	<i>Anas undulata</i>	Anatidae	47	7.51	Least Concern
<b>African Grass Owl</b>	<b><i>Tyto capensis</i></b>	<b>Tytonidae</b>	<b>1</b>	<b>0.16</b>	<b>Vulnerable</b>
Marsh Owl	<i>Asio capensis</i>	Tytonidae	1	0.16	Least Concern
African Snipe	<i>Gallinago nigripennis</i>	Scolopacidae	20	3.19	Least Concern

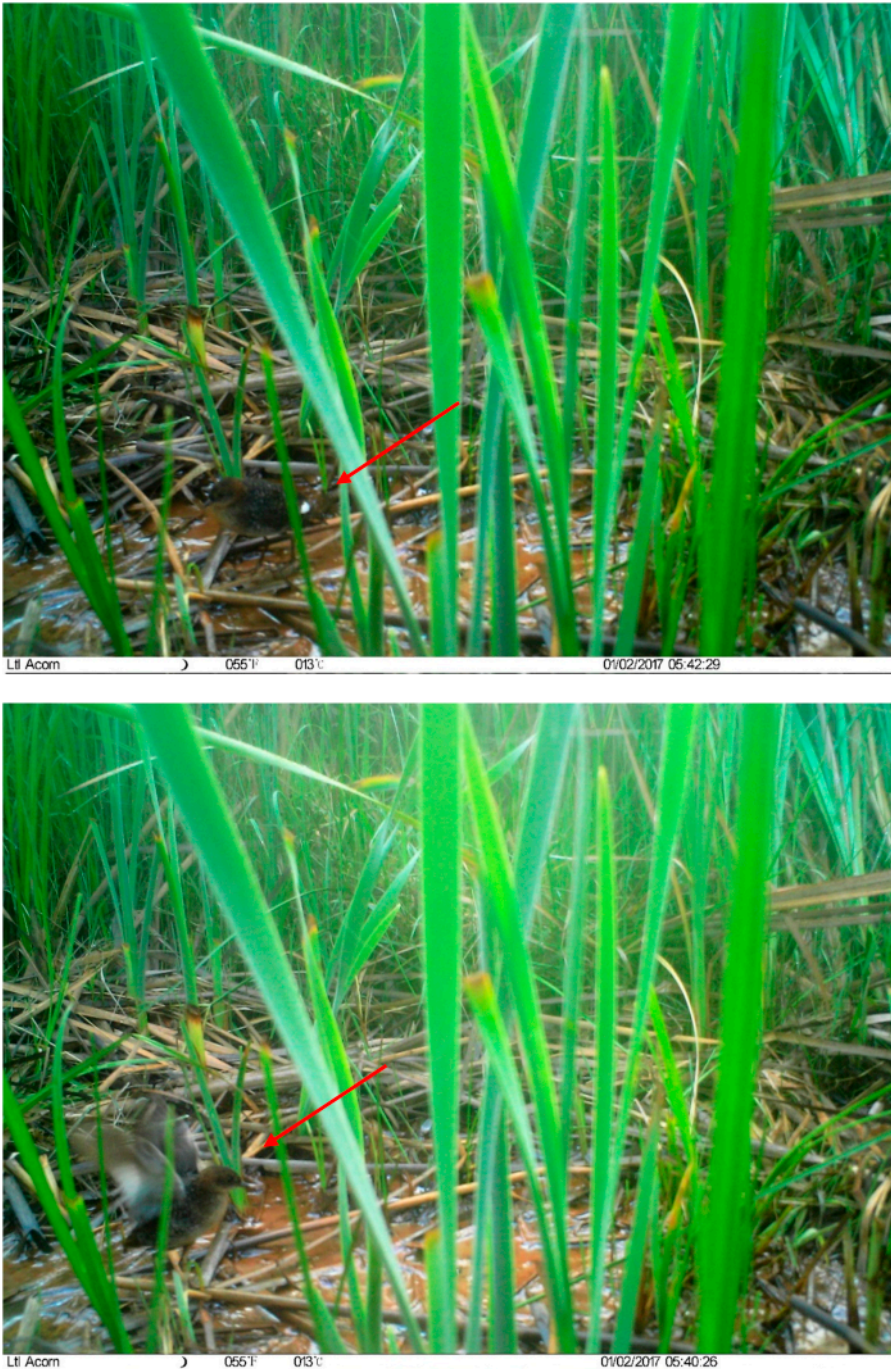


Figure 2. Selected images of a female White-winged Flufftail *Sarothrura ayresi* recorded during the study (indicated by arrow) displaying a distinctive white patch (i.e. secondaries) whilst walking with wings folded in (above) and conducting an apparent territorial wing-flapping display (below).

Table 2. Summary of the Akaike Information Criterion (AIC) model selection criteria for the two best model fits per species assessed. \*Mean occupancy ( $\psi$ ) and detection (P) probabilities displayed represent the best model fit.

Model	AIC	$\Delta$ AIC	AIC weight	Model Likelihood	No. of Par.	$\psi \pm SE^*$	$P \pm SE^*$
<b>White-winged Flufftail</b>							
psi(basal cover),p(water depth)	10.77	0.00	0.42	1.00	4	0.20 $\pm$ 0.18	0.22 $\pm$ 0.07
psi(basal cover + canopy cover),p(water depth)	12.77	2.00	0.15	0.37	5		
<b>Red-chested Flufftail</b>							
psi(canopy cover),p(water depth)	57.53	0.00	0.72	1.00	4	0.41 $\pm$ 0.21	0.22 $\pm$ 0.07
psi(canopy cover),p(canopy cover)	61.28	3.75	0.11	0.15	4		
<b>Spotted Crane</b>							
psi(canopy cover),p(.)	13.64	0.00	0.15	1.00	3	0.20 $\pm$ 0.19	0.67 $\pm$ 0.19
psi(basal cover),p(.)	13.64	0.00	0.15	1.00	3		
<b>African Rail</b>							
psi(vegetation height),p(vegetation height)	112.40	0.00	0.72	1.00	4	0.67 $\pm$ 0.28	0.28 $\pm$ 0.04
psi(vegetation height + water depth),p(vegetation height)	114.24	1.84	0.29	0.40	5		
<b>African Snipe</b>							
psi(vegetation height),p(water depth)	58.76	0.00	0.25	1.00	4	0.37 $\pm$ 0.19	0.41 $\pm$ 0.20
psi(canopy cover),p(canopy cover)	59.80	1.04	0.15	0.59	4		

late December to early January), the average vegetation height, water depth, basal cover and canopy cover at the exclusive presence locality were 150 cm, 15 cm, 80% and 45% respectively. This area differed significantly ( $P < 0.05$ ) in relation to average canopy ( $P = 0.01$ ) and basal ( $P = 0.003$ ) cover when compared to the other sampled units. Furthermore, the respective sites varied significantly in average water depth across three ( $P = 0.006$ ,  $P = 0.02$ ,  $P = 0.01$ ) of the surveyed localities. Water depth across surveyed localities were not significantly associated with dominant vegetation communities sampled ( $P = 0.17$ ), but seemingly a factor of local topographic relief (e.g. depressions, channels and sediment compaction). Conversely, as expected, dominant vegetation types sampled varied significantly in average height ( $P < 0.05$ ).

Three changes in environmental covariate data were noted during the absence of White-winged Flufftail records between the core group of sightings recorded up to early January and the solitary and last sighting logged in late January. Firstly, the last sighting preceded a significant rainfall (flooding) event that increased water depths across all surveyed localities at the study site. At the exclusive presence locality, water depth preceding the rainfall event (mean 15 cm) varied significantly to that directly after the event (mean 30 cm,  $P = 0.004$ ). Water depth remained relatively high for 12 days from the onset of the rainfall event, after which it became comparable ( $P = 0.28$ ) to when White-winged Flufftail were first recorded at the locality. Secondly, basal and canopy cover reduced notably following the core group of White-winged Flufftail sightings (early January). Basal cover was significantly reduced by 40% ( $P < 0.05$ ), whilst canopy cover was marginally reduced by 10% ( $P = 0.07$ ). Potential disturbance factors of vegetation cover noted during this period included primarily flooding of basal cover and disturbance of sections of canopy cover through the respective rise in water levels. Southern Reedbuck *Redunca arundinum* were observed moving through this camera locality over the same period, but the associated disturbance impact was thought to be negligible. Significantly, following the absence of White-winged Flufftail records over this period when water depth and vegetative cover (basal and canopy) were altered, a solitary and final sighting was recorded. At the time of the sighting the water depth was comparable to when White-winged Flufftail were first recorded, whilst basal and canopy cover were still significantly lower ( $P < 0.05$ ,  $P = 0.07$ ) following the flooding event. Surveying commenced



for a further 279 camera days within the survey period (December–February) following this sighting and yielded no additional records.

Three other rallid and four non-rallid avian species were recorded during the survey (Table 1). Other rallid species recorded included Red-chested Flufftail, Spotted Crake *Porzana porzana* and African Rail *Rallus caerulescens* with 14, 12 and 303 independent sightings recorded respectively. Spotted Crake ( $cf = 1.92$ ) and Red-chested Flufftail ( $cf = 2.24$ ) were relatively comparable in capture frequency to White-winged Flufftail ( $cf = 1.28$ ), whilst African Rail yielded a significantly greater capture frequency ( $cf = 48.40$ ) than the other rallid species. Mean occupancy ( $\psi$ ) and detection ( $P$ ) probability estimates for other rallid and non-rallid species assessed were in the range 0.20–0.67 and 0.22–0.67 (Table 2). Vegetation height influenced both the occupancy ( $\beta = 1.62$ ) and detection probability ( $\beta = 2.06$ ) of African Rail positively, whilst canopy ( $\beta = 89.02$ ) and basal ( $\beta = 65.08$ ) cover strongly influenced the occupancy of Spotted Crake. Red-chested Flufftail occupancy was influenced positively by canopy cover ( $\beta = 3.14$ ), whilst detection probability was influenced negatively by water depth ( $\beta = -5.45$ ). The last species assessed, African Snipe *Gallinago nigripennis*, yielded occupancy estimates that responded negatively to vegetation height ( $\beta = -1.98$ ) and detection probability that responded positively water depth ( $\beta = 0.45$ ).

Spotted Crake was only recorded across a consecutive three-day period in mid-December. However, during this very brief period, it exhibited a high level of activity and associated captures when compared to other species present across the entire study period (Table 1). Furthermore, Spotted Crake was only recorded at the same exclusive camera trap that recorded White-winged Flufftail. The temporal difference at the exclusive spatial location being occupied by Spotted Crake and White-winged Flufftail was six days. The environmental covariate data with regards to water depth and vegetative cover were comparable ( $P > 0.05$ ) over the peak temporal period of occupancy across the two species. Additionally, both species occupancy estimates were influenced positively by basal and canopy cover (Table 2).

Non-rallid species recorded included 'Vulnerable' African Grass Owl *Tyto capensis*, Marsh Owl *Asio capensis*, African Snipe and Yellow-billed Duck *Anas undulata* (Table 1). Non-target species recorded included 13 bird, five mammal and one reptile species (Table S2).

### *Activity patterns, inter-species interactions, demographics and behaviour*

White-winged Flufftail kernel density estimates of activity patterns display peak periods of activity at dawn and dusk (Figure 3). Based on the distribution of sightings recorded, a strong preference for activity surrounding sunrise was displayed, with 60% of sightings registered between 05h00 and 06h00. Of the rallid species assessed, Spotted Crake yielded the highest degree of overlap with White-winged Flufftail, with a resultant overlap coefficient of 0.62 (0.33–0.86) (Figure 4). Red-chested Flufftail and African Rail yielded lower and comparable levels of overlap with White-winged Flufftail: 0.44 (0.17–0.71) and 0.39 (0.17–0.59) respectively (Figure 4). Confidence intervals were relatively wide as a result of the small sample size obtained for White-winged Flufftail (Linkie and Ridout 2011). White-winged Flufftail yielded the highest kernel density estimates over the sunrise activity period when compared to the other three rallid species (Figure 4).

When activity patterns were assessed over the entire seasonal cycle of the study period (i.e. December–February), our results displayed a spatial niche avoidance between White-winged Flufftail and Red-chested Flufftail (Figure 5). Although both species occurred at the respective camera site by day 16 of the survey, once White-winged Flufftail activity peaked, Red-chested Flufftail activity diminished. Furthermore, Red-chested Flufftail activity was once again noted and increased significantly following the absence of White-winged Flufftail from day 35 of the survey (Figure 5). This significant increase in activity by Red-chested Flufftail led to a breeding attempt and successfully fledged juvenile that was recorded frequently following day 60 of the survey.

Demographics of White-winged Flufftail sightings included an adult female, adult male and juvenile (sex unknown). Noted behaviour included a female utilising a perch site to presumably display. These displays incorporated wing-flapping from the perch, followed by the display of

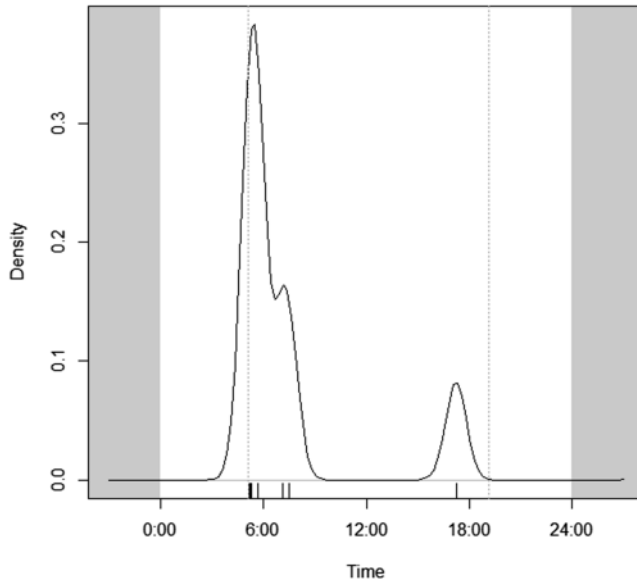


Figure 3. Kernel density estimates of daily activity patterns of White-winged Flufftail in high altitude palustrine wetland habitat, South Africa. Dotted lines indicate approximate time of sunrise and sunset over the respective period.

white secondaries while walking in the immediate area. The voluntary display of white secondaries whilst the wings were folded in, seemed comparable to that of pectoral tuft displays recorded in other species (Evans and Hatchwell 1992). The voluntary nature of this display was evident in that comparable images of other adults failed to produce these white patches. This wing-flapping and voluntary display of secondaries whilst walking was noted twice from the same perch site over a three-day period. Furthermore, following both these sightings, a male was observed coming into the area shortly after the female had left (8 min and 4 min respectively).

## Discussion

The ecological application of technological advances has yielded increased capacity and ongoing improvements for surveying rare and elusive species worldwide (Nichols *et al.* 2011). Our study confirms camera trapping as the first non-invasive method of surveying the CR White-winged Flufftail. Results from this study represent more independent sightings of this species than that accumulated through four consecutive years of rope dragging surveys at the same respective site (Davies *et al.* 2015). Additionally, camera trapping provided the first assessment of site occupancy and fine-scale activity patterns of this species. This study also accumulated the first photographic material of this species behaving and interacting within its natural habitat in an undisturbed state. Building on the foundational work conducted using traditional survey methods (Taylor 1994, Allan *et al.* 2006, Davies *et al.* 2015), this study demonstrates the applicability and potential of camera trapping as a non-invasive, accurate and reliable survey method for elusive rallids.

Habitat covariates most influencing White-winged Flufftail occupancy included basal and canopy cover (Table 2). Although the species has a known association with dense wetland vegetation (Evans *et al.* 2015), our study confirms the importance that intact canopy and basal cover could have on species occupancy. This further highlights the potential threat of activities that lower vegetative cover, such as overgrazing and excessive trampling by domestic stock, could have on species persistence in a given area (Evans *et al.* 2015). Furthermore, our results confirm the

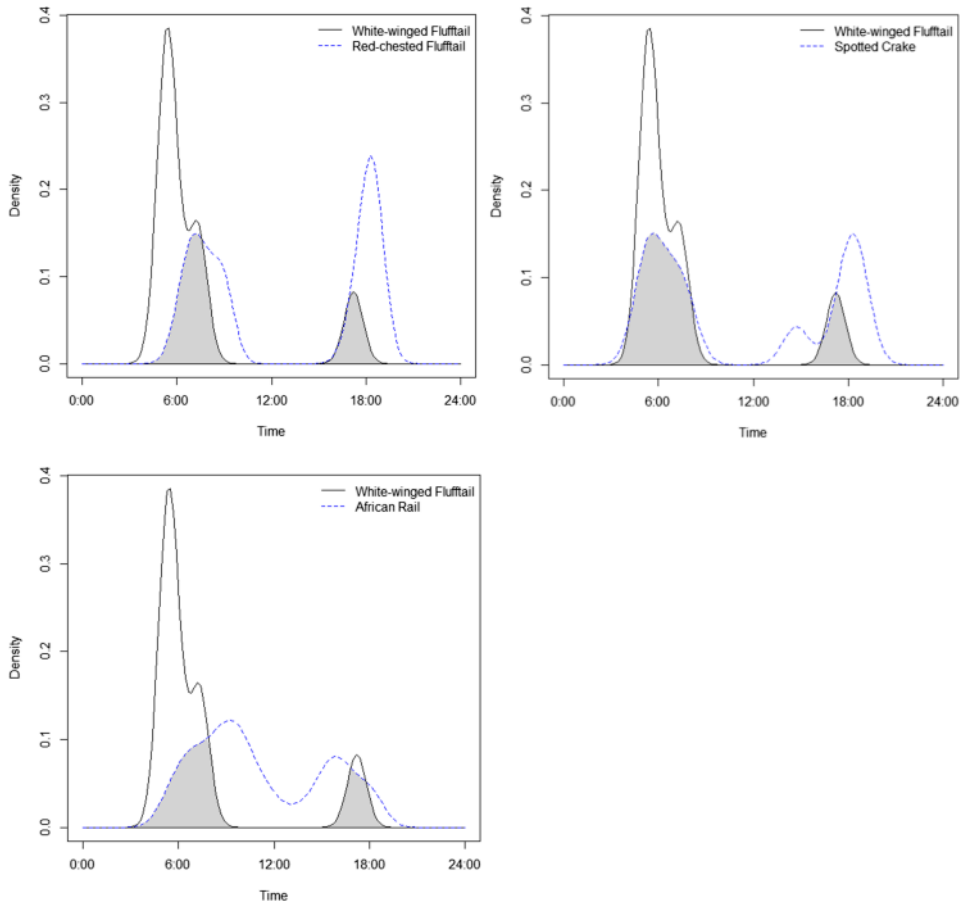


Figure 4. Estimated daily activity patterns (lines) and coefficient of overlap (grey-shaded area) of White-winged Flufftail (solid line) and three other rallid species (dotted line) recorded during the study, namely Spotted Crake, Red-chested Flufftail and African Rail.

noted preference of White-winged Flufftail for shallower water levels within wetlands, as seen by water level negatively influencing detection probability within our study. Also corroborated by our study is the sensitivity of this species to microhabitat alteration, whereby any significant reduction in vegetative cover and increase in water level could lead to the local abandonment of that site. The local abandonment of a microhabitat noted in our study was caused by a natural flooding event and therefore also highlights the need for sufficiently sized wetlands and patch connectivity across the landscape to accommodate this species. The low resultant capture frequency and occupancy estimate of White-winged Flufftail from our study corroborate the supposition that this species is rare and currently represented by very low densities (Evans *et al.* 2015). These results are further supported by low genetic diversity confirmed in the innate immune regions (Dalton *et al.* 2016). The low diversity, rendering the species more vulnerable to changes in the environment, needs to be further elucidated as it may ultimately contribute to the extinction of the species.

Many rallids are known to be territorial in both the breeding and non-breeding range (Taylor 1987, 1994, Taylor and van Perlo 1998). Spotted Crake, the only other migratory rallid recorded in our study, has been noted to display aggressive territorial behaviour in the non-breeding

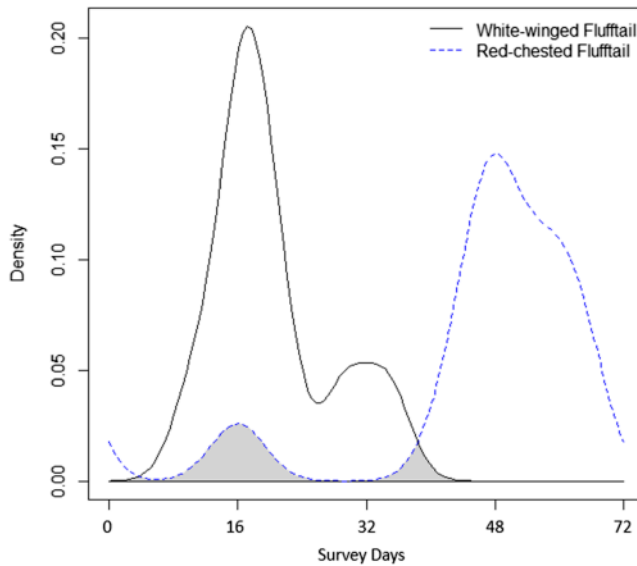


Figure 5. Kernel density estimates of sighting distribution across the study period (December–February) for White-winged (solid line) and Red-chested Flufftail (dotted line) at the individual camera trap where the focal species (White-winged Flufftail) was exclusively recorded.

stop-over sites (Taylor 1987). Furthermore, Mendelsohn *et al.* (1983) noted that although Red-chested and White-winged Flufftail were found at the same wetland, there seemed to be little overlap between them. Our study confirms that spatial avoidance between the two species does seem to occur, with Red-chested Flufftail seemingly abandoning the local microhabitat after the arrival and peak activity of White-winged Flufftail (Figure 5). Other studies have noted that White-winged Flufftail occur singly, in pairs or small family groups (Taylor 1994), but our study only recorded solitary birds. The peak period hosting the majority of sightings yielded one intra-specific interaction. Two consecutive sightings of a female White-winged Flufftail utilising a perch to presumably display, followed by a male moving into the area shortly thereafter, but never overlapping in site utilisation. Although based on a limited sample size, the inter-species spatial avoidance and lack of intra-species spatial overlap, together with noted displays, suggest that White-winged Flufftail exhibit territorial behaviour in the respective austral summer range.

The migration strategy employed by most migratory species involves alternation between flights and stopover foraging periods (Schaub *et al.* 2001, Strandberg and Alerstam 2007). Most migratory ground-foraging species undertake a full stop incorporating intensive foraging activity to accumulate fuel reserves along the migration journey (Schaub *et al.* 2001, Lindstrom 2003). Although White-winged Flufftail is thought to be a migratory species based on the available data (Taylor 2005), the exact status is disputable (Davies *et al.* 2015). Furthermore, DNA analysis of mitochondrial (COI, Cytb, 12S/Val/16S) and nuclear (ADH-5, GPD3-5 and bfib7) markers revealed only three interspecific genetic variations between South African and Ethiopian birds, suggesting that these birds are not different species or subspecies but are rather one migrating population (Dalton *et al.* 2016). Our study provides further support for the postulation that White-winged Flufftail is a migratory species. The species was only recorded across a restricted temporal period, whereby the bulk of the sightings occurred across a consecutive 10-day period. Furthermore, the level of activity during the short temporal period of occupancy was higher than other non-breeding resident rallid species, suggestive of typical intensive stopover foraging exhibited by migratory species (Schaub *et al.* 2001, Lindstrom 2003). Furthermore, the short

temporal period of intensive activity closely resembled that of Spotted Crake documented in this study, which is a known Palearctic breeding migrant (Taylor 1987).

White-winged Flufftail are known to prefer short sedge, grass and Asteraceae meadows in the Ethiopian breeding range (Taylor and van Perlo 1998, Taylor 2005). Similarly, in the non-breeding austral range the species seemingly shows a preference for shorter (< 60 cm) sedge and grass meadows (Taylor and van Perlo 1998, Taylor 2005, Davies *et al.* 2015). However, the species has been noted to occupy taller vegetation habitats in the austral summer range, including mixed stands of sedge and taller reeds (Taylor 2005, Evans *et al.* 2015). Our results exclusively recorded the species within a taller (mean 170 cm) mixed *Typha*-sedge community, but failed to detect the species in the preferred sedge meadows in which 66% of the camera localities were situated. Further studies are required to ascertain if the absence of sightings within sedge meadows is a reflection of true absence or pseudo-absence. Survey design potentially requires refinement to accommodate alternative microhabitat camera placement methods that prevent bias in detection probability and increase the reliability of detection histories accumulated across camera localities.

Management recommendations for existing habitat should limit the excessive reduction of vegetative cover within wetland habitats by maintaining low stocking densities to prevent overgrazing and/or extensive trampling within the respective management units. Given the species' noted preference for good quality peat wetlands (Davies *et al.* 2015), frequent (annual) intense fires in the wintering months should be avoided as these will adversely impact on peat condition and accumulation (Hamilton 1984, Kirkman *et al.* 2000). Furthermore, fire not only impacts on peat characteristics, but can influence the development of dominant wetland vegetation communities (Hamilton 1984, Timmins 1992, Kirkman *et al.* 2000). A complete lack of fire could potentially alter grass-sedge wetland communities to taller dense stands of vegetation, whilst more frequent fires could benefit prevalence of grass-sedge community (Kirkman *et al.* 2000).

## Conclusion

White-winged Flufftail was noted in our study as a low-density, habitat specialist species that proved sensitive to habitat alteration, particularly reduction in vegetative cover (basal and canopy) or increase in water level. Furthermore, the species' short temporal period of occupation across an austral summer season within our study site suggests a reliance on multiple wetland sites across its migratory journey. Our study supports the need for conservation initiatives focused on securing contiguous sections of suitable wetland habitat in order to accommodate the persistence of this 'Critically Endangered' species. Imperative elements of conservation networks would include replication and representation (Redford *et al.* 2011), whereby numerous local wetland sites are secured at multiple localities across the species' range.

In order to progress our understanding of site occupancy and population trends for this species, further refinement of the survey technique and/or survey design is required to increase detection probabilities and subsequent datasets obtained. One particular area of concern is the lack of any sightings at any of the camera traps located in sedge meadows, which is a preferred habitat type for the species (Davies *et al.* 2015). We postulate that this possibly was not a reflection of occupancy, but an artefact of the current survey design. Sedge meadows yielded a significantly shorter and denser vegetation structure than in other mixed vegetation units sampled, which could necessitate an alternate camera placement strategy. Furthermore, given the noted relationship observed in our study between site occupancy and vegetation cover, vegetation cropping in front of cameras as part of the camera placement technique would need to be carefully considered. Lack of cropping would not allow for efficient camera surveying as vegetation would obscure the detection arc (Colyn *et al.* 2018), whilst cropping more than is absolutely needed could bias resultant detection probabilities. Identifying the optimal camera placement technique for ground-dwelling species inhabiting dense short wetland habitats therefore requires further investigation.

A survey technique that can reliably and accurately determine presence and be replicated across the species range would significantly aid the understanding of the species' population status and

more efficiently direct conservation initiatives. Furthermore, this method would be applicable to other rare and elusive rallid species for which data deficiencies exist, such as ‘Endangered’ Slender-billed Flufftail *Sarothrura watersi*, ‘Vulnerable’ Yellow Rail *Coturnicops noveboracensis* and ‘Vulnerable’ Swinhoe’s Rail *Coturnicops exquisites*.

## Supplementary Material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0959270918000400>

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