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Natural or anthropogenic disturbances (stimuli that trigger a behavioural response from animals) can have direct consequences on fitness and population trends. This study aimed at investigating the relative influence of three types of disturbances (mammalian herbivores, terrestrial threats from ground predators and aerial threats) on the responses by waterbirds at waterpans in Hwange National Park (HNP, Zimbabwe) and adjacent land uses. Thirteen waterpans were monitored during daylight hours between years 2015 and 2017 and responses of waterbirds to the three forms of disturbances were recorded. Logistic regressions revealed that the likelihood of responding was highest after terrestrial threats; with individuals/groups that were initially engaged in non-feeding activities that allowed vigilance, responding the most. Wildfowl species spent significantly longer time flying (compared to waders and generalists), more so in communal areas (CAs) than HNP, and after terrestrial threats compared to aerial threats and herbivore disturbances. We did not find any differences in probability of responding across land uses probably because there is less human disturbance in HNP, but predation risk is high. Further, even though there are less terrestrial predators in CAs, domestic dogs may be maintaining the stimuli. We conclude that terrestrial threats are least tolerated, with species most susceptible to human predation (i.e. wildfowl) losing more time avoiding them. Interestingly, only acute aerial threats induced departure from waterpans. Our findings have a direct implication for waterbird conservation as herbivore and human density in this area are currently increasing.

Key words: disturbances, escape, Hwange National Park, protected areas

Wetlands face various forms of disturbances because they are focal habitats for humans and wildlife; with activities such as resource extraction and tourism; taxa reliant on them have not been spared. Wildlife populations can be impacted by disturbances especially on focal habitats such as wetlands (Schüttler et al. 2009, Rajashekara and Venkatesha 2017). Disturbances negatively affect several aspects of wildlife including foraging behaviour (Guillemain and Fritz 2002), reproduction (Goering and Cherry 1978, Barr 2017) and spatiotemporal occupation of habitats (Duriez et al. 2005). Waterbirds, being wetland species with particular behaviours and migration patterns (Boere et al. 2006), have a large conservation attention on them (Ma et al. 2009) and are supported by a growing interest of bird watchers around the globe (Herget et al. 2016). They can therefore be good biological models to study the effects of disturbances on wildlife species. Conservationists may be interested in characterizing the various sources of disturbances to waterbirds and evaluate their sensitivity to them. Various levels of sensitivity have direct consequences on individual fitness (Livezey et al. 2016, Tablado and Jenni 2017).

With human population expansion, wetlands are being increasingly used (England et al. 2015) thus disturbances to waterbirds are likely to become more acute. For example, wetlands in agricultural areas close to large protected areas (PAs) are mainly used by humans and livestock where noise, swimming, fishing, hunting, gardening and livestock drinking are strong disturbance stimuli (Gill et al. 1996, Ian 2000, Delany et al. 2007, Tablado and Jenni 2017) in addition to terrestrial carnivores and raptors (Schüttler et al. 2009, MacLeod et al. 2014). Anthropogenic activities around waterpans may temporarily force waterbirds to leave nest areas exposing the eggs/chicks to predation and harsh weather conditions (Wang et al. 2015). In PAs, waterbirds

are disturbed by vehicles, birdwatchers, researchers, micro-aircrafts, natural predators and also other wildlife species as they compete for resources (Raeside et al. 2007, Barr 2017, Coetzer and Bouwman 2017). All these forms of disturbances and threats are known to shift waterbird behaviour (Gill et al. 1996, Blumstein 2006, England et al. 2015). While the understanding of disturbances in agricultural areas can help in evaluating human impacts on waterbirds, it is also important to explore mostly natural processes in PAs. Also, tourists have high expectations to experience nature in its most wild form in PAs because of reduced anthropogenic disturbances when compared to areas outside (Ian 2000).

With their sensitivity to disturbances waterbirds may avoid sites with high disturbances (Borgmann 2011, Moore et al. 2016), modify their spatiotemporal distribution (Duriez et al. 2005) or habituate (Ian 2000). Behaviourally, they may show no visible reaction; become more attentive (head up while scanning the environment or focus on the disturbance agent); continue their original activity while increasing scanning rate; walk, run or swim away; fly away for a certain period and return in a short while; or fly away without returning that day (Fernández-Juricic and Tellería 2000, Blumstein et al. 2003, Fernández-Juricic et al. 2005). Excessive and persistent disturbances may lead to effective habitat loss by forcing waterbirds to abandon otherwise suitable feeding areas (England et al. 2015). However, for the species that can persist in high disturbance sites, foraging bouts have been observed to be reduced (Guillemain and Fritz 2002). Although some researchers have shown a clear link between the levels of disturbance to species and the size of their local populations (Schulz and Stock 1993), in some cases disturbances act in a more subtle way, by reducing access to resources such as food supplies or nesting sites (Gayet et al. 2011). Disturbances are also known to affect reproductive success in some species; for example in families of gulls, terns and skimmers (Barr 2017). Increased disturbance frequency also triggered nest abandonment in black-crowned night herons *Nycticorax nycticorax* in Canada (Tremblay and Ellison 1979), but reproductive success was not affected in the tricolored heron *Egretta tricolor* in Florida (Frederick and Collopy 1989).

Based on the group vigilance hypothesis (Roberts 1996, Blumstein 2006, Beauchamp 2008), large groups of waterbirds may be able to detect threats earlier due to the 'many eyes' compared to small ones. Also, the 'dilution effect' hypothesis proposes that individuals' probability of being preyed upon in a large group is small hence they can be less vigilant and feed more (Foster and Treherne 1981, Lima 1996). However, the benefits of the dilution effect may be species or context specific. In several waterbirds species that can gather in large numbers, individuals may tend to fly away when a potential threat is detected far from them by other members of the group. Individual flight behaviour may also be triggered by a disturbance response coming from a zone outside their visual control (McFadden et al. 2017). Models relating energetic gains versus mortality risks in animals suggest that risk-taking would be minimized in large species compared to small ones (Grand 1999) and that the energy-demanding escape attempts (e.g. flying) should occur when body reserves allow it (Beale and Monaghan 2004). Waterbirds feeding in dense vegetation may make fewer responses to potential disturbances because they fail to detect them or

they can quickly take refuge if the threat gets closer (Whittingham and Evans 2004). Individuals feeding on rich habitat patches may make fewer escape responses from threats to maximize food acquisition (Lim 1999). Also, when disturbed, breeding waterbirds may not frequently leave sites with their nests to protect their eggs or chicks (Palestis 2005).

In semi-arid regions of Africa, several PA management goals have focused on supplementing surface water to support large mammal populations (Owen-Smith 1996) mostly targeted by increasing tourism (Smit et al. 2007). In most of these PAs, the populations of large and megaherbivores increased, particularly African elephant *Loxodonta africana* whose densities rank high in southern Africa (Chamaillé-Jammes et al. 2007). Such herbivores have been found to alter access to water by other wildlife species (Valeix et al. 2009), and it may be possible that their presence and noise may alter waterbirds' behaviour especially during the dry season when surface water is a limiting resource. Herbivore congregations at water sources may result in prolonged disturbances and in this regard waterbirds may habituate (Ian 2000) or switch to other sites if food availability is not a limiting factor in the landscape (Wen et al. 2016). However, other waterbird guilds are able to swim into the waterpan interior (e.g. wildfowl) and may tolerate herbivore disturbances compared to those that cannot swim (e.g. waders).

In this study, we aimed at investigating the relative influence of various forms of disturbances (mammalian herbivores, potential terrestrial ground predators, and aerial threats) on the responses by waterbirds at waterpans in Hwange National Park (HNP, northwest Zimbabwe) and adjacent communal areas (CAs), dominated by subsistence agriculture. This area is very important for waterbird breeding in the country (Godfrey 1992) and also hosts a wide variety of raptor species (Hustler and Howells 1990), large herds of herbivores (Chamaille-Jammes et al. 2007) and various levels of access by humans (Guerbois et al. 2013). Our study describes the disturbances and associated responses of birds, which will improve our understanding of the risks that influence the use of wetlands by waterbird communities and the implications for conservation planning.

We defined a disturbance as any stimulus (natural or anthropogenic) that triggers a behavioural response from waterbirds (e.g. people, wild and domestic herbivores, carnivorous mammal and reptile species, raptors, bird alarm calls and vehicles), a modification from Van de Voorde et al. (2015). We expected a waterbird size effect (H1) in which smaller species would respond more by escaping from raptors as birds of prey can easily kill and lift them compared to larger ones. Also, we thought that large species, when disturbed, would be conservative in opting to fly away as this is more energetically taxing compared to smaller ones (MacLeod et al. 2014). The group vigilance effect (H2) was hypothesised to influence reactions in which large waterbird groups would be able to detect and consequently respond more to potential disturbance agents compared to smaller ones. Since people in CAs may practice subsistence hunting on waterfowl species (Bloom et al. 2013), we expected an anthropogenic disturbances effect (H3) in which these waterfowl, when disturbed by humans, are more likely to react by flying away as compared to other guilds; and we also expected more escape responses from waterbirds in CAs compared to those in PAs. A habitat effect (H4) was also hypoth-

esised in which birds occupying sites with more vegetation (emergent and shore line cover) would have less responses compared to those on less vegetated waterpans. Lastly, we expected to detect a seasonal effect (H5) in which the probability of waterbirds making escape responses to disturbances during the wet season is low compared to the dry season. This could be because most waterpans are flooded during the wet season and hence offer safer habitats for breeding birds from terrestrial predators that may not easily target.

Methods

Study area

The study was conducted in two protected areas (Main Camp area of Hwange National Park (HNP) and Sikumi Forestry Area (FSA)) and the adjacent communal areas (CAs) as illustrated in Fig. 1. These areas are part of the southern Kavango Zambezi Trans-frontier Conservation Area (KAZA TFCA). The Main Camp area covers ca 1500 km², SFA ca 544 km² and the CAs are under Tsholotsho and Hwange districts. The area receives about 600 mm of rainfall, falling between November and May (Chamaillé-Jammes et al. 2007) and is characterised by poorly drained Kalahari sands and patches of clay that form a system of more than 40 000 mostly shallow seasonal waterpans in HNP and surrounding areas (Childes and Mundy 2001). In addition to the seasonal waterpans, HNP and SFA have boreholes to supplement water to wildlife during the dry season, while in CAs some dams were constructed. For sites that retained water between the peak dry seasons of 2014–2016, the surface area averages for HNP, SFA and CAs waterpans were 1337, 1200 and 4085 m² respectively.

The waterpans are utilised by various waterbird species including waterfowl (e.g. ducks, geese and grebes), carnivores and piscivores (e.g. storks, egrets, herons, terns and kingfishers) and waders (e.g. sandpipers and lapwings). Since waterpans are small in size (Goudie and Wells 1995), numbers of waterbirds hosted on them are usually small as well, making observational studies easier when compared to large water bodies such as dams, floodplains and coastal areas. Waterpans are accessed by several mammalian species, chiefly the African elephant and African buffalo *Syncerus caffer* mostly in the PAs during the dry season, while those in CAs are also used by local cattle breeds *Bos* species (usually accompanied by cattle herders). Waterpans are also visited by a wide array of wild and domestic carnivorous species that potentially prey on waterbirds or their eggs.

Waterpan selection and observations

We purposively selected 13 waterpans that retained water throughout the year in the study area. We selected pumped and unpumped waterpans in HNP (6 and 2 respectively), SFA (1 and 2 respectively) and CAs (1 unpumped waterpan and 1 dam). Our waterpans were at least 5 km from each other to reduce risk of pseudo-replication when recording waterbird behaviour. Between July 2015 and March 2017 we monitored the activities of waterbirds at each waterpan during the day from 06:00 h to 18:00 h. Each site was visited at least twice in the wet season (between December and April) and also twice in the dry season (May–November), a total of 724 h of monitoring. Each time the monitoring team consisted of four people, one recorder and three observers (with 10×50 magnification binoculars) to cover the whole waterpan. This team size was sufficient in monitoring these small wetland systems. As it was unavoidable to cause some disturbances to waterbirds upon our arrival at a waterpan, we waited for at least 10 min to allow the waterbirds to resume their normal behaviours. We then noted all waterbirds present and their relative positions to the waterpan edge. We constantly scanned (after every minute) the waterpan area to note any changes as waterbirds arrived/left the waterpan area or when they changed their positions. We also constantly scanned (at one minute intervals) the sky for any predatory birds (or any other large bird that could possibly disturb waterbirds) that flew by the waterpan area, hereinafter a flyover. Upon seeing the flyover, we immediately recorded the original activity engaged by all the different waterbird species; any behavioural changes in response to the flyover danger (see the guide in Table 1); and any associated changes in relative position to water. However, in the cases that waterbirds did not show any immediate response after the flyover, we continued to monitor their activity for another one minute before concluding that there was no response. Likewise, we also recorded the position and activity changes when other forms of disturbances occurred (e.g. from carnivores, large herbivores, people and other noises). We also recorded the numbers of individuals that responded to each disturbance as it was possible to have multiple responses from one disturbance. The monitoring team took 30 min break between 10:00–10:30 h and 13:00–13:30 h to feed and rest. We believe that these intensive scans allowed us to record the waterbird responses timeously.

For the waterbirds that responded by flying away, we used a stopwatch to record the time taken (in seconds) before they returned to the waterpan (we considered individuals to have completely left the waterpan if they did not return within 2 h, a time in which local feeding conditions e.g. day time temperature and composition of herbivores visiting the waterpan is likely to have changed). We used group composition (e.g. numbers, sex and ages of individuals where possible) and any notable individuals (with distinct breeding plumage, broken limbs, rings etc.) to identify returning groups or individuals. With our experience of the study area and the predictable movements of species after disturbances, we could identify returning birds with a high degree of certainty. Disturbances triggered by our monitoring team were minimised as we observed the waterbirds from established observation platforms, or hiding places located at least 100 m from the waterpan. However, when we noted that our team had triggered the response, we recorded them accordingly.

Categorisations of species, their activities, source of disturbances, time and waterpans

All waterbirds recorded during the study were grouped according to their taxonomy, size and feeding guilds or their nearest group as generalist medium and large (herons, ibises, storks and egrets), large wildfowl (Egyptian geese *Alopochen aegyptiaca*, knob-billed duck *Sarkidiornis melanotos* and

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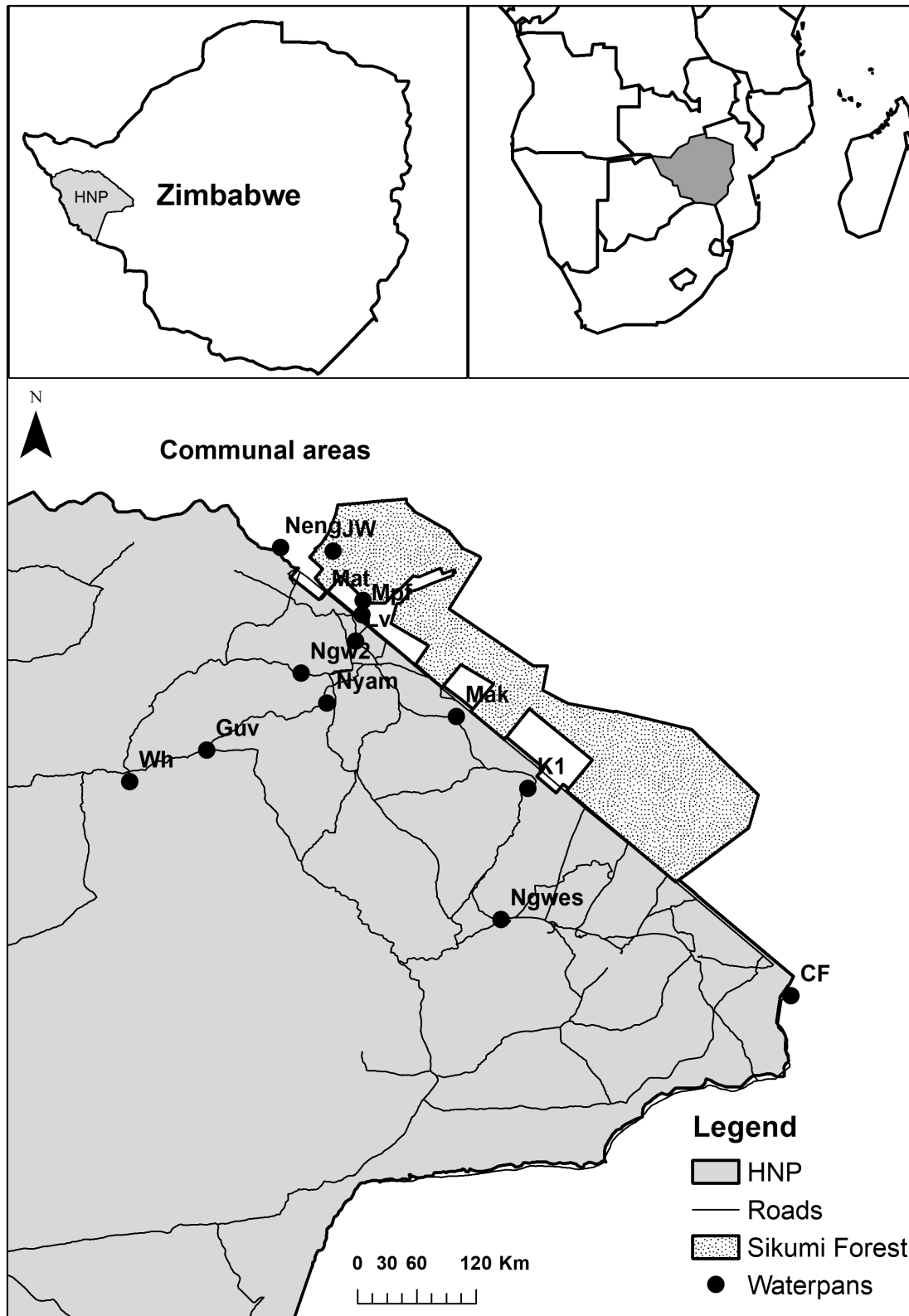
Figure 1. Distribution of waterpans across the three land-use types. The abbreviated waterpan names are defined in Table 4.

spur-winged geese *Plectropterus gambensis*), small wildfowl (teal, grebes, moorhens and white-faced duck *Dendrocygna viduata*) and waders (lapwings, sandpipers, stilts and jacanas) as shown in Table 2. We categorised original species activity, distinguishing if activities could allow for some form of vigilance, e.g. swimming with head up, or grazing in short grass (Guillemain et al. 2001); or preventing any vigilance, e.g. underwater feeding, sleeping with head under wings (Thomas 1982, Guillemain et al. 2007) and other responses (continued in non-vigilant activities or became more alert

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Table 1. Description of behaviours used to categorise the original activity and responses of waterbirds to disturbances. In the original activity category, F.V = Feeding allowing vigilance, F.nV = feeding not allowing vigilance, nF.V = non-feeding allowing vigilance, nF.nV = non-feeding not allowing vigilance; and in the response categories, Vig = vigilance, noRes = no response and Esc = escape.

Code	Code description	Original activity category				Response category		
		F.V	F.nV	nF.V	nF.nV	Vig	noRes	Esc
B	Filter feeding, only bill underwater	✓					✓	
H	Feeding with head underwater		✓				✓	
N	Neck underwater		✓				✓	
U	Feeding with body upside down		✓				✓	
V	Vigilant			✓		✓		
W	Walking			✓				✓
PR	Preening				✓		✓	
PS	Pruning grass seeds	✓					✓	
R	Resting (head up)			✓			✓	
RS	Roosting (with head under wing)				✓		✓	
S	Swimming			✓				✓
P	Picking from the surface	✓					✓	
I	Immobile			✓		✓		
SH	Swimming with head underwater		✓				✓	
SB	Swimming with only bill underwater	✓					✓	
SV	Swimming but vigilant			✓				✓
SP	Swimming but picking food items	✓					✓	
F	Flying				✓			✓
D	Drinking water	✓					✓	
DI	Diving		✓					✓

and escaping from the danger) as shown in Table 1. We categorised the type of disturbance as aerial (raptors and any flying birds that initiated a response), terrestrial (including wild carnivorous mammal species that potentially eat waterbirds, crocodiles *Crocodylus niloticus*, people, domestic dogs *Canis familiaris* and noise from vehicles) and herbivores (wild herbivores and livestock). We categorised the time of day as early morning (06:00–09:00 h), mid-morning (09:01–12:00 h), early afternoon (12:01–15:00 h) and late afternoon (15:01–18:00 h). Observations done between December and April were categorised as wet season and the rest as dry season.

As habitat type may influence responses by waterbirds, we used vegetation characteristics and waterpan size data collected in July 2014 and January 2015 as part of a broader survey of waterpans in our study area. We conducted assess-

Table 2. Waterbird species (alongside allocated guilds) and frequency of disturbances recorded from 2015 to 2017 in and around Hwange National Park.

Guild	Species local name	Scientific name	Type of disturbance		
			Aerial	Terrestrial	Herbivores
Generalist	Abdim's stork	*Ciconia abdimii*	15	1	3
	African darter	*Anhinga rufa*	1	0	1
	Black stork	*Ciconia nigra*	0	0	1
	Cattle egret	*Bubulcus ibis*	13	3	5
	Crowned crane	*Balearica regulorum*	10	3	6
	Grey heron	*Ardea cinerea*	19	4	5
	Hamerkop	*Scopus umbretta*	2	0	0
	Squacco heron	*Ardeola ralloides*	3	1	0
	White stork	*Ciconia ciconia*	1	1	0
	White-breasted cormorant	*Phalacrocorax carbo*	4	0	0
	Woolly-necked stork	*Ciconia episcopus*	9	4	7
Large wildfowl	Egyptian geese	*Alopochen aegyptiaca*	106	30	51
	Knob-billed duck	*Sarkidiornis melanotos*	25	7	7
	Spur-winged geese	*Plectropterus gambensis*	3	0	0
Small wildfowl	Common moorhen	*Gallinula chloropus*	1	1	0
	Hottentot teal	*Spattula hottentota*	28	0	2
	Lesser moorhen	*Gallinula angulata*	6	0	0
	Little grebe	*Tachybaptus ruficollis*	30	3	1
	Maccoa duck	*Oxyura maccoa*	1	0	2
	Red-billed teal	*Anas erythrorhyncha*	102	38	42
	White-faced duck	*Dendrocygna viduata*	32	15	11
Waders	African jacana	*Actophilornis africanus*	11	6	0
	Blacksmith lapwing	*Vanellus armatus*	240	30	43
	Black-winged stilt	*Himantopus himantopus*	29	1	4
	Common sandpiper	*Actitis hypoleucos*	11	0	1

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ments of the surrounding vegetation at each waterpan by establishing 30 m long transects along the cardinal and intercardinal directions from the water edge. On each transect we placed a 1-m^2 quadrat about 10 cm from the water's edge and recorded the grass cover (visual estimate) and representative grass height (using a standard calibrated wooden ruler). We repeated these measurements at 10, 20 and 30 m away from the water's edge for all the eight transects, which is a modification from Trash (2000). We also used a range-finder to measure the distance from the water's edge to the nearest tree line (bush edge) for each transect direction. Surface area and perimeter of each waterpan were calculated by walking right round its shores while marking our tracks on a handheld GPS. Visual estimations of the percentage of the waterpan covered by emergent and submerged aquatic vegetation approximately 3m from the shore were made (Raeside et al. 2007). The vegetation and waterpan size variables were used to distinguish four groups of waterpans using a Euclidean distance based cluster analysis to produce groups described in Table 3.

Analysis

We excluded from our analysis observations where waterbirds responded to anything that we did not see and those when our monitoring team had initiated the response (these comprised 2.2% of the original dataset). We wanted to specifically test for a group vigilance effect (H2) but also tested for a possible confounding effect with the waterbird guilds, as group size may vary widely among waterbird species and guilds. Although we noted that group sizes were significantly different across waterbird guild (using one way ANOVA), the average group sizes fell within the same order of magnitude (between 12 and 21), and thus any effect of group size was unlikely to be explained uniquely by our waterbird guild. We therefore used a set of independent variables (land use, season, waterbird guild, group size, original activity, disturbance type, waterpan cluster group, waterpan identity and time of day) that we thought could influence the probability of reacting to disturbance and length of time spent flying after a disturbance. Accordingly, we used a mixed-effects logistic regression model in which the response variable was treated as 'no response' (when waterbirds showed non-vigilance behaviour) or 'response' (vigilant and/or an escape of some form). The site identity was treated as a random variable, and also in all subsequent mixed-effects models used in this study. Since various response types have

different energetic requirements and associated costs in lost feeding or resting opportunities, we created two subsets of our main data to explicitly test for factors associated with each reaction category. We termed the first 'mild', which excluded observations with escape responses (i.e. restricted to vigilance); and the second 'extreme', included individuals that swam/walked/ran or flew away. We used our set of independent variables to investigate the factors that resulted in waterbirds showing 'mild' responses (i.e. becoming vigilant without moving away from their original position) and 'extreme' responses (i.e. when waterbirds engaged in escaping activities) using mixed-effects logistic regressions.

We wanted to further investigate which disturbance would trigger flying, as it is the most energetically costly response. We thus also performed a mixed-effects logistic regression (with our set of independent variables) to determine factors that caused waterbirds to respond by flying away as opposed to remaining at the waterpan. To assess the consequences of this extreme response, we also distinguished waterbirds that responded by flying away and then returned to the waterpan, as opposed to those that did not return in 2 h. For the former, we used our set of independent variables to investigate factors that affected the time spent flying (in seconds) using a generalised mixed-effects model. For the latter, we also used a mixed effect logistic regression to determine the probability of flying away and not returning (given its guild and disturbance type). As there is a conservation issue related to anthropogenic disturbance, not only outside PAs but also mildly inside, we specifically tested for the anthropogenic disturbance effect for terrestrial threats (with the re-categorised disturbance source – people/not people), and we used a generalised mixed-effects model on our set of independent variables to investigate the relative influence of anthropogenic disturbance (across the guilds) on the probability of flying, and time spent flying. Our analysis for time spent flying only included comparisons between HNP and the CA since we did not have enough records for SFA.

For all our analyses, we included single variables and two-way interactions (between waterbird guild and disturbance type, original activity, season, land use and waterpan cluster) according to our main predictions in the models. We used the 'dredge' function in the MuMln package (Barton 2011) to select candidate models where delta AIC was less than 2 and then considered the best model from the list as the one with the lowest Akaike information criteria (Burnham and Anderson 2002). All analysis was done in the R package for statistical computing (<www.r-project.org>).

Table 3. Characteristics of waterpan clusters as distinguished through cluster analysis on waterpans in the study area.

Group	Wet season description	Dry season description
1	Small waterpans (mean 2120 m^2 in area), with shores mostly bare, little submerged and emergent vegetation, large distance to tree line.	Shores very bare, with submerged and emergent vegetation almost non-existent.
2	Medium sized pans (mean 6487 m^2 in area), close to half of waterpan area covered in submerged and emergent vegetation, shoreline is mostly vegetated.	Half of shorelines open up, almost all emergent vegetation lost but retain most submerged vegetation, only half of their water capacity lost.
3	Large waterpans (mean 23 235 m^2 in area), about ¾ of shoreline vegetated, high emergent vegetation and short distances to tree line.	Short grasses around pans, emergent vegetation decreases drastically but submerged vegetation higher than wet season.
4	Medium sized pans (mean 6934 m^2 in area), with about 30% of shoreline bare, with low submerged and emergent vegetation.	Very sparse shoreline vegetation to almost bare, submerged vegetation almost non-existent, only half of their water capacity lost.

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Results

We recorded a total of 1042 responses across 25 species of waterbirds (Table 2), with records in which birds were initially engaged in non-feeding allowing vigilance being 53.8%, feeding allowing vigilance (22.6%), non-feeding not allowing vigilance (21%) and feeding not allowing vigilance (2.6%). A summary of recorded waterbird guild group size and range across the three areas surveyed is presented in Table 4. There were significant differences in the group sizes of the waterbird guilds ($F = 17.642$, $df = 3$, $p < 0.0001$) with mean group sizes ($\pm$ standard deviation) for waders, generalists, large and small wildfowl being 19.1 ± 15.6, 12.1 ± 14.5, 17.8 ± 17.3 and 23.6 ± 15.6 respectively, mostly due to the difference between generalists and small wildfowl group sizes. The majority of observations were made at waterpans inside the PAs (84.4%) while CAs constituted 15.6%. Waders, small wildfowl, large wildfowl and generalists constituted 36.1, 34, 18.2 and 11.7% respectively of the total observations. Most of the waterpans inside HNP overall had more aerial disturbances on them compared to the rest (Table 5). Humans and domestic dogs constituted 58.1% of all the terrestrial disturbances recorded (86 out of the 143 cases).

The probability of responding to any disturbance

The best model describing the probabilities of overall responses (i.e. response or no response) only retained the single effects of waterbird original activity, guild and the type of disturbances. Waterbirds were more likely to respond if they were engaged in non-feeding allowing vigilance activities before the disturbance when compared to the rest of the states (Fig. 2a, Supplementary material Appendix 1). Small wildfowl were least likely to respond (Fig. 2b) when compared to the other guilds. Terrestrial disturbances had greater chances of stimulating responses compared to herbivores and aerial disturbances (Fig. 2c).

Probability of mild, extreme and escape responses after a disturbance

The single effects of waterbird original activity, guild and the type of disturbances constituted the best model explaining mild responses (probability of responding by vigilant activities). Waterbirds were likely to respond using mild behaviours if they were engaged in non-feeding allowing vigilance activities prior to the disturbance (Fig. 2d) compared to other activities. Small wildfowl were also less likely to respond with mild responses (Fig. 2e) when compared to the rest of the guilds. Terrestrial disturbances were significantly more likely

to stimulate mild responses (Fig. 2f) compared to aerial and herbivores disturbances.

For extreme responses, waterbirds were most likely to escape if they were engaged in non-feeding allowing vigilance activities prior to the disturbance but least likely in feeding allowing vigilance states (Fig. 2g, Supplementary material Appendix 1). The likelihood of escaping was greater in waders and generalists when compared to small and large wildfowl (Fig. 2h); and when they were disturbed by terrestrial threats (in comparison to herbivores and aerial ones, Fig. 2i). We did not detect any significant effects of land use, seasonality and habitat on the probability of waterbirds to react to disturbances in our study area.

Time spent flying

The best model explaining variation in time spent flying included the interacting effects of guild with land use and disturbance type. Overall, terrestrial and aerial threats stimulated significantly longer periods (35.8 (29.6–43.3 CI) and 27.0 (22.6–32.2 CI) seconds respectively) when compared to herbivore threats (13.7 (11.1–16.8 CI) seconds). Across these disturbance types, large and small wildfowl took significantly more time to return to waterpans after a disturbance when compared to waders and generalist species (Fig. 3a, Supplementary material Appendix 2). On average, waterbirds took significantly longer periods to return to waterpans in the CAs (30.7 s (22.2–42.4 CI)) when compared to those in HNP (18.2 s (15.6–21.0 CI)). However, in both land uses (CAs and HNP), large and small wildfowl took significantly longer periods to return to waterpans after disturbances when compared waders and generalist species (Fig. 3b).

Overall, disturbances by people elicited longer periods of flying compared to those stimulated by non-human sources. Time taken flying after humans and non-human disturbance sources was not different in generalist species; waders and small wildfowl had significantly longer flight periods after disturbances by humans compared to non-human sources (Fig. 4a, Supplementary material Appendix 2). Waterbirds took significantly less time to return to waterpans inside HNP (8.1 (5.7–11.4 CI) s) compared to CAs (20.4 (14.7–28.4 CI) s) as illustrated in Fig. 4b.

The probability of flying away from a disturbance and not return

For the majority of instances (94.5%, 398 cases out of 421 cases of fly-aways), waterbirds generally returned to the waterpans. For most cases when birds did not return to the waterpan (82.6%, 19 out of 23) the disturbance type was

Table 4. The mean waterbird guild size ($\pm$ standard deviation) and ranges of across the three areas in and around Hwange National Park. The dash (–) denotes cases where no observation was made.

	Area					
	CA		SFA		NP	
Waterbird guild	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Generalist	14.6 ± 11.6	2–47	–	–	14.4 ± 12.2	2–49
Large wildfowl	24.1 ± 16.3	2–45	–	–	17.6 ± 17.3	1–47
Small wildfowl	22.6 ± 14.9	2–49	29.4 ± 25.5	1–48	24 ± 15.8	1–57
Waders	17.5 ± 11.7	3–41	–	–	19.1 ± 15.7	2–57

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Table 5. Summary of waterbird disturbances at waterpans in and around Hwange National Park during the study period. The asterix (*) on waterpans denotes those that are pumped. The waterpan names in brackets refer to those used in Fig. 1.

Area	Waterpan	Waterpan group	Daily mean disturbances (±SE)		
			Aerial	Terrestrial	Herbivores
CA	Nengasha (Neng)	3	14.6 ± 10.5	5.5 ± 6.2	20.7 ± 6.8
	Campfire (CF)	3	1.2 ± 0.8	1 ± 1.2	12.1 ± 7.8
SFA	Jwapi (Jw)	1	3 ± 1.5	1.8 ± 0.2	0
	Mataka (Mat)	4	3 ± 2.3	0	2 ± 0.7
	Mpofu (Mpf)*	2	3 ± 2.7	0	0
HNP	Guvalala (Guv)*	2	35.1 ± 23.9	3.1 ± 3.2	8.1 ± 6.5
	Kennedy 1 (K1)*	1	6.8 ± 6.1	4.1 ± 3.4	5.1 ± 1.9
	Livingi (Lv)*	4	1.0 ± 0.8	0	0
	Makwa (Mak)*	4	12.8 ± 4.7	7.8 ± 6.6	1.1 ± 0.9
	Ngwenya 2 (Ngw2)	1	2.3 ± 1.1	0	0
	Ngweshla (Ngwes)*	2	47.4 ± 24.8	7.8 ± 2.6	4.2 ± 1.4
	Nyamandlovu (Nyam)*	4	49.8 ± 26.6	1.8 ± 1.6	9.8 ± 4.2
	Whitehills (Wh)	2	4 ± 1.7	3 ± 0.9	0

aerial. The probability of not returning was significantly higher in large wildfowl (0.357 (0.208–0.341 CI)) compared to the rest of the guilds all of which had probabilities lower than 0.09.

Discussion

We used direct observations to evaluate the relative influence of various disturbance stimuli on waterbirds in and around HNP, a PA. We acknowledge that what we measured as the disturbances may be an under-representation of the actual pressure around waterpans as we could have missed some flyovers, noises or minor behavioural adjustments to things we did not see (Marchant-Forde 2015, Payne et al. 2017). We also do not rule out the possibility of waterbirds reacting to more than one stimulus (Krüger 2016), but these could be very few instances since we were scanning the waterpan area after every minute. Thus we believe that for the disturbances we detected, we were able to capture the responses and that the inferences we made in this study reflect the general pressures faced by the waterbirds in our area. Also, because waterpans are small water bodies that often host few waterbirds, it was possible to monitor the activities of the birds with a high degree of precision (including identifying individuals that flew away and came back or not return).

Waterbirds that were engaged in non-feeding activities that allowed some form of vigilance responded more to disturbances. These activities (e.g. standing and swimming) allow waterbirds to monitor their surroundings (Blumstein et al. 2003), even if not truly alert, and can therefore quickly detect threats and react accordingly (Borgmann 2011, Livezey et al. 2016). In addition, this state can be engaged by individuals that have been disturbed (Frid and Dill 2002, Blumstein 2006), exposed to prolonged threats (Fernández-Juricic et al. 2005) and those defending their territory (Earnst 2002, Fritz et al. 2002) and therefore are ready to react to various stimuli. Although individuals may be able to detect and respond to threats when they are constantly engaged in non-feeding vigilant activities, they could be losing opportunities to acquire food or rest (Blumstein 2006, Raeside et al. 2007) with direct disadvantages on fitness (Schulz and Stock 1993). Most (76.4%) of the

responses to disturbances were recorded from waterbirds that were engaged in vigilance-compatible behaviours prior to the threat. The low frequency of responses by waterbirds that were engaged in feeding non-vigilant could be a reflection that they had greater energy requirements and were not apt to respond so that the feeding opportunities are not lost. Such tendencies have been observed for birds when they are energy stressed (Guillemain et al. 2001, Beale and Monaghan 2004).

We did not find a significant influence of the group vigilance effect (H2) on probability of responding although such patterns are often reported in behaviour studies (Frid and Dill 2002, Blumstein 2006, Beauchamp 2008, Borgmann 2011). It is possible that the group size effect is already captured in our waterbird guild categorisation as the guilds tend to have defined social groupings (Green and Elmberg 2014) and we have also shown that group sizes were different across guilds. As waterpans are in this study were small, and did not host numerous birds on them as is the case with other wetlands types, it may also be possible that the range of possible group sizes that we observed on them (Table 4) were not wide enough to allow detection of a group size effect across the species. The small size of the waterpans may also implies that individuals could not afford to rely on conspecific detection (Lima 1995), as predators could appear in sights only a few seconds before predation could occur (Quinn and Cresswell 2005). Also, although our data did not allow us to separate single species groups from mixed ones, mixed species groups may change the effect of group size as individuals benefit from the vigilance of the more vulnerable individuals or species (Beauchamp 2008).

Types of disturbances and associated responses

Terrestrial disturbances triggered the most responses (including escape reactions), although these threats were not the most frequent at our waterpans (Table 5). For the instances that waterbirds flew away from terrestrial threats, individuals took significantly longer time to come back to the waterpan area when compared to aerial and herbivore disturbances. This suggests that terrestrial threats are the least tolerable in our study area and indicates the high levels of risk associated with them. Since our terrestrial disturbance class mostly
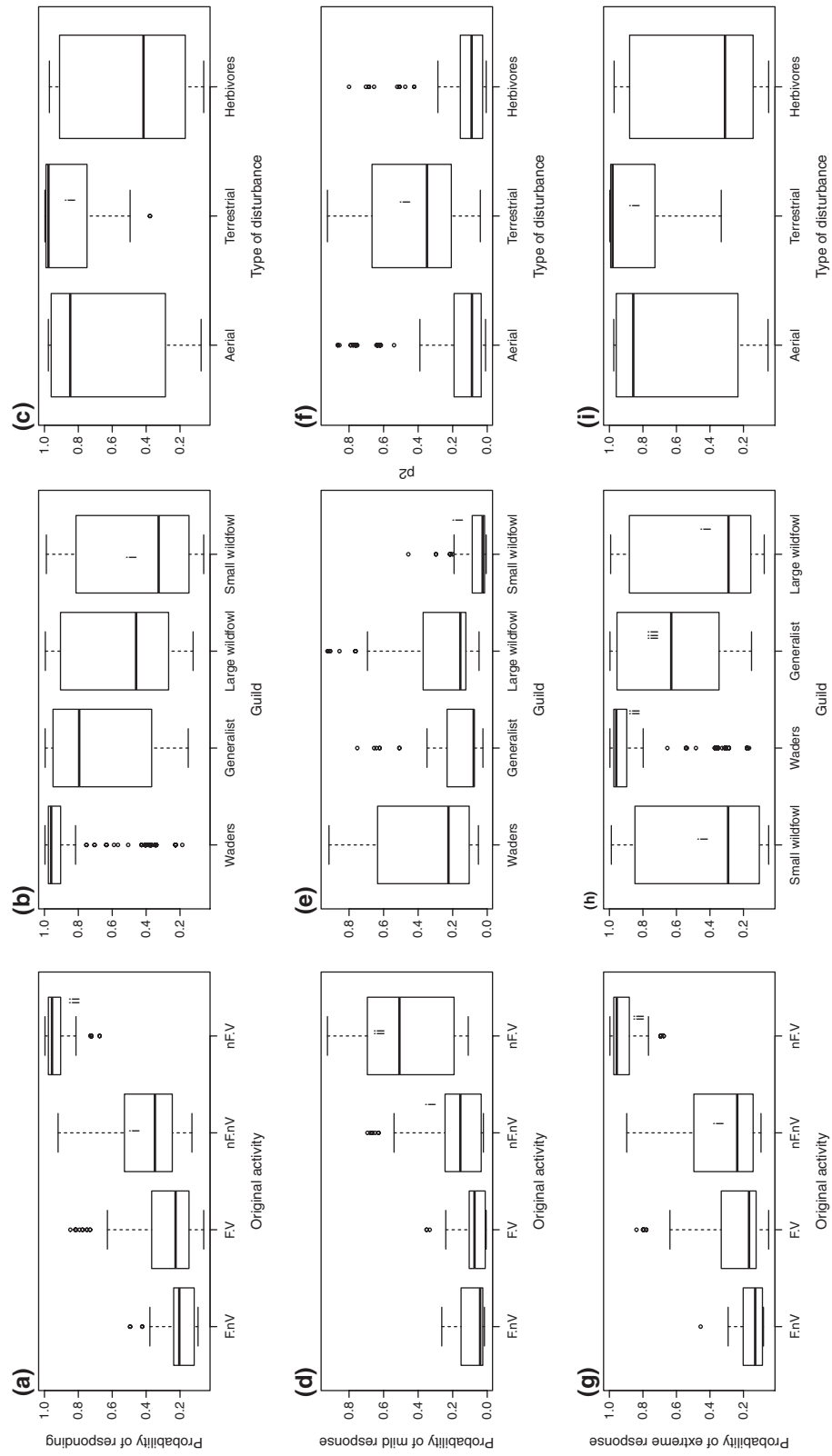
8

Figure 2. Schematic presentation of the likelihood of waterbirds to respond to disturbances plotted from model estimates. The top panel shows the probability of waterbirds to respond, the middle one presents the probability of reacting with a mild response (i.e. becoming vigilant without change of position) and the bottom panel shows the likelihood to show extreme response (i.e. flying away). The plots a, d and g illustrates comparisons across original activities classes; b, e and f shows comparisons across guilds; and c, f and i illustrates differences across disturbance types. Different numeric superscripts (i,ii,iii) represent groups that are statistically different.
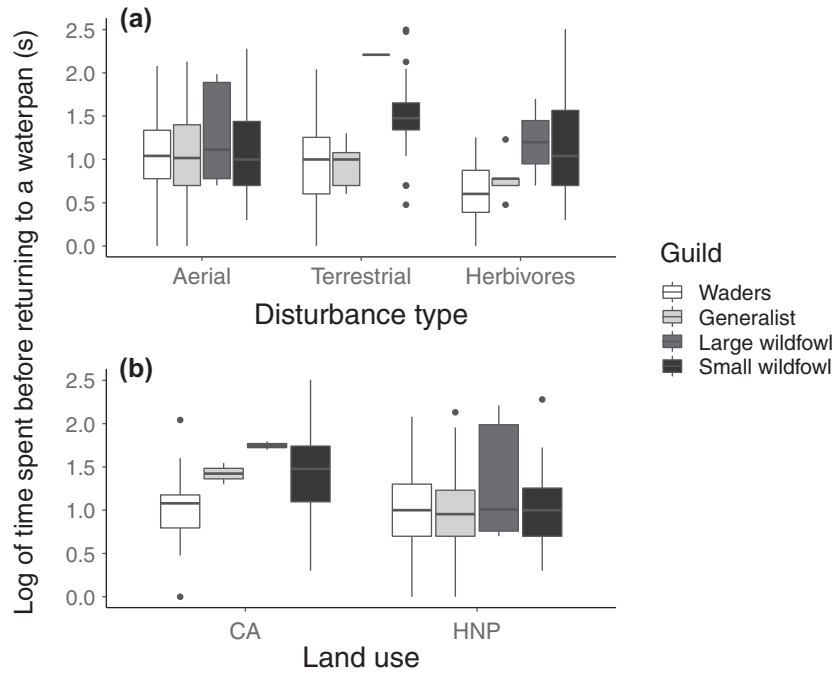
Figure 3. Plots from raw data of time taken flying by the different waterbird guilds (a) after being disturbed by various threat types and (b) across land uses.

included humans, noise from vehicles and domestic dogs (all anthropogenic sources contributing to 58.1% of cases), the perceived threats of people seem to be high as was recorded elsewhere (Klein et al. 1995, Banks and Bryant 2007, Krüger 2016, Moore et al. 2016). Probably the most threatening human activities for waterbirds in our study area is domestic dogs and their use in subsistence hunting and noises around waterpans, especially in the CAs (Tarakini et al. 2018). In line with our anthropogenic disturbance effect hypothesis

(H3), we expected waterbirds from the PAs (where hunting is prohibited and therefore some possibility of habituation) to have less escape responses from people, but this was not so. Our results suggest that risk levels associated with terrestrial threats are similar in CAs and HNP, and could imply that waterbirds from the park sometimes visit and utilise waterpans in CAs where they are also exposed to human predation (Borgmann 2011). However, for the waterbirds that flew away, those in CAs took significantly longer periods to
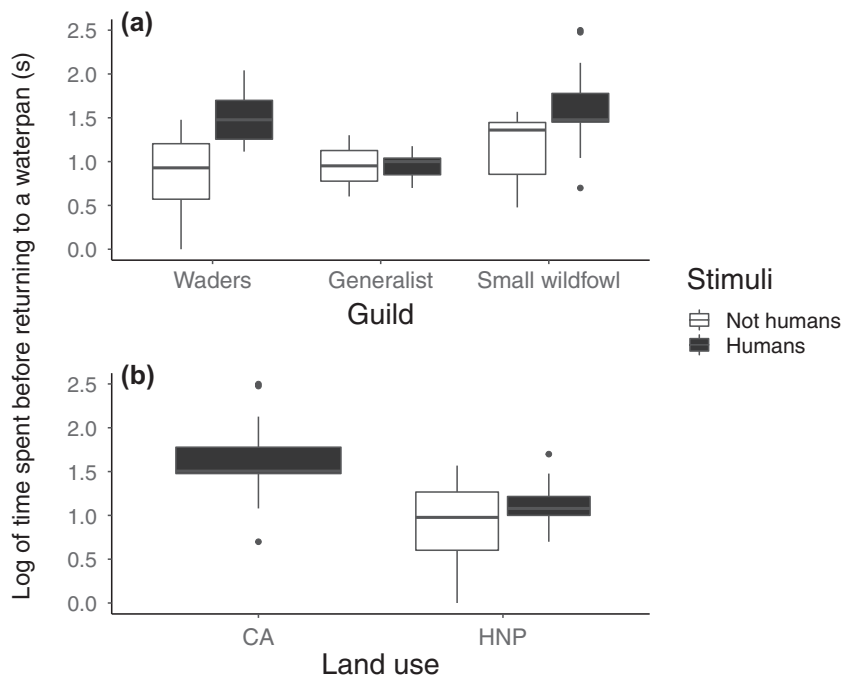

Figure 4. A schematic presentation of raw data illustrating time spent flying by waterbirds after disturbances by humans or not across (a) guilds and (b) land uses..

return to waterpans, thus greater fear could be associated with returning to them when compared to HNP. We also think that the effect of disturbance type overshadowed the habitat type effect (H4) which did not significantly influence the likelihood of responding and the time spent flying.

The waders (which normally forage on the shores and do not swim) responded more to threats compared to those that do swim (small and large wildfowl) and those that normally forage away from shores (generalist). Also, when disturbed by people, waders, which mostly comprised the blacksmith lapwing *Vanellus armatus* (83.2%, Table 2), took the longest time to return to the waterpans (compared to other guilds). This could be associated with the lower energetic requirements (because of light weight) by these species (Grand 1999) when compared to small wildfowl and generalists. In addition, several waders are known for prolonged territorial flight behaviour especially close to their feeding or nesting areas (Goss-Custard 1970, Coetzer and Bouwman 2017). The tendencies of flying for long periods before returning were also observed in large and small wildfowl, particularly in the CAs where they are normally targeted for meat by humans (Tarakini et al. 2018), but those facing less human predation pressure such as generalists and waders (Hancock et al. 2010) took less time in flying. Our results therefore failed to show a clear waterbird size effect (H1) on waterbird responses to threats.

The disturbances (especially the terrestrial ones) triggered more flight responses from waterbird guilds that do not usually swim (waders and generalists in our case) when compared to others. Previous studies have observed that swimming to safer or unreachable areas is commonly used by waterbirds, especially for small wildfowl, which is an energetically less demanding escape option (England et al. 2015, McFadden et al. 2017). However, the long periods taken by large wildfowl to return after flying away suggest that risk-taking is low (Grand 1999). If these species are constantly under threats that trigger flight, a significant proportion of foraging time could be lost making such sites unfavourable for them (Klein et al. 1995, Blumstein 2006). Therefore, if all the other factors are constant, sites that experience constant disturbances will progressively be selected by communities skewed towards species that can swim (Rajashekara and Venkatesha 2017). Such biases will not meet tourist expectations for greater species diversity (Ian 2000), and may ultimately result in skewed ecosystem processes, for example, some food resources may remain underutilised (Gill et al. 2001, McFadden et al. 2017) or waterbirds may shift their feeding times and locations accordingly (Guillemain and Fritz 2002). The implications of such a scenario could be worse inside the park, especially if tourist numbers visiting waterpans negatively affect waterbird communities.

Returning to a site after a fly away

Only about 5.5% of flying responses did not return to the same waterpan in 2 h after being disturbed. Whether or not waterbirds return to the original site can also depend on the quality of habitat (such as food abundance, cover, the frequency of disturbances when compared to other sites) (Ian 2000, Coetzer and Bouwman 2017). Some breeding waterbirds (constructing nest, tending to eggs or chicks)

may be compelled to return to sites after disturbances more than the non-breeding ones (Hernández-Matías et al. 2003, Gayet et al. 2011). However, our study did not reveal differences across seasons (i.e. in contrast to our seasonal effect hypotheses (H5)) but we acknowledge that our sample size was too small to test for the breeding status of each species. Some studies used rates of disturbances and food acquisition to relate to the fitness consequences for waterbirds (Goss-Custard et al. 2006), and have suggested threshold disturbance levels for different scenarios of food availability. Thus further research is needed in our study area to investigate how waterbirds tradeoff reacting to various stimuli under varying food availability and such work will be critical as the area is important for breeding waterbirds (Godfrey 1992).

Our study has shown that in the few instances that waterbirds did not return, it was due to aerial disturbances. The aerial threats frequency was high at Nengasha, Guvalala, Nyamandlovu and Ngweshla (Table 5). The large wildfowl had the highest probability of flying away and not return, which could be related to the greatest flight energy costs related to their body weight. It could be argued that they would be the least likely to engage in a return flight when they have escaped to an alternative waterpan after disturbance (in comparison to the rest of the guilds). Although we found no significant interactive effects of disturbance type and waterbird guild on responses to threats, we think that if raptor pressure increases on waterbirds such species will abandon the high risk sites (Guillemain et al. 2007). This may not only affect the large species but also the small that can be carried away on the wing (Goss-Custard et al. 2006).

Conclusions

Our results do not generally support the waterbird size hypothesis but we have shown that waders responded most to threats and large wildfowl took the longest time to fly back after disturbances. We do not think that terrestrial threats are currently a problem inside HNP, though wild predators are often present at waterpans. However, these threats inside HNP may be enough to maintain the response behaviour that waterbirds mostly expressed when using waterpans in the matrix of land uses around the PA. As we failed to find any evidence of habituation to humans in the PA, waterbirds may face more terrestrial disturbances as plans are underway to promote tourism inside HNP (Andersson et al. 2017), herbivore pressure continues to increase around waterpans (Tshipa et al. 2017) and human population is growing in the surrounding CAs (Guerbois et al. 2013). Although some waterbirds species can forage during the night as a coping strategy against disturbances (Guillemain et al. 2002), some are inactive at that time. The level of predation risk may actually be high at night due to the very large array of nocturnal mesopredators, an aspect of waterbird ecology that warrants more studies. With waterbirds facing increased levels of disturbances, the establishment of tourist-free waterpans especially inside the PAs may offer some form of refuge (but not necessarily from natural forms of predation and disturbances). The availability of such tourist-free waterpans will be critical when food resources decline in the major sites (Goss-Custard et al. 2006), commonly during the dry sea-

son in our study area. Also, large waterpans/dams may also have safe areas (such as islands) where threats will be greatly reduced (Adams et al. 2000).

Although we failed to detect the influence of seasons and habitats in this study, the frequency of disturbance occurrences is not uniform throughout the year. Herbivores, subsistence hunting and aerial predations are likely to be low in the wet season because surface water is abundant in the Hwange system and wild animals do not congregate in large numbers at waterpans; people will be working in the fields and cattle herders utilise the ephemeral streams to water livestock; and raptors will be spread out in the landscape even over puddles with water. Due to the differences in frequency of disturbances, the negative impacts of these disturbances could be expected to be more important during the dry season if threat pressures increase.

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