

Water scarcity exacerbates feral ungulate use of ephemeral savanna waterholes in northern Australia

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ABSTRACT

Context. Australian savannas evolved in the absence of hooved mammals and are therefore prone to disturbance from exotic ungulates. Several ungulate species have established feral populations in Australia's northern savannas. Because most ungulate species have high water requirements, seasonal and interannual changes in water availability are likely to affect their behaviour and the extent of their impacts on native ecosystems. However, few studies have investigated how water scarcity affects feral ungulate use of waterpoints in Australia. **Aims.** The aim of this study was to determine whether seasonal and interannual water scarcity affected the visitation behaviours of feral pigs, cattle and water buffalo at ephemeral savanna waterholes within Limmen National Park, Northern Territory, Australia. **Methods.** We used motion-triggered wildlife cameras to study feral ungulate visitation and behaviour at 20 waterholes. Generalised linear mixed-effects models were used to investigate whether the number of visits, duration of visits and number of individuals visiting waterholes varied with year and dry season progression. We also investigated whether these factors affected the amount of time ungulates spent foraging, drinking and wallowing at waterholes. **Key results.** All three species visited waterholes more often, for longer periods and in larger numbers during a drought year compared with an average rainfall year. Cattle and buffalo spent more time drinking from waterholes during the drought, and pigs and cattle spent longer periods foraging. Buffalo also wallowed more during the drought. Responses to dry season progression varied among species. Cattle visited waterholes more frequently, for longer durations and in larger herd sizes as the dry season progressed, whereas buffalo use did not change. Pigs only increased their visitation to waterholes when water scarcity was most extreme, at the end of the dry season during the drought. **Conclusions.** Our results demonstrate that water scarcity exacerbates feral ungulate use of savanna waterholes. Management and control programs for feral ungulates in Australian savannas may benefit from targeting different species under specific water scarcity conditions. **Implications.** Because climate change is predicted to reduce surface water availability in northern Australia, feral ungulate use of savanna waterholes may intensify, risking further biodiversity losses and irreversible ecosystem damage.

Keywords: cattle, drought, feral ungulates, invasive species, pig, tropical savanna, water buffalo, waterhole visitation.

Introduction

Northern Australia supports one of the largest savanna ecosystems in the world, which covers approximately 1 500 000 km² (Woinarski *et al.* 2007). Australian savannas are thought to be particularly susceptible to disturbance from introduced ungulate species (Freeland 1990; Ash and McIvor 1998), because they did not evolve with native ungulates and have been devoid of large herbivores (>100 kg) since the extinction of the megafauna ~45 000 years ago (Skarpe 1991; Scogings and Sankaran 2019). However, several ungulate species have been introduced to the region since the 1800s (Ridpath 1991), and pastoralism is now a major land use (Woinarski and Ash 2002; Holmes 2010). Pigs (*Sus scrofa*), cattle (*Bos taurus*, *B. indicus*) and Asian water buffalo (*Bubalus bubalis*) have established

widespread feral populations in tropical savanna habitats (Mihailou and Massaro 2021), including in conservation reserves, indigenous protected areas and national parks (Bayliss and Yeomans 1989; Kakadu National Parks Board of Management 2016). In addition, domestic cattle in pastoral areas of northern Australia are typically allowed to roam freely across vast areas (average paddock size in the Barkly region is 364 km²; Bubb 2004) of 'unimproved' native savanna rangeland until mustering (Karfs and Trueman 2005; Walsh and Cowley 2011; Chilcott *et al.* 2020). Fenced boundaries between pastoral properties and protected land are rarely effective barriers to ungulates, due to the high cost of maintenance and monitoring for breaks (Hunt *et al.* 2014). Therefore, domestic cattle often make their way into national parks (at least until the next tenured muster), where they likely cause the same damage to the landscape as feral populations, making the distinction between the two more academic than ecological.

The pervasiveness of pastoralism and the difficulty of controlling ungulates in protected areas in northern Australia raises concern that refugia for native wildlife may not be as extensive as it appears. Over the last few decades, many native mammal and bird species have suffered sudden and severe declines in their distribution and abundance in northern Australia, including in protected areas such as Kakadu National Park (Woinarski 2000; Woinarski *et al.* 2001, 2011; Franklin *et al.* 2005). These declines are often attributed to predation by feral cats (*Felis catus*) and the impacts of altered fire-regimes on native habitat (Pardon *et al.* 2003; Firth *et al.* 2010; Fisher *et al.* 2014; Lawes *et al.* 2015). However, researchers are increasingly considering the impacts of introduced ungulate species on vegetation communities as a factor that exacerbates the combined effect of both cats and fire on native wildlife (Legge *et al.* 2011, 2019; McGregor *et al.* 2014; Woinarski 2015). In addition, recent research has highlighted the potential competitive impacts of introduced ungulates on native herbivores in Australia, primarily due to dietary overlap and potential exclusion from resources (Reid *et al.* 2020a, 2020b, 2023; Mihailou *et al.* 2022).

Most ungulates, particularly grazing species, need to drink regularly due to their dry diets, so they are often distributed near waterpoints (Tomkins and O'Regain 2007; Graz *et al.* 2012). Ungulate visitation to waterholes can reduce water quality through faecal contamination and by increasing turbidity through the overturning of benthic soils (Skeat *et al.* 1996; Finlayson *et al.* 1999; Pettit *et al.* 2012; Waltham and Schaffer 2017), reducing the suitability of waterholes for native wildlife. Additionally, ungulates can drink up to 10% of their body weight daily (Hunt *et al.* 2013; Bray *et al.* 2015) and can increase the evaporative potential of waterholes through pugging and wallowing (Skeat *et al.* 1996), directly reducing the amount of water available for native wildlife. In northern Australia, rainfall can vary greatly between years, and surface water availability declines as the dry season progresses each year, resulting in interannual (i.e. during

years of below-average rainfall) and seasonal (i.e. as the dry season progresses each year) periods of water scarcity (Cook and Heerdegen 2001; Kanniah *et al.* 2013). Such periods concentrate animal activity around those areas where surface water is still available (Pettit *et al.* 2012). Both permanent and ephemeral waterholes provide important drought and dry season refugia for many savanna species (Thrash *et al.* 1995; Redfern 2002; Valeix 2011). Thus, ungulate visitation and use of savanna waterholes may have greater impacts on native biota when water scarcity is high compared with times when water is more readily available across the landscape, especially considering that some feral ungulates move in larger group sizes towards the end of the dry season (Reid *et al.* 2020b). Despite this, there is a lack of research in Australia on the behaviour of ungulates in the wild and whether water scarcity affects how they use waterholes in savanna environments. Understanding how feral ungulates respond to water scarcity may inform land managers and conservationists about potential threats to native biota due to changes in ungulate disturbance and allow targeted control and management of ungulates in protected areas.

In this study, we used remote-triggered wildlife cameras to investigate changes in the annual and seasonal visitation behaviours of three feral ungulate species (pigs, cattle and buffalo) at ephemeral savanna waterholes in Limmen National Park in northern Australia. Rainfall varied considerably over the 2 years the study was conducted. The first year received a relatively normal amount of rainfall, but the second year was a drought year with well below average rainfall, so surface water availability within the landscape varied considerably between years, as well as over the progression of the two dry seasons (i.e. with increasing time since last rainfall each year). We hypothesised that ungulates would respond to increasing water scarcity (both during the drought and as the dry season progressed) in the following ways: (1) visiting waterholes more frequently; (2) visiting waterholes for longer time periods; (3) visiting waterholes in larger numbers; and (4) spending more time drinking, foraging and wallowing at waterholes.

Materials and methods

Study area

This study was conducted in Limmen National Park, a large savanna reserve (>1 000 000 ha) in the Northern Territory, Australia. Vegetation communities in the region comprise a mosaic of grasses, shrubs and trees in a range of densities depending on fire history, soil type and landscape hydrology (Woinarski *et al.* 2007). Dominant flora species in savanna lowland areas of the park include native perennial grasses such as *Chrysopogon fallax*, *C. latifolia*, *Eulalia aurea* and *Eriachne obtuse*, and trees such as *Eucalyptus microtheca*, *Bauhinia cunninghamii* and *Atalaya hemiglauca* (Vincent and Mihailou 2023). Rainfall follows a monsoonal wet–dry cycle, whereby

rain predominately falls between November and April (wet season), and the months of May to October (dry season) receive little or no rain. Rainfall can be highly variable between years (Taylor and Tulloch 1985; Haynes *et al.* 1991), so surface water availability can be restricted on both a seasonal (i.e. as the dry season progresses each year) and interannual basis (i.e. during years of below-average rainfall). On average, the park receives 859 mm of rain annually (as measured at Nathan River Ranger Station; Bureau of Meteorology 2021). The park received totals of 970 mm and 371 mm of rain over the 2017/2018 (hereafter 2018) and 2018/2019 (hereafter 2019) wet seasons respectively (Bureau of Meteorology 2021).

Data collection

Ephemeral waterholes within the park are typically small clay basins, which dry completely by the end of the dry season and are refilled by rain each wet season. To collect pig, cattle and buffalo visitation data, we selected 10 main waterholes of comparable size, depth, soil type and surrounding vegetation. Because pilot sampling in 2017 indicated pig numbers within the study area were lower than the other ungulates studied, we selected a further 10 sites for pig sampling only (following the same selection criteria). All waterholes were situated in open, mixed-savanna woodland. Those at the base of ridgelines or within 1 km of rivers and permanent billabongs were excluded.

Field work was conducted from April–October in 2018 and March–August in 2019. The length of the field season varied between these years due to the accelerated drying of waterholes during the drought (2019). Because data was collected from multiple sites per day, the total number of sampling days also varied between years and for different species (Table 1). All species were sampled for a total of 173 calendar days in 2018, and in 2019, cattle and buffalo were sampled for 138 calendar days, and pigs for 150. The duration of sampling in 2019 and the number of sampling days per year was higher for pigs than for cattle and buffalo because pigs were sampled over 20 sites instead of 10 sites. Four study sites were sampled each week on a 5-week rotation over the course of each dry season. Accessibility to sites at the start of the dry season determined their sampling order, which was maintained thereafter. To sample ungulate visitation to and use of study waterholes, three Reconyx Hyperfire HC600 motion-triggered wildlife cameras (‘camera traps’) were mounted to trees around waterholes at ~1.2 m above ground level and positioned to capture as much of the waterline as possible (see Fig. 1 for photo capture examples showing each ungulate species utilising study waterholes at various times of season and year). When triggered by movement or body heat, cameras captured three photos at 1-s intervals (key settings used: trigger, sensitive; night mode, max range; quiet period, no delay). Once set, cameras were left to sample waterhole visitation for ~5 continuous day/night cycles (i.e. average camera deployment = 5.17 days).

Table 1. Sampling day averages and standard deviations of the number of visits, visit duration, number of visiting individuals, time spent drinking, foraging and wallowing by pigs, cattle and buffalo.

Species	Factor	Number of sampling days	Number of visits	Duration of visits (min)	Number of individuals	Variable		
						Time spent drinking (min)	Time spent foraging (min)	Time spent wallowing (min)
Pig	Year	446	0.036 ± 0.257 (16)	0.117 ± 1.342 (52)	0.148 ± 1.339 (66)	–	0.061 ± 0.628 (27)	–
	2019	294	0.133 ± 0.467 (39)	1.415 ± 8.889 (416)	0.643 ± 3.105 (189)	–	0.503 ± 3.133 (148)	–
	Overall	740	0.074 ± 0.358 (55)	0.632 ± 5.729 (468)	0.345 ± 2.228 (255)	–	0.237 ± 2.043 (175)	–
Cow	Year	226	0.159 ± 0.444 (36)	1.580 ± 8.692 (357)	0.482 ± 1.797 (109)	0.181 ± 0.782 (41)	0.637 ± 5.311 (144)	–
	2019	168	0.512 ± 0.997 (86)	6.655 ± 26.460 (1118)	3.083 ± 7.988 (518)	1.077 ± 3.682 (181)	1.976 ± 8.967 (332)	–
	Overall	394	0.310 ± 0.752 (122)	3.744 ± 18.630 (1475)	1.591 ± 5.533 (627)	0.564 ± 2.512 (222)	1.208 ± 7.124 (476)	–
Buffalo	Year	226	0.297 ± 0.664 (67)	2.301 ± 8.460 (520)	0.836 ± 2.524 (189)	0.208 ± 1.329 (47)	1.407 ± 6.509 (318)	0.133 ± 0.952 (30)
	2019	168	0.476 ± 0.868 (80)	3.833 ± 14.420 (644)	1.345 ± 3.521 (226)	0.583 ± 2.260 (98)	1.423 ± 5.166 (239)	0.506 ± 2.445 (85)
	Overall	394	0.373 ± 0.762 (147)	2.954 ± 11.400 (1164)	1.053 ± 2.996 (415)	0.368 ± 1.793 (145)	1.414 ± 5.966 (557)	0.292 ± 1.759 (115)

Values in parentheses represent raw totals (over all sampling days). Dashes denote variables not included in analysis.

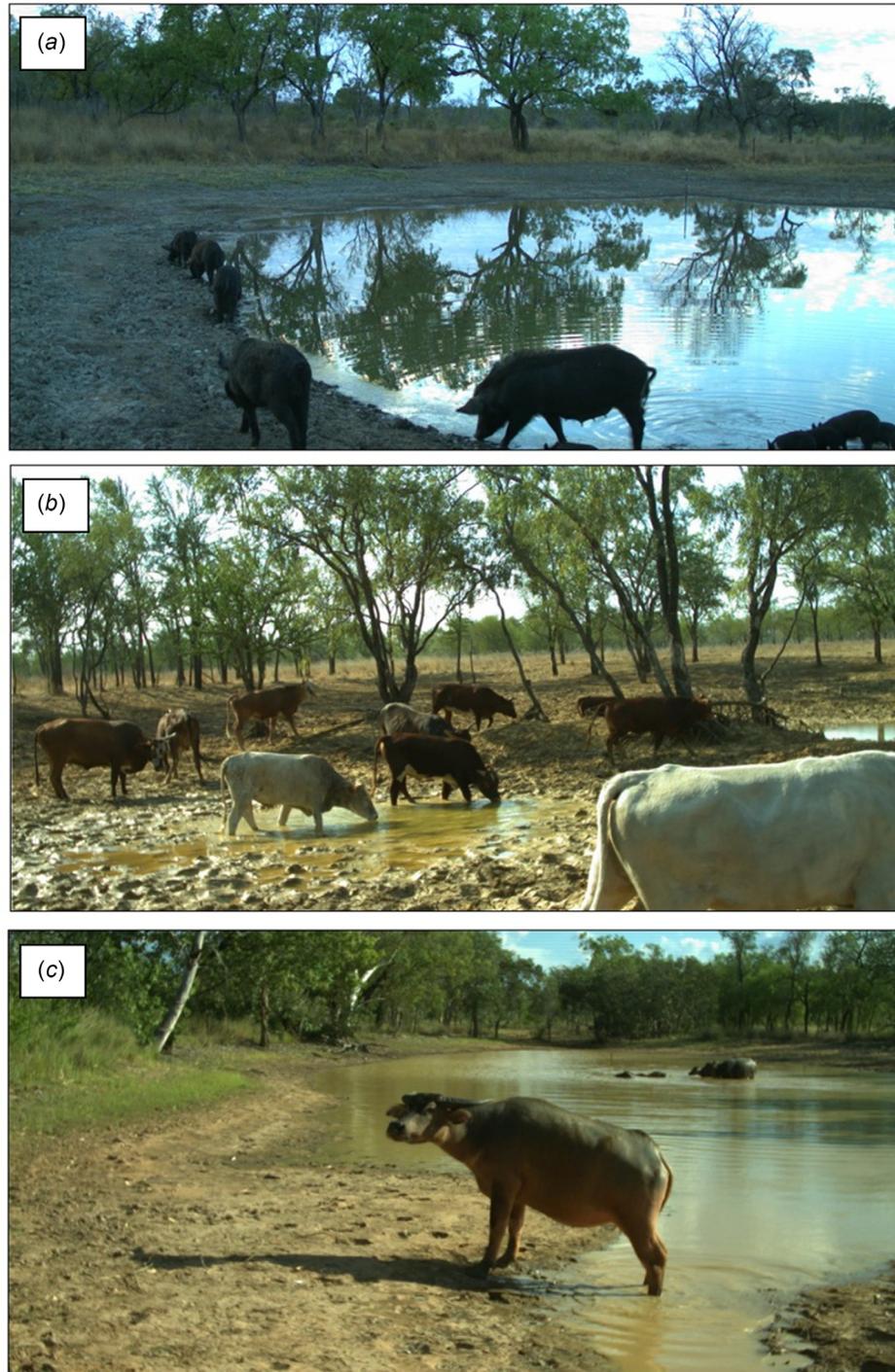


Fig. 1. Feral ungulates using study waterholes captured by Reconyx automated wildlife cameras. (a) Pigs grubbing for food around a waterhole verge – mid-dry season 2018. (b) Cattle drinking from an almost dry waterhole – late dry season 2019. (c) Buffalo wallowing – early dry season 2019).

Collation and processing of data

Photos captured by cameras were processed using the database program CPW Photo Warehouse ver. 4.3.0.5 (Newkirk 2016). A visit was defined as any event where target species

were caught on camera. A visit began when a camera was triggered by an ungulate and ended when the last individual of that species left the camera field of view. Multiple visits within a 30-min time frame were not considered to be independent events, unless the animals involved could be

identified as different individuals/groups that appeared to be moving independently from each other within the 30-min time frame. For example, if a mixed group of female buffalo and calves entered the trigger zone from the right and began grazing for several minutes before eventually moving off to the left, and then 25 min later, a male buffalo entered from the right before exiting to the right – this series of triggers would be considered two distinct visits. The total number of individuals in a visit was determined by looking at all cameras stationed around a waterhole and counting the lowest possible number of individuals present, based on their identifiable markings (e.g. coat colour, horn/tusk shape, gender, size).

The behaviour of ungulates during visits was then classified into several categories, including drinking, foraging (either grazing or grubbing with head down posture moving slowly over fodder) and wallowing (for buffalo only). Other behaviours, such as moving through sites, resting (other than wallowing) and fighting were not included in the analysis. To account for slight variations in camera times and to prevent double counting of behaviours, a time buffer of 3 min was applied when multiple cameras stationed around a waterhole captured activity within a single visit. This buffer was determined by turning on all 20 cameras used for sampling at once and observing the maximum and minimum times displayed, then calculating the offset required so that no time overlap was possible. Where multiple cameras simultaneously captured activity in a visit and the 3-min buffer had to be applied, the configuration of cameras that captured the most activity was used.

Data were analysed at a daily scale per site (i.e. per sampling day). Visitation response variables included the number of visits, the total duration of visits and the total number of individuals visiting per sampling day. Behavioural response variables included time spent foraging (i.e. grazing in cattle and buffalo, grubbing in pigs), drinking (cattle and buffalo) and wallowing (buffalo). Although pigs were also observed drinking and wallowing, there were not enough records to allow analyses of these behaviours. The estimated time (in minutes) spent conducting a given behaviour in each sampling day was calculated as a function of camera triggers by dividing the number of camera triggers in which a given behaviour was observed by the total number of camera triggers, and then multiplying this by the total duration (in minutes) of all visits in that sampling day.

Data analyses

We used generalised linear mixed models (GLMMs) to analyse all data because they are well suited for modelling count data correlated by repeated sampling of study sites (Bolker *et al.* 2009; Bolker 2015). GLMMs modelled each response variable against two fixed factors (predictor variables): year, and days since the dry season started (i.e. year + days since the dry season started), as well as the interaction between the two

(i.e. year × days since the dry season started). Days since the dry season started was included as a continuous variable. Study site was included as a random effect to account for repeated sampling. Given that much of the data was over-dispersed and zero-inflated (because there were many days when species did not visit waterholes), we tested the suitability of the two model variations for each response variable that included different model families (e.g. poisson, quasi-poisson, negative binomial, hurdle) and several zero-inflation factors (including year, days since the dry season started, year + days since the dry season started and year × days since the dry season started). The most parsimonious model was then determined using Akaike's information criterion (AIC; Akaike 1973). If more than one model was supported (i.e. $\Delta\text{AIC} \leq 2$, Akaike weight of most parsimonious model <0.9), we produced a model that included all the variables (and their interactions) contained in the set of supported models (following Haslem *et al.* 2015). Full model component details and AIC values for the most parsimonious model for each response variable are presented in Supplementary Table S1. Results for co-efficients are presented for the conditional models using a quasi-poisson or negative binomial family with a log-link, and zero-inflation models used a logit-link. All data were analysed using the statistical program 'R' (R Core Team 2020), with library 'glmmTMB' (Brooks *et al.* 2017). Model dispersion was assessed using the 'testDispersion' and 'simulateResiduals' functions from the 'DHARMA' package (Hartig 2020). Figures were generated by using models to calculate predicted values for each response variable using the 'ggpredict' function from library 'ggeffects' (Lüdtke 2018) and plotted with 'ggplot2' (Wickham 2016).

Ethics approval

Approval to conduct this study was granted by the Animal Care and Ethics Committee of Charles Sturt University (Approved protocol number A17035).

Results

Number of visits

Both cattle and buffalo visited waterholes more frequently during the drought (2019) compared with the non-drought year (Table 2, Fig. 2a). Cattle also significantly increased their number of visits to waterholes as the dry season progressed, whereas buffalo did not. For pigs, the interaction between year and dry season progression was significant and positive – they visited waterholes more frequently towards the end of the dry season during the drought year (for full results, see Table S2).

Visit duration

The duration of cattle and buffalo visits to waterholes increased during the drought (2019) compared with the

Table 2. Results of most parsimonious GLMMs determined from model selection.

Species	Model component	Factor	Variable co-efficients					
			Number of visits	Duration of visits (min)	Number of individuals	Time spent drinking (min)	Time spent foraging (min)	Time spent wallowing (min)
Pig	Conditional	Year	-0.683	-1.696	-3.145*	-	-0.981	-
		Dry season progression	-0.100	-0.0002	-0.005	-	0.015	-
		Interaction	0.028**	0.069**	0.072***	-	0.060*	-
	Zero-inflation	Dry season progression	-	0.261	0.245	-	0.334	-
Cow	Conditional	Year	1.068***	1.319***	1.565***	3.578**	1.316**	-
		Dry season progression	0.006*	0.018***	0.018***	0.041***	0.012*	-
		Interaction	-	-	-	-0.019	-	-
	Zero-inflation	Dry season progression	-	0.022	0.014	0.115	-	-
Buffalo	Conditional	Year	0.426*	0.401*	0.432*	0.809*	0.388	1.044**
		Dry season progression	-0.001	-0.001	-0.001	0.004	-0.005	-0.001

All results represent values per sampling day sampled for different species (e.g. time spent drinking (minutes)/sampling day). Both conditional and zero-inflation components of models are presented where applicable. Significant values are presented in bold and significance levels are as follows: *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$). Dashes denote factors not included in models. 'Interaction' denotes the interaction between year and dry season progression.

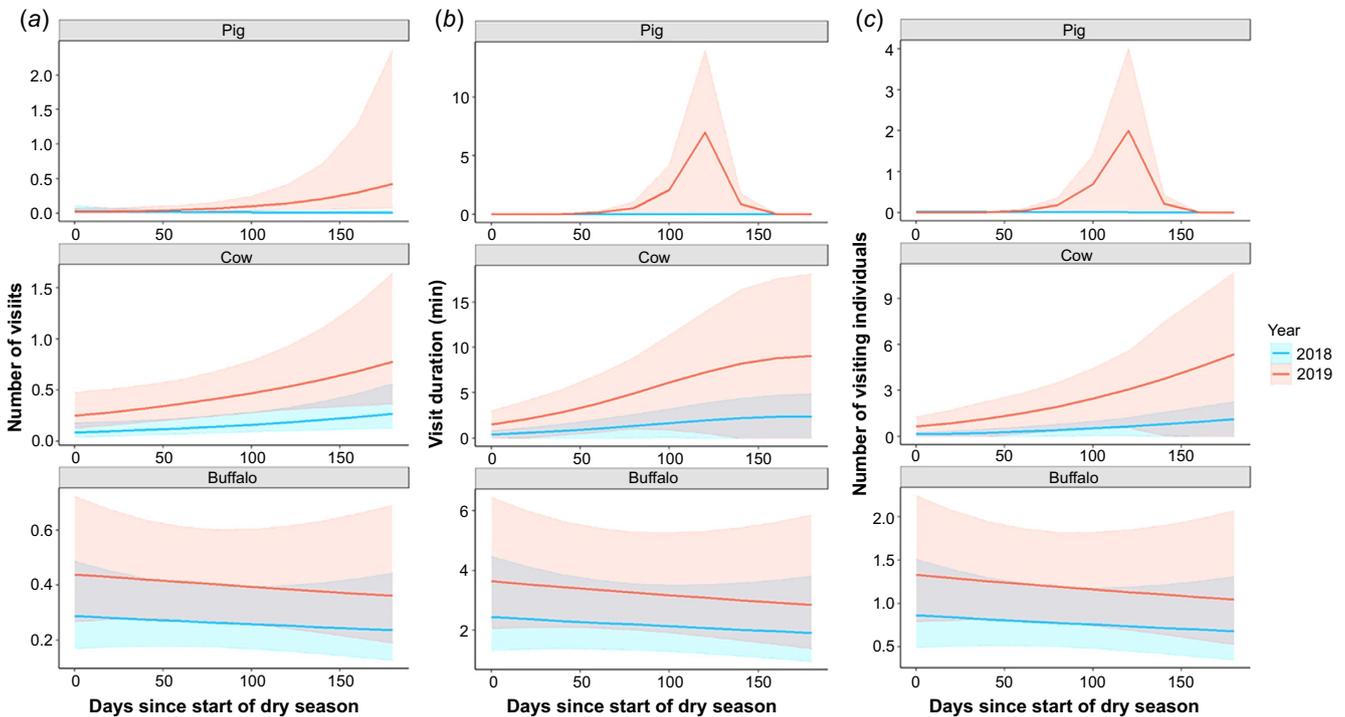


Fig. 2. Effects of year and dry season progression on the waterhole visitation behaviours of feral ungulate species. (a) Number of visits by feral ungulate species per sampling day. (b) Duration of feral ungulate visits per sampling day (min). (c) Number of visiting individuals per sampling day. Solid lines represent predicted mean values and shaded areas represent upper and lower 95% confidence intervals. Colours of lines and shaded areas correspond to different years: blue (2018 – normal rainfall year) and red (2019 – drought year).

non-drought year (Table 2, Fig. 2b). In addition, cattle significantly increased the duration of their visits as the dry

season progressed, whereas buffalo did not. For pigs, the interaction between year and dry season progression was

significant and positive – the durations of their visits increased towards the end of the dry season during the drought year. Dry season progression was included as a zero-inflation factor in the pig model but was not significant (for full results, see Table S3).

Number of individuals visiting

The numbers of cattle and buffalo visiting waterholes increased significantly during the drought year (Table 2, Fig. 2c). Cattle numbers also increased significantly as the dry season progressed, but buffalo numbers were not significantly affected. For pigs, the interaction between year and dry season progression was significant and positive – their numbers

increased towards the end of the dry season during the drought year. Dry season progression was included as a zero-inflation factor in the pig model but was not significant (for full results, see Table S4).

Time spent foraging

Cattle spent significantly more time foraging around waterhole verges during the drought and as the dry season progressed, but buffalo did not alter their behaviour in response to either factor (Table 2, Fig. 3a). For pigs, the interaction between year and dry season progression was significant and positive – they spent more time foraging towards the end of the dry season during the drought year. Dry season

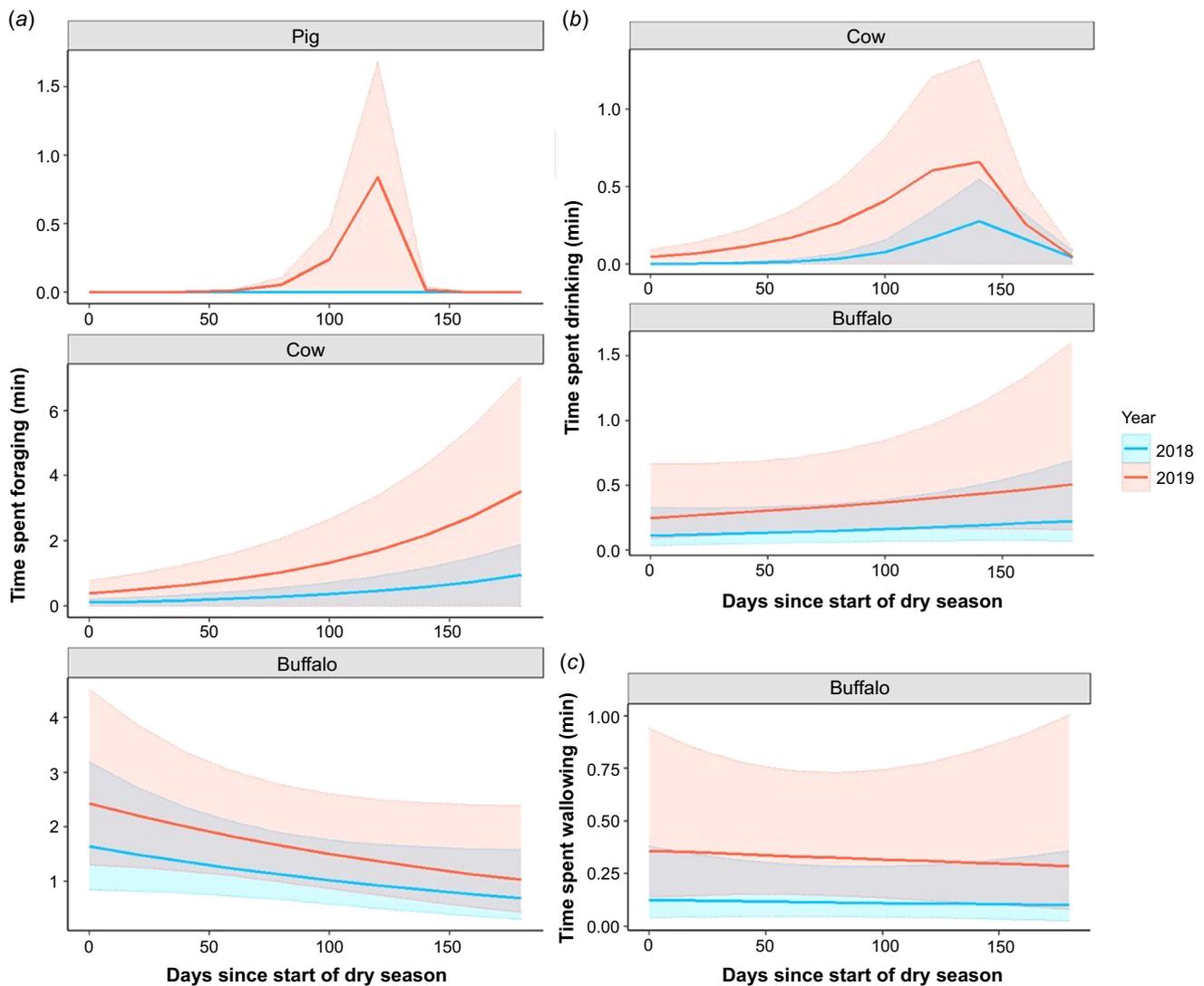


Fig. 3. Effect of year and dry season progression on the waterhole use behaviours of feral ungulates. (a) Time feral ungulate species spent foraging around waterholes per sampling day (min). (b) Time cattle and buffalo spent drinking at waterholes per sampling day (min). (c) Time buffalo spent wallowing per sampling day (min). Solid lines represent predicted mean values and shaded areas represent upper and lower 95% confidence intervals. Colours of lines and shaded areas correspond to different years: blue (2018 – normal rainfall year) and red (2019 – drought year).

progression was included as a zero-inflation factor in the pig model but was not significant (for full results, see Table S5).

Time spent drinking

The time cattle and buffalo spent drinking at waterholes increased significantly during the drought year (Table 2, Fig. 3b). Cattle also spent significantly more time drinking as the dry season progressed, but buffalo did not. Model selection supported the inclusion of an interaction term between year and dry season progression for the cattle model, but this result was not significant (i.e. the time cattle spent drinking at the end of the dry season was not significantly different between years; for full results, see Table S6).

Time spent wallowing

Buffalo spent significantly more time wallowing during the drought compared with the non-drought year (Table 2, Fig. 3c). However, dry season progression had no significant effect on their wallowing behaviour (for full results, see Table S7).

Discussion

Responses to drought

In this study, we found that water scarcity exacerbated feral ungulate use of ephemeral waterholes in Limmen National Park. All ungulates increased their number of visits to waterholes, visited for longer durations and visited in greater numbers during the drought year. We also found that the behaviours ungulates exhibited during visits were significantly affected by drought: cattle and buffalo spent more time drinking, pigs and cattle spent more time foraging and buffalo spent more time wallowing during the drought year. Our findings support the hypothesis of Illius and O'Connor (2000) that seasonal and climactic variability leads to the spatial concentration of ungulates around key resource areas, such as waterholes.

High waterhole use by ungulates can lead to severe defoliation of vegetation communities in a spherical gradient surrounding waterpoints, known as a piosphere (Thrash and Derry 1999; Illius and O'Connor 2000). Our findings suggest that drought may exacerbate ungulate impacts on vegetation communities surrounding savanna waterholes. Piospheres have been shown to have long lasting (>100 years) and possibly irreversible effects on vegetation and soil characteristics in Australian arid areas, even after grazing pressure is removed (Croft et al. 2007). Accordingly, further research defining how feral ungulates affect vegetation communities surrounding Australian savanna waterholes during drought, and how this may impact native fauna communities, is needed. Additionally, studies over longer time periods of fluctuating water availability (>2 years) are needed to verify our findings.

Responses to dry season progression

Dry season progression affected waterhole visitation and behaviour of cattle, pigs and buffalo differently. Cattle were the most responsive to water scarcity: they significantly increased their number of visits, they visited for longer durations and more individuals visited per sampling day as the dry season progressed. They also spent significantly more time drinking and foraging when visiting waterholes as the dry season progressed. Cattle were the most numerous feral ungulates observed during the study (Table 1) and were detected 4.6 and 1.5 times more per sampling day than pigs and buffalo, respectively. The number of cattle we detected across just 10 small waterholes is concerning, because each adult can drink ~40–80 L of water daily depending on sex and body condition (Hunt et al. 2013; Bray et al. 2015). Therefore, increased cattle visitation to savanna waterholes during dry and hot conditions (i.e. drought, end of dry season) may deplete already scarce water resources available to native fauna. In addition, cattle presence may affect patterns of waterhole visitation by native fauna (Mihailou et al. 2022), as has been observed with other feral ungulate species in water limited habitats (e.g. Perry et al. 2015; Hall et al. 2016; Gooch et al. 2017; Brim Box et al. 2019). For example, feral camel presence at waterholes in central Australia reduces the frequency of visits by native dingoes (*Canis lupus dingo*) and birds and impacts their temporal activity patterns (Brim Box et al. 2019).

Pigs only changed their visitation and behaviours at waterholes at the end of the dry season during the drought, when water scarcity was most extreme. They visited waterholes more, for longer periods and in greater numbers, and spent more time foraging at the end of the dry season during the drought than at any other times. This suggests that pigs are more reliant on larger waterbodies (e.g. lagoons, swamps and billabongs) than cattle and buffalo – they provide better foraging opportunities for pigs than the small, ephemeral waterholes studied here (Ridpath 1991). Lower surface water availability during the drought may have led pigs to move into less preferred habitat as the year progressed and many of the larger billabongs in the study area prematurely dried out. This also explains why pigs spent more time foraging around our 20 focal waterholes as the drought progressed, because larger waterbodies may have dried earlier than in the previous year (i.e. did not fill to capacity), forcing pigs to find alternative foraging sites.

Buffalo only changed their waterhole visitation and use in response to drought, and not dry season progression. This may be because buffalo evolved in hot, humid wetland habitats (Ridpath 1991) where evaporative cooling from sweating is impaired. Buffalo have highly vascularised skin and rely on frequent wallowing to keep cool (Tulloch and Litchfield 1981; Ridpath 1991), and their water requirements appear to be high year-round. This may explain why their visitation and use of waterholes was relatively consistent across the dry

season. By contrast, drought may have had greater impacts on buffalo behaviour because reduced surface water availability would have increased their dependence on those waterholes still containing water (e.g. our study waterholes). Unlike cattle, buffalo did not spend more time grazing riparian vegetation on waterhole verges with increasing water scarcity. This may be explained by the wider dietary niche of buffalo, whose diet consists of <30% grasses (Bowman *et al.* 2010), compared with ~50% grasses for cattle (Reid *et al.* 2020a). Unlike cattle, buffalo may selectively browse more woody vegetation with higher moisture content than desiccated grasses in the wider savanna as water scarcity increases (Reid *et al.* 2020a), limiting their reliance on riparian food resources.

Broader implications of feral ungulate aggregations at ephemeral waterholes

Feral ungulates have extensive impacts on Australian savanna habitats and cause substantial detrimental flow-on effects for native wildlife, particularly the destruction or degradation of primary habitat (Mihailou and Massaro 2021). Our study indicates that water scarcity increases ungulate presence and activity at savanna waterholes, and that these areas are particularly vulnerable to ungulate disturbance. Negative flow-on effects of this disturbance for wildlife are potentially worsened at critical times, when water sources are limited. In a related study, we found that waterhole visitation by native macropods (Family Macropodidae, including kangaroos and wallabies) increased during periods of water scarcity, but their activity rapidly declined as cattle visitation peaked at the end of the dry season (Mihailou *et al.* 2022). This finding that feral ungulate presence at waterholes may deter visitation by native fauna is supported by other studies in Australia (cattle: Mihailou *et al.* 2022; Reid *et al.* 2020a, camels: Brim Box *et al.* 2019) and North America (horses: Ostermann-Kelm *et al.* 2008; Hall *et al.* 2018). Vulnerable fauna already suffering declines in Australia's northern savannas, such as small mammals (Woinarski *et al.* 2011; Woinarski 2015) and granivorous birds (Franklin 1999; Franklin *et al.* 2005), may also be negatively affected by ungulate disturbance around waterholes during water scarcity events. Ungulate damage to understorey vegetation surrounding waterholes may be particularly detrimental for small species with frequent drinking requirements (e.g. granivores), because habitat simplification around watering points increases vulnerability of these species to predators, such as feral cats (Fisher *et al.* 2014; McGregor *et al.* 2014; Stobo-Wilson *et al.* 2020).

Our findings suggest that management and control programs for feral ungulates in northern savannas may benefit from targeting different species under different water scarcity conditions. To make the most out of aerial and ground-based control operations, cattle should be targeted around waterholes in the late dry season, irrespective of annual rainfall, because this is when their activity is most concentrated around waterpoints. By contrast, pigs are best targeted (at least

around ephemeral water sources in savanna) during extreme water scarcity events (i.e. late dry season during drought years). Because buffalo utilise waterholes consistently across the dry season, land managers should instead focus control programs during years of low rainfall.

Climate change is predicted to reduce surface water availability in northern Australia (Dai *et al.* 2018; NESP Earth Systems and Climate Change Hub 2020), so increasing feral ungulate use of waterholes may exacerbate stress on native flora and fauna communities. This could lead to the loss of resilience of ecosystems to recover from severe water scarcity events and potentially lead to irreversible damage to sensitive habitats. Therefore, more research is warranted to assess how different densities of feral ungulates impact native species. Furthermore, the social and economic value of ungulates complicate conservation efforts in the region (Robinson *et al.* 2005; Spear and Chown 2009; Sloane *et al.* 2021). Many local stakeholders view feral ungulates as a source of income (e.g. tourism operators and safari hunters – buffalo), or as a self-sustaining food source (e.g. recreational hunters – pigs and buffalo; some traditional Aboriginal landowners – cattle and buffalo), rather than a threat to native ecosystems (Skeat *et al.* 1996; Robinson *et al.* 2005; Ens *et al.* 2016). Further research is needed to assess the impacts of feral ungulate populations on native flora and fauna in northern Australia, especially in national parks and conservation areas intended to provide protection for native species.

Supplementary material

Supplementary material is available [online](#).

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Data availability. All data analysed during this study are available in the supplementary material.

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Code availability. The modelling used for the statistical analysis is described in detail in the text and supplementary material, including the 'R' packages used.

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