



## Research Article

# Human Disturbance Affects Latrine-Use Patterns of Raccoon Dogs

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**ABSTRACT** Although urbanization is a leading threat to wildlife conservation, some species have adapted to a synanthropic lifestyle. We used a population of raccoon dogs (*Nyctereutes procyonoides*) in the Akasaka Imperial Grounds in central Tokyo, Japan to investigate how latrine-using carnivores can maintain their socio-spatial organization with human disturbance. Between 2012 and 2014, we selected 4–11 latrines per year (from a max. of 18 latrines recorded in the area) using 1 camera per latrine. We focused on latrines that included varying levels of human disturbance. We analyzed the temporal patterns of 3,257 latrine visits, of which 878 included defecation events. Overall, latrine use (i.e., visits with and without defecation events) increased as winter approached, coinciding with dispersal, and showed a seasonal shift from diurnal to nocturnal use patterns as days got shorter. Generalized linear mixed model results confirmed that temporal visiting and defecation patterns were affected by human disturbance and shifted from diurnal to nocturnal, although overall frequency of visits and defecation events did not decrease at disturbed latrines and raccoon dogs continued to use disturbed latrine sites. Raccoon dogs likely perceive human disturbance as predation risk and avoided this by shifting their temporal, but not spatial, activity pattern to minimize disturbance. Minimizing the amount of disturbance around raccoon-dog latrines at sensitive sites and times of day would allow them to co-exist with people with the minimal compromise to their latrine-centered socio-spatial organization. © 2018 The Wildlife Society.

**KEY WORDS** activity shift, avoidance behavior, human disturbance, latrine, *Nyctereutes procyonoides*, olfactory communication, raccoon dog, risk disturbance hypothesis, scent marking, synanthropic.

Urbanization is one of the leading threats to wildlife conservation (Czech et al. 2000, McKinney 2002), often resulting in local extinction events (McIntyre 2014). Nevertheless, some species, including several large and

medium-sized carnivores (e.g., red foxes [*Vulpes vulpes*], Harris 1981; coyotes [*Canis latrans*], Gehrt et al. 2009; golden jackal [*Canis aureus*], Gupta et al. 2016; raccoons [*Procyon lotor*], Prange et al. 2003; black bears [*Ursus armericanus*], Don Carlos et al. 2009), can be tolerant to living sympatrically with humans (i.e., synanthropic; Bateman and Fleming 2012), resulting in certain species occurring at high population densities in urban environments (McIntyre 2014). In general, foraging generalists appear to be the most

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adaptable carnivores to urbanization (Nilon and Paris 1997, Pickett et al. 2001, Saito and Koike 2015), although many alter their activity patterns to avoid human presence or activities (e.g., European badger [*Meles meles*], Davidson et al. 2008; coyote, Kitchen et al. 2000; bobcat [*Lynx rufus*], Riley et al. 2003; golden jackals, Rotem et al. 2011). Often, field signs, such as feces, are the only indication of their presence (Wilson and Delahay 2001, Barea-Azcón et al. 2007). Nevertheless, although the mechanisms of species adaptation to urban environments are well researched in terms of obtaining ecological resources (e.g., food, shelter) and changes in activity patterns (McIntyre 2014, Sálek et al. 2015), adaptations facilitating intra-specific communication in the context of territoriality, individual and reproductive advertisement, and socio-spatial interactions in general, have been largely neglected.

Among carnivores, olfactory signals are the predominant mode of communication (Brown and Macdonald 1985). In contrast to specialized glandular secretions, which are often costly to produce (Gorman and Trowbridge 1989), urine and feces are free, naturally pungent metabolic by-products that typically encode a wealth of individual-specific information (Buesching and Stankowich 2017). Many carnivores use latrines (i.e., sites where  $\geq 2$  fecal deposits accumulate over time because of repeated use). Additional roles of latrines, including territory maintenance or conveyance of information about the species' spatio-temporal activity patterns, are established for such mesocarnivores as golden jackals (Macdonald 1979), spotted hyenas (*Crocuta crocuta*; Gorman and Mills 1984), European badgers (Jordan et al. 2007, Buesching et al. 2016), banded mongooses (*Mungos mungo*; Jordan et al. 2010), European rabbits (*Oryctolagus cuniculus*; Sneddon 1991), San Joaquin kit foxes (*Vulpes macrotis*; Ralls and Smith 2004), and ocelots (*Leopardus pardalis*; Moreno and Giacalone 2006). Nevertheless, in urbanized areas, people often remove these fecal deposits on account of the potential health risks to humans and their pets through zoonotic diseases and parasites (Mackenstedt et al. 2015); although this may risk perturbing the socio-spatial integrity of resident animals' territories, which we investigate here.

A recent review on latrine use in carnivores (Buesching and Jordan 2018) postulated a research framework to investigate latrine function based on 4 data categories: spatial distribution patterns, temporal usage patterns, individual visits and contribution patterns, and the information content of the scent signal itself. Although frequency and temporal patterns of latrine use can provide basic information on a species' ecology and physiology (Buesching and Macdonald 2001, Jordan et al. 2007, 2010, Buesching and Stankowich 2017), for most species, information on temporal latrine-use patterns is still scarce. Nonetheless, the potential for delayed olfactory communication at latrines (signal latency) has been proposed to be crucial in territorial species to maintain their socio-spatial organization (Buesching et al. 2002, Buesching and Jordan 2018).

We used the raccoon dog (*Nyctereutes procyonoides*) as a model species to investigate the behavioral adaptations necessary to maintain effective intra-specific communication in urban environments. Raccoon dogs are hibernating

opportunistic foragers that typically live in pairs (Kauhala and Saeki 2004). Olfactory information exchanged at latrines (Yamamoto 1984) plays an important role in their intra-specific communication (Ikeda 1984). But although latrine-use patterns in raccoon dogs have been suggested to be partly affected by social relationships with neighbors, or closely related individuals (Ikeda 1984), a detailed analysis of their defecation pattern is lacking.

Until the 1970s, raccoon dogs inhabited the western part of Tokyo (Ohara 1982) and, although absent for the intervening roughly 20 years, they re-colonized green areas in central Tokyo in the 1990s (Teduka and Endo 2005, Sako et al. 2008), where their successful adaptation to urban living is largely due to their opportunistic feeding behavior (Saito and Koike 2015). We analyzed daily and seasonal variation in their latrine-use patterns, in terms of timing and frequency of latrine visits and timing and number of fecal deposits, in a region of urban Tokyo, Japan and related them to varying levels of human disturbance.

We hypothesized that if raccoon dogs perceive human activity as a predation risk (Clinchy et al. 2016), they may alter or modify their behavior in accord with the risk-disturbance hypothesis (Frid and Dill 2002), shifting activity patterns towards nocturnal latrine use (Benítez-López 2018, Gaynor et al. 2018). Thus, we predicted that level of human disturbance would affect timing of latrine visits and defecation events, but that overall latrine-use frequency would not be affected by disturbance, and that raccoon dogs would continue to use disturbed latrines because olfactory information exchanged at latrines is crucial in this species to maintain stable socio-spatial networks.

## STUDY AREA

We conducted latrine-use surveys from August to November 2012, September to November 2013, and June to August 2014 in the Akasaka Imperial Grounds, Tokyo (Table 1). The Akasaka Imperial Grounds are located in the eastern part of central Tokyo (Fig. 1) and comprise approximately 51 ha. They include buildings such as the Crown Prince's Palace and the Royal Family's residence, complemented by Japanese gardens comprising lawns, ponds, and several small wooded areas, both deciduous (e.g., Itajii [*Castanopsis sieboldii*], Japanese evergreen oak [*Quercus acuta*], Chinese evergreen oak [*Quercus myrsinifolia*], muku [*Aphananthe aspera*], Japanese zelkova [*Zelkova serrata*], maples [*Acer* spp.]) and coniferous (e.g., hinoki cypress [*Chamaecyparis obtusa*]; Fig. 1; Abe 2005, Mitsunashi et al. 2018). The area belongs to the warm-temperate climate zone type (see classification in Hisano et al. 2018), with mean annual temperature of 16.7°C and mean annual precipitation of 1,664 mm (2012–2014; Japan Meteorological Agency 2018). The area was relatively flat, ranging in elevation from 11–34 m (Iwasaki et al. 2017). Masked palm civets (*Paguma larvata*) and feral cats (*Felis catus*) were also sympatric (Teduka and Endo 2005). Because the area was closed to the public, few people frequented the gardens except for management staff and guards (who were also present at night). For security reasons, the Akasaka Imperial Grounds

**Table 1.** Summary of camera trapping surveys ( $n = 12$ ) of raccoon dog latrines in the Akasaka Imperial Grounds, Tokyo, Japan, 2012–2014.

Year	2012	2013	2014	Total
Survey period	3 Aug–6 Nov	7 Sep–5 Nov	2 Jun–27 Aug	
Number of survey days	97	60	87	244
Number of monitored latrines	11	10	4	25
Number of camera nights	1,056	590	344	1,990
Number of raccoon dogs filmed	2,200	618	439	3,257
Number of defecation events	568	164	146	878
Number of visits	1,632	454	293	2,379

were protected by a 2-m-high wire-mesh fence with gated access. The area was surrounded by busy roads with  $\leq 4$  lanes, developed business districts, and densely populated residential areas. Consequently, this study population was relatively contained and discrete, although gaps under the fence may have allowed animals occasional ingress and egress (Saito et al. 2017).

Raccoon dogs have been recorded at the Akasaka Imperial Grounds continuously since the early 1990s (Teduka and Endo 2005) and were also confirmed to breed there during the study period. Concurrent studies estimated that latrines

were used by approximately 26 different individuals in 2012 and 2013 (Iwasaki et al. 2017).

## METHODS

### Latrine-Use Patterns

At the start of each annual survey period, we mapped all active raccoon dog latrines in the Akasaka Imperial Grounds (Table 2; Fig. 2). We recorded the immediate environment (e.g., lawn, parking lot, proximity to garden management track) and extent of canopy cover and understory vegetation for each latrine site (Table 2). We categorized latrines as disturbed (i.e., daily human activity within 10 m of the latrine such as being adjacent to a parking lot or close to high-traffic areas and garden management work) or undisturbed (e.g., latrines situated away from any human presence within 10 m of the latrine).

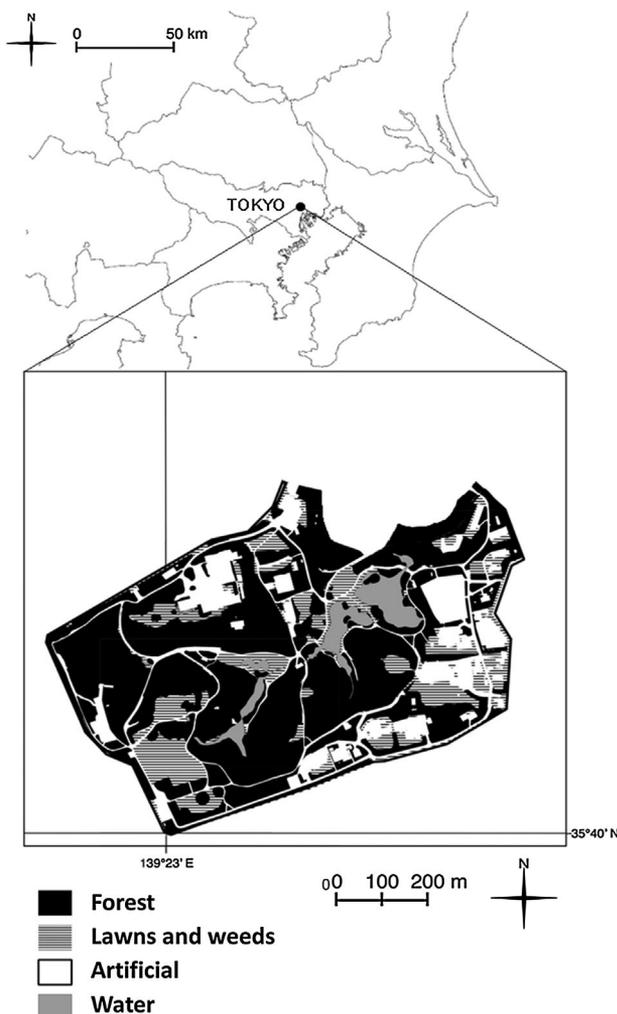
We selected between 4 and 11 focal latrine sites annually (according to the number of latrines in active use and camera availability) from 18 total latrines recorded in the area during the study period, to achieve contemporaneous coverage of disturbed and undisturbed latrine sites each year. We monitored 12 different latrines over the course of the survey period, of which 3 (latrines 1, 2, and 11) were filmed every year (Fig. 2; Table 2). At each latrine, we deployed 1 Bushnell wildlife camera with an infra-red motion detector (Trophy cam XLT; Bushnell, Overland Park, KS, USA), programmed to record 30 seconds of video each time it was triggered, with a 1-second interval between subsequent events.

For each latrine visit, we recorded date, time (from the camera's time stamp), and defecation (yes or no; defined as the visible evacuation of feces). We defined latrine visits without defecation as visits, and visits that included defecation as defecation events. If a further video-clip was recorded within 60 seconds of the first event, we categorized both clips as 1 event.

All study protocols were authorized by the ethical review board according to the 6th edition of the Tokyo University of Agriculture and Technology Regulations on Animal Experiments and complied with the Guidelines for the Treatment of Animal Samples (The Mammal Society of Japan 2009), which imposes regulations similar to American Society of Mammalogists (Sikes et al. 2016).

### Data Analysis

We used generalized linear mixed models (GLMM) with a Poisson error distribution to assess how month (Jun to Nov), time, and human disturbance affected hourly frequency of



**Figure 1.** Akasaka Imperial Grounds, Tokyo, Japan (based on the map in 2009).

**Table 2.** Classification of level of human disturbance for all monitored raccoon dog latrines ( $n = 12$ ) in the Akasaka Imperial Grounds, Tokyo, Japan, 2012–2014. We observed different latrine combinations in each year.

Latrine identification	Canopy vegetation <sup>a</sup>	Understory vegetation <sup>b</sup>	Disturbance	Monitored years	Notes
1	1	1	Undisturbed	2012, 2013, 2014	In shrub
2	1	1	Undisturbed	2012, 2013, 2014	In shrub
3	1	1	Undisturbed	2012, 2014	In shrub
4	1	1	Undisturbed	2012, 2013	In shrub
5	1	1	Undisturbed	2012	In shrub, became inactive in 2014
6	1	1	Undisturbed	2012, 2013	In shrub
7	1	1	Undisturbed	2012, 2013	In shrub near a passway
8	1	1	Undisturbed	2012, 2013	In shrub
9	1	1	Undisturbed	2012, 2013	In shrub
10	1	0	Disturbed		Near garden management track
11	1	0	Disturbed	2012, 2013, 2014	Near parking lot
12	1	0 <sup>c</sup>	Disturbed	2012, 2014	Near parking lot and a building; became inactive in 2014
13	0	1	Disturbed		On the lawn near garden management track
14	0	0	Disturbed		In parking lot
15	1	1	Disturbed	2013	Near garden management track; became inactive in 2014
16	0	1	Disturbed		On the lawn near garden management track
17	1	1	Disturbed		On the lawn near garden management track
18	1	0	Disturbed		Near garden management track; formed in 2014

<sup>a</sup> Latrines with (1) and without (0) canopy vegetation.

<sup>b</sup> Latrines with (1) and without (0) understory vegetation.

<sup>c</sup> Latrine 12 had understory vegetation only in 2012.

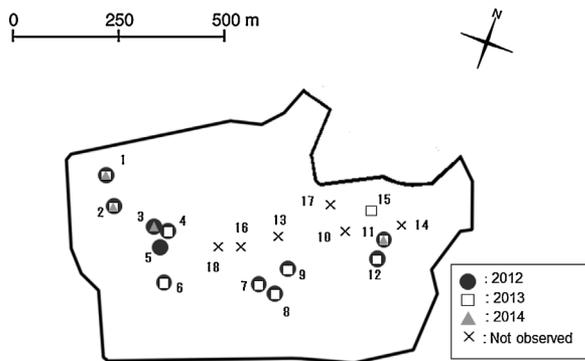
visits and defecation events at latrines where defecation events occurred. We used the hours that included sunrise and sunset (obtained from the Ephemeris Computation Office Public Relations Center National Astronomical Observatory of Japan database; Ephemeris Computation Office Public Relations Center NAOJ 2015) to define day and night. We then applied categorical (binary) variables to attribute the temporal conditions during the hour when the latrine event occurred: sunset (1) or not (0), daytime (1) or not (0), and sunrise (1) or not (0). We included human disturbance as a categorical (binary) variable: undisturbed (1) or disturbed (0). Additionally, we included the following interaction effects as explanatory variables: month  $\times$  daytime and disturbance  $\times$  daytime. Because sampling effort (i.e., number of working camera days) per month differed among latrines, we added

the logarithm of camera days to the GLMM as an offset term. Because frequency of latrine use could differ among years and latrines (Ikeda 1984, Akihito et al. 2016), we included year and latrine identification as random effects. We selected the most supported model by performing a best-subset selection procedure based on Akaike's Information Criterion values (AIC) to assess which parameters affected hourly frequency of latrine visits and defecation events. We regarded a model with the least AIC as the best-fitted model. We also took other models with  $\Delta AIC < 2$  into consideration, and if the explanatory variables in the best-fitted model were also contained in the majority of these alternative models, we assumed that the variable affected the response variable. Based on our hypothesis, we were particularly interested in the effect of disturbance or disturbance  $\times$  daytime on latrine use. We performed all analyses in the R software environment, version 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria). We conducted GLMM analyses using the `glmer` function in the `lme4` version 1.1.12 package, and model selection using the `dredge` function in the `MuMIn` version 1.15.6 package.

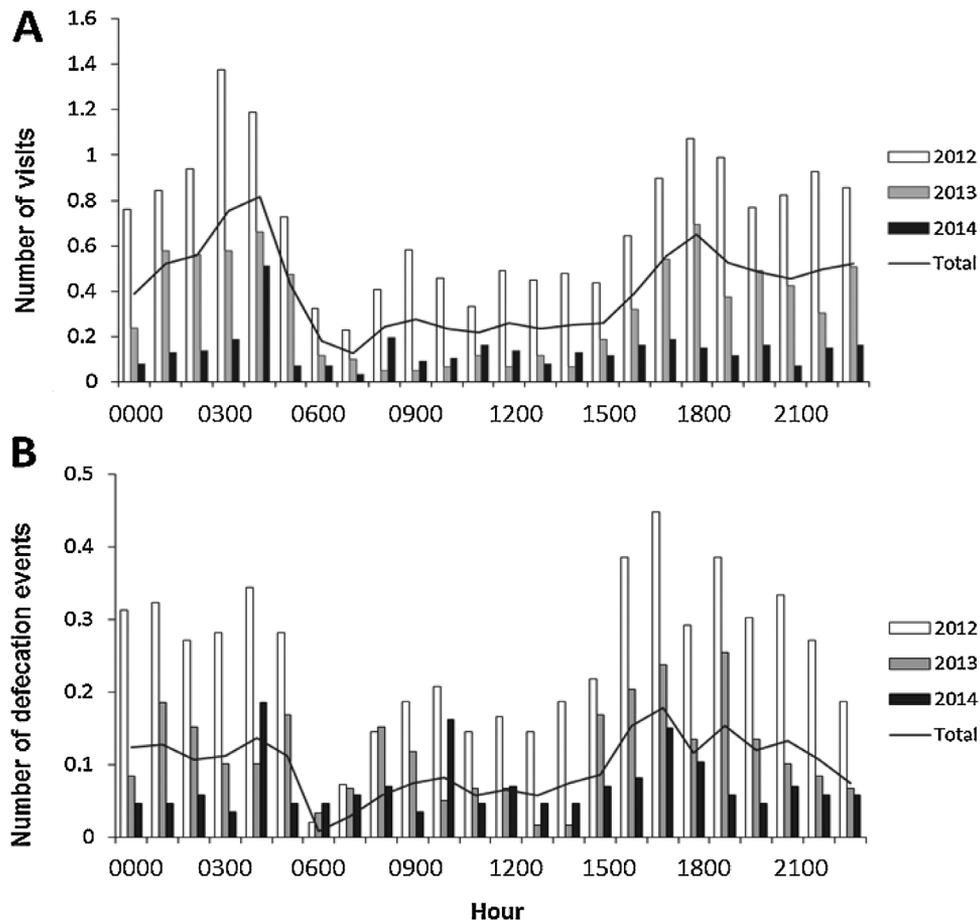
## RESULTS

Most latrines were situated under canopy (14 of 18) and 12 of 18 were located under understory vegetation (Table 2). Half of the monitored latrines (9 of 18) were located in disturbed environments and the other half were located in undisturbed environments (Table 2). Fourteen of 18 latrines were active throughout the study period, 3 became inactive in 2014, and a new latrine was established in 2014 (Table 2).

The camera deployment returned 3,257 raccoon dog observations, including 878 defecation events and 2,379 visits during which the animal sniffed or searched for invertebrates at latrines but did not defecate (Table 1).



**Figure 2.** Location of raccoon dog latrines in the Akasaka Imperial Grounds, Tokyo, Japan. We deployed camera traps at focal latrines ( $n = 12$ ) subjected to varying degrees of human disturbance in 2012 ( $n = 11$ , Aug–Nov), 2013 ( $n = 10$ , Sep–Nov), and 2014 ( $n = 4$ , Jun–Aug). Latrines marked with  $\times$  were not included in the surveys because activity was sporadic or absent.



**Figure 3.** Daily patterns of A) visits and B) defecation events at raccoon dog latrines in the Akasaka Imperial Grounds, Tokyo, Japan ( $n = 12$ ) per year. The bar charts show the hourly visits or defecation events at each latrine per day for each year. The line indicates the number of hourly visits or defecation events for each day across the complete study period (2012–2014).

Latrine visits (1,567 of 2,379; 65.9%) and defecation events (497 of 878; 56.6%) occurred mostly at night. We observed visits at all latrines but did not record defecation events at 2 latrines (latrine 7 and 12) during the study period. Most visits and defecation events occurred around dusk (between 1700 and 1900), and the fewest visits and defecation events occurred around dawn (between 0600 and 0800; Fig. 3).

With regard to latrine visits, the most supported GLMM model (top model with lowest AIC value:  $AIC = 4,673.5$ ) included month, month  $\times$  daytime, disturbance  $\times$  daytime, sunrise, sunset, and daytime. All the alternative models of latrine visits with  $\Delta AIC < 2$  included our main variable of interest (disturbance  $\times$  daytime; Table 3).

Overall, temporal patterns of all latrine visits proved to be affected primarily by time of day with significantly more visits to latrines being made during night-time compared to any other time, which is apparent from the coefficient estimates for daytime being negative (with  $P < 0.001$ ) but those for sunrise and sunset being insignificant (Table 3; Fig. 3A). The effect of disturbance was such that disturbed latrines were visited significantly less (2.31%) than were undisturbed sites but notably (39.52%) less during daytime.

With regard to defecation events, the most supported model (AIC value:  $AIC = 3,264.2$ ) included month, month

$\times$  daytime, disturbance  $\times$  daytime, and sunset, and all valid alternative models included disturbance  $\times$  daytime (Table 3). At all latrines, frequency of defecation events was significantly greater around sunset than during any other time period (Table 3). Again, human disturbance affected temporal defecation patterns significantly with the frequency of daytime defecation events being significantly greater at undisturbed latrine sites than at disturbed sites (Table 3; Fig. 4).

In addition, overall latrine use (i.e., applying equally to visits and defecation events) at each latrine increased towards winter from a minimum of  $0.88 \pm 0.87$  (SD)/day in June to  $2.41 \pm 2.59$ /day in November, and that there was a seasonal shift between June and November from diurnal to nocturnal latrine visits and defecation events. Both behaviors occurred more frequently during the nighttime towards winter, reflecting the seasonal decrease in day length towards winter solstice (Table 3; Fig. 5).

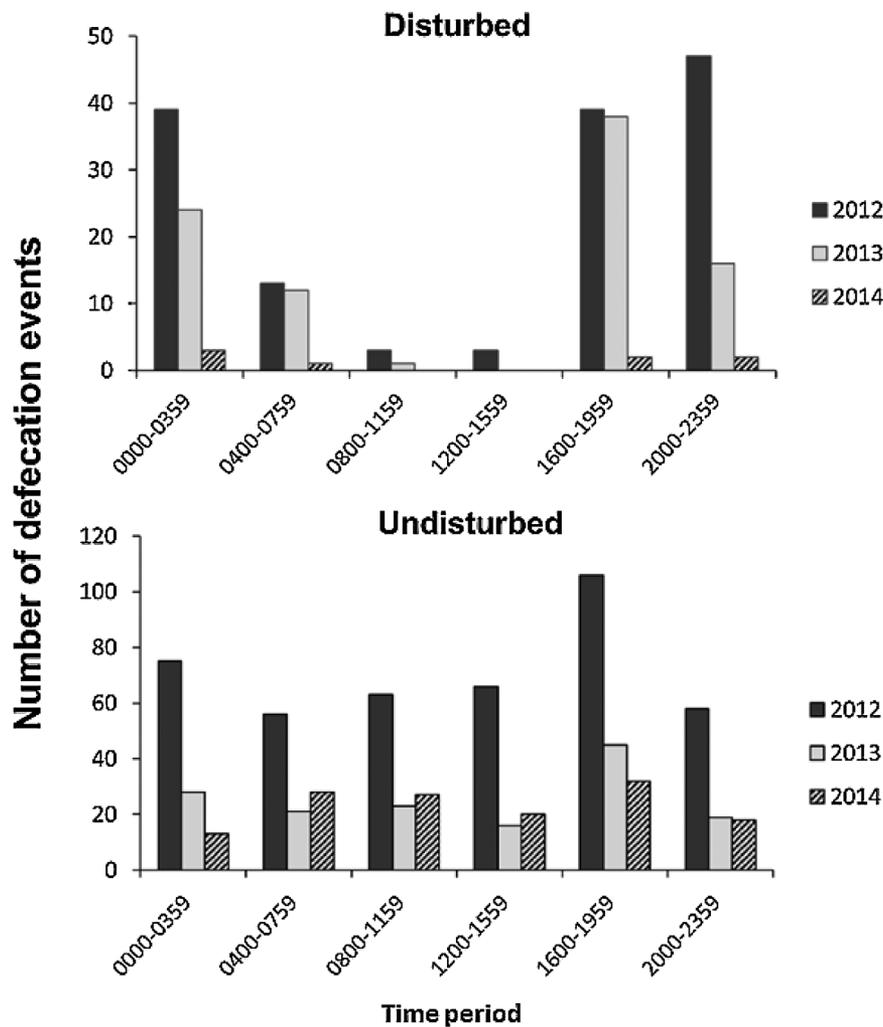
## DISCUSSION

Our initial hypothesis, that human disturbance might alter the temporal latrine-use patterns of raccoon dogs was supported. Independent of human disturbance, latrine use was significantly more frequent during nighttime than at any

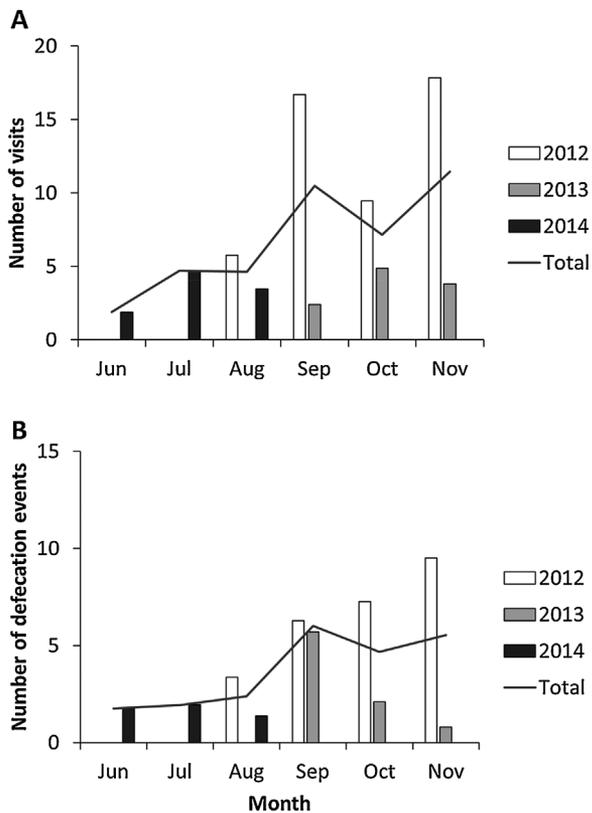
**Table 3.** Coefficients of selected variables from generalized linear mixed models (GLMMs) explaining latrine use by raccoon dogs in the Akasaka Imperial Grounds, Tokyo, Japan, 2012–2014, and Akaike's Information Criterion (AIC) values of the GLMMs with  $\Delta AIC < 2$  by model selection.

Model rank	Coefficient of each variable <sup>a</sup>								AIC	$\Delta AIC$
	Intercept	Month	Daytime	Month $\times$ daytime	Disturbance	Disturbance $\times$ daytime	Sunrise	Sunset		
Visits										
1	-6.06 ( $<0.001$ )	0.30 ( $<0.001$ )	-2.08 ( $<0.001$ )	-0.17 ( $<0.001$ )		3.44 ( $<0.001$ )		0.15 (0.095)	4,673.5	0.00
2	-6.03 ( $<0.001$ )	0.30 ( $<0.001$ )	-2.11 ( $<0.001$ )	-0.17 ( $<0.001$ )		3.44 ( $<0.001$ )			4,674.2	0.69
3	-5.88 ( $<0.001$ )	0.30 ( $<0.001$ )	-2.09 ( $<0.001$ )	-0.17 ( $<0.001$ )	-0.22 (0.645)	3.45 ( $<0.001$ )		0.15 (0.095)	4,675.3	1.79
4	-6.05 ( $<0.001$ )	0.30 ( $<0.001$ )	-2.09 ( $<0.001$ )	-0.17 ( $<0.001$ )		3.44 ( $<0.001$ )	-0.04 (0.708)	0.14 (0.110)	4,675.4	1.86
Defecation events										
1	-6.12 ( $<0.001$ )	0.24 ( $<0.001$ )		-0.29 ( $<0.001$ )		2.53 ( $<0.001$ )		0.39 ( $<0.001$ )	3,264.2	0.00
2	-6.11 ( $<0.001$ )	0.24 ( $<0.001$ )		-0.29 ( $<0.001$ )		2.53 ( $<0.001$ )	-0.14 (0.327)	0.37 ( $<0.001$ )	3,265.2	1.01
3	-5.74 ( $<0.001$ )	0.24 ( $<0.001$ )		-0.29 ( $<0.001$ )	-0.47 (0.367)	2.54 ( $<0.001$ )		0.39 ( $<0.001$ )	3,265.5	1.23
4	-6.02 ( $<0.001$ )	0.23 ( $<0.001$ )	-0.34 (0.556)	-0.26 ( $<0.001$ )		2.61 ( $<0.001$ )		0.39 ( $<0.001$ )	3,265.9	1.65

<sup>a</sup> *P* values are shown in parentheses.



**Figure 4.** Annual raccoon dog defecation patterns at focal raccoon dog latrines ( $n = 12$ ) located in the Akasaka Imperial Grounds, Tokyo, Japan, 2012–2014. We classified observed latrines as disturbed or undisturbed based on human activity.



**Figure 5.** Monthly changes in A) visits and B) defecation events at raccoon dog latrines in the Akasaka Imperial Grounds, Tokyo, Japan ( $n = 12$ ) per year. The bar charts show the monthly visits or defecation events at each latrine for each year. The line indicates the number of monthly visits or defecation events across the total study period (2012–2014).

other time. At disturbed latrines, the frequency of daytime visits and defecation events was depressed even further. This is similar to observations in other carnivore species that have adapted to a synanthropic lifestyle (e.g., red foxes, coyotes, raccoons, European badgers; Sálek et al. 2015), often by changing their activity patterns to become predominantly, or even exclusively, nocturnal (McIntyre 2014, Benítez-López 2018, Gaynor et al. 2018). Other studies (Zhou et al. 2013) reported that a wide variety of other carnivore species (e.g., yellow-throated martens [*Martes flavivula*], masked palm civets) were deterred from defecating close to areas of heightened human activity, and thus changed their temporal and spatial latrine-use pattern. Our observations showed a similar pattern with raccoon dogs using undisturbed latrines more than disturbed latrines, demonstrating an effect of disturbance on both their temporal and spatial use of under human disturbance.

Previous literature indicates that prey are more vigilant when the perceived risk of predation is greater (i.e., risk-disturbance hypothesis; Frid and Dill 2002, Shannon et al. 2014), and there is evidence that other carnivores may perceive human presence as a predator threat (e.g., European badgers, Clinchy et al. 2016; pumas [*Puma concolor*], Smith et al. 2017). Nevertheless, defecation is a necessary by-product of any heterotrophic diet and this behavior cannot be eliminated in response to human disturbance or predation risk.

One possible explanation for the shift in activity patterns we observed is that raccoon dogs perceive human-caused disturbance as predation risk (Frid and Dill 2002) and do not want to expose themselves to danger but still need to remain informed on their socio-spatial network via the information that is encoded in the scent of feces deposited at latrines (Tinnesand et al. 2015, Buesching and Stankowitch 2017, Buesching and Jordan 2018). Scent provisioning experiments have reported that raccoon dogs can recognize individuals (Yamamoto 1984) and group membership (Ikeda 1984) from fecal odor profiles. By defecating at latrines predominantly at sunset (i.e., at the onset of their activity period), animals may thus try to update their olfactory information regarding their socio-spatial network (Ikeda 1984, Yamamoto 1984) as soon as a reduction in human disturbance allows. Indeed, Gaynor et al. (2018) reported that a wide variety of taxa shift their activity towards nocturnality in response to human disturbance, which is a cumulative effect of human disturbance that had not been quantified before.

Season also affected raccoon dog latrine-use patterns. Typically, latrines are visited, and used by, several individuals belonging to the same or to neighboring pairs or groups (Ikeda 1984, Koizumi et al. 2017), and the seasonal increase in latrine visits and defecation events towards winter we observed coincides with the typical dispersal peak reported for raccoon dogs (Kauhala and Saeki 2004). Our findings corroborate reports from other areas that raccoon dogs are more nocturnal in winter (Yamamoto 1993, Kaneshiro et al. 2000, Kauhala et al. 2007, Rudert et al. 2011). Although the exact reasons are still unclear, this might be partly a function of shortening day length during winter in the northern hemisphere (in Japan on average by  $\sim 5$  hr to an average day length of 9.4–10.2 hr in winter compared to 14.2–15.3 hr in summer (Hisano et al. 2018)).

## MANAGEMENT IMPLICATIONS

In our study, raccoon dogs clearly sought to minimize defecating at sites, or at times of day, when disturbance by people was likely to be greatest. This demonstrates that raccoon dogs are able to co-exist with humans, but still maintain their use of latrines, by altering temporal and spatial pattern of latrine use. In terms of conserving native raccoon dogs in Japan, or in enhancing their welfare, especially during sensitive periods such as breeding, we recommend human activities should avoid areas where raccoon dogs are actively using latrines, especially around sunset and particularly in the winter months.

More broadly our work shows that latrine sites are important to the spatial relationships of raccoon dogs. If feces were removed from raccoon dog latrines in accord with the recommendations of urban by-laws in Japan (Joetsu City 2016; Wildlife Repelling Number 110 2018), or if repellents (e.g., wood, bamboo vinegar) were used to discourage raccoon dogs from re-establishing latrines, we would predict that this would be detrimental to their social organization and thus their well-being. We would not, therefore, recommend actually undertaking such an experiment on account of these potential ethical implications. Nevertheless,

our inference is that municipalities should weigh carefully the hygienic and zoonotic benefits of removing urban carnivore feces (Di Cerbo et al. 2008, Mackenstedt et al. 2015) against the disturbance this could cause to animals.

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