

1 TITLE: Temporal patterns of waterhole use as a predator avoidance strategy

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ABSTRACT

Animals that depend on water sources in dry environments must balance their water demands with predation risk. In settings of water scarcity, predators may strategically exploit prey's dependence on water; prey may adjust their use of water sources either spatially or temporally to avoid overlapping with predators. To examine the spatiotemporal dynamics of predators and prey at water sources, we studied the use of semi-permanent waterholes in the dry season by red-fronted lemurs (*Eulemur rufifrons*), a primate species that exhibits flexible circadian activity patterns and inhabits a dry deciduous forest in western Madagascar. We hypothesized that lemurs avoid predators in their spatiotemporal use of waterholes. We analyzed the patterns of camera-trap activations at waterholes by red-fronted lemurs and their two main predators: fossa (*Cryptoprocta ferox*) and Madagascar harrier hawks (*Polyboroides radiatus*). We found that red-fronted lemurs were unlikely to use waterholes at times of day when predators were commonly present, and that the distributions of times of waterhole use differed between red-fronted lemurs and each of their predator species. Red-fronted lemurs frequently used waterholes that were also used by predators within the same week in part because the predators used a variable set of water resources. In this system, predators did not appear to exploit waterholes for the high density of red-fronted lemurs attracted to them, but instead likely used waterholes primarily to meet their own water demands. Our findings suggest that when predators and prey share water sources, prey may adjust their behavior to reduce their risk of overlap with predators, including through avoidance of indirect cues of predation, such as waterholes at particular times of day.

KEYWORDS: camera trap, carnivore, predator-prey interactions, primate, raptor

INTRODUCTION

In water-scarce environments, water sources present a dilemma for animals that drink from them (Valeix et al. 2009; Sirot et al. 2016). Due to physiological demands, some animals have no choice but to use the few available sources of water, leading to higher population densities and more intense habitat use near lakes, rivers, waterholes, and other sources of water (Boroski and Mossman 1996; Bleich et al. 2010; Valeix 2011). Higher densities of prey are predicted to attract predators, increasing predation risk (Freese 1978; Valeix et al. 2009). Predators also need access to water, and water sources in open areas of habitat may visibly expose prey to predators. In other words, waterholes may provide an indirect cue of predation risk (Orrock et al. 2004). Water sources, therefore, have the potential to shape the landscape of predation risk for prey in these systems.

Semi-permanent waterholes in arid environments represent an especially acute example of how water impacts predation risk and prey counter-strategies to predation. In these settings of water scarcity, predators may be able to exploit prey's dependence on water. In African savanna habitats, for example, lions (*Panthera leo*) frequently ambush prey from the vegetation surrounding waterholes (Makin et al. 2017). Previous research has demonstrated that the preferred prey species of lions employ a variety of strategies to reduce the risk of predation at waterholes, including increased vigilance, reduced waterhole use at night, and increased group size at riskier waterholes (Valeix et al. 2009).

Understanding the role of waterholes in shaping predator risk in a wide variety of systems requires systematic study of predation risk at these sites. However, observing predation events directly can be challenging, and many accounts of predation are anecdotal or comprise small

sample sizes (Heymann 1987; Wright et al. 1997; Matsuda et al. 2008; Fichtel 2009; Goheen & Swihart 2005). In addition to these challenges, ecological characteristics of some predator and prey species, such as non-diurnal activity periods, make these dynamics even more challenging for researchers to observe directly (Müller et al. 2000; Kappeler and Erkert 2003).

Recent studies have attempted to circumvent these challenges through the use of automated technologies, including motion-activated camera traps to monitor the activity patterns of predators and their prey (Linkie and Ridout 2011). With this approach, researchers have demonstrated that leopards (*Panthera pardus*) prioritize encounters with prey species over avoiding lions, their competitors, in their diel activity periods (Mugerwa et al. 2017). Similarly, other studies found that mammalian species partitioned their use of artificial water sources in dry habitats, perhaps as a strategy to minimize competition at these small, highly valuable resources (Edwards et al. 2015, 2017). Temporal overlap between predators and prey as inferred from camera traps concords with scat analyses of predators' diets, implying that data from camera traps accurately reflect predation risk (Torretta et al. 2017).

Herein, we examined the patterns of waterhole use by a water-dependent species, the red-fronted lemur (*Eulemur rufifrons*), in a seasonally water-scarce environment. Red-fronted lemurs are cathemeral, i.e., they exhibit a habitual pattern of activity that is characterized by flexible periods of activity and rest throughout the 24-hour period (Kappeler and Erkert 2003). As a result, their patterns of circadian activity, both at waterholes and generally, might be more flexible and less constrained than those of a more strictly diurnal or nocturnal species. Given this temporal flexibility, red-fronted lemurs' patterns of waterhole use could respond to dynamic ecological pressures that vary throughout the diel period, such as predation risk. In this system, red-fronted lemurs select among several available waterholes along a riverbed (Scholz and

Kappeler 2004; Amoroso et al. 2019). Variation in predation risk among these waterholes could impact patterns of usage by the lemurs.

Using camera traps, we assessed how lemurs navigated this presumably high-risk environment relative to the presence of their two main predators, the fossa (*Cryptoprocta ferox*) and the Madagascar harrier hawk (*Polyboroides radiatus*) (Goodman et al. 1993). Both of these species have been observed to drink from waterholes, but it remains unknown whether they also exploit the waterholes for the high density of prey or primarily visit these locations for the purpose of meeting their water demands. Previous research using scats from fossa in the study population estimated that red-fronted lemurs comprise around 5% of the diet of the largest Malagasy carnivore (Rasoloarison et al. 1995). Fossa are also cathemeral (Dollár 1999; Merson et al. 2018), and this activity pattern has been hypothesized to drive the cathemerality of lemurs (Colquhoun 2006). Madagascar harrier hawks have been observed to predate red-fronted lemurs (Karpanty 2006). Accordingly, in prior experiments in this study population, red-fronted lemurs performed referential alarm calls in response to harrier hawk vocalization playbacks (Fichtel and Kappeler 2002). This call also elicited a response of scanning the sky and moving lower in the tree canopy from exposed positions, behaviors that functioned to reduce aerial predation risk (Fichtel and Kappeler 2002). Madagascar harrier hawks are diurnal, and may also exert pressures on red-fronted lemur activity periods (Karpanty and Wright 2007).

We aimed to understand how and whether lemurs balance their water demands with potential predation risk. Successful predation events of red-fronted lemurs have not been observed directly by human observers. Prior to the present study, however, one of the authors (CF) observed an unsuccessful predation attempt by a Madagascar harrier hawk on a group of red-fronted lemurs that was in the trees around the edge of a waterhole. Consistent with this

observation, the lemurs commonly perform vigilance and threat perception behaviors as they approach waterholes, such as “woof” vocalizations and “tail wagging,” which are common responses to terrestrial predators (Pereira and Kappeler 1997; Fichtel and Hammerschmidt 2002; Fichtel and Kappeler 2002). Specifically, we investigated the hypothesis that lemurs avoid predators in their spatiotemporal use of waterholes. We investigated two predictions. First, we predicted that lemurs would avoid waterholes that were frequently visited by predators. Second, we expected that lemurs would use waterholes at times of the day when predator species were less commonly present at waterholes. Given the multiple waterholes available for red-fronted lemurs and their predators to use and the flexibility of red-fronted lemurs’ activity patterns, this setting provides a valuable opportunity to investigate these predictions.

MATERIALS AND METHODS

Study system

This study took place in Kirindy Forest/Centre National de Formation, d’Etudes et de Recherche en Environnement et Foresterie, a protected core area of the Aire Protégée Menabe Antimena. Kirindy Forest is a dry deciduous forest occupied by a population of red-fronted lemurs that has been studied for over two decades (Kappeler and Fichtel 2012). This population comprises several groups that are habituated and collared and an unknown number of uncollared groups.

In this habitat, red-fronted lemurs drink water from small standing waterholes that form as the river stops flowing during the local dry season between April and November (Scholz and Kappeler 2004). Previous work in this population suggests that these waterholes are a driver of red-fronted lemur habitat use during the dry season, when water is not available elsewhere (Scholz and Kappeler 2004). Given the dependence of the red-fronted lemur population on these

waterholes, the waterholes are sites of overlap between resident groups (of which six are definitively known and collared) and an unknown number of non-resident groups that travel from beyond the extent of the study site to reach the water sources. During the period of this study, the collared lemur groups ranged in size from 3 to 13 individuals. In addition to red-fronted lemurs, a number of other species drink from waterholes during the dry season, including the fossa and the Madagascar harrier hawk.

Data collection

To quantify the use of waterholes by lemurs, fossa, and harrier hawks, we monitored a subset of between 6 and 12 (out of 35 total waterholes at the start of data collection) waterholes using motion-activated video camera traps (Bushnell 119875C Trophy Cam) positioned around the edge of waterholes along a 2-km stretch of the riverbed continuously from July-September 2017. The subset of waterholes that was monitored was chosen arbitrarily to capture variation in waterhole size, location, and qualitative characteristics, and was varied from week to week as waterholes dried across the course of the dry season. Our choice of the number of waterholes to monitor depended in part on the number of cameras required to provide adequate coverage around the edge of differently-sized waterholes. These cameras were active 24 hours per day and recorded one-minute videos during daylight and 15-second videos in the dark using an infrared illuminator. From these videos, we extracted the dates and times of camera activations by all three species. From videos of red-fronted lemurs, we also recorded the group ID if the lemurs were collared. If multiple groups (e.g. two collared, or one collared and one uncollared) activated the camera, that was also noted. If more than one uncollared group overlapped at the waterhole edge, we developed a heuristic for counting the number of groups. Specifically, for uncollared

individuals, we considered repeated camera activations less than one hour apart to comprise one waterhole visit. Repeated camera activations by uncollared individuals extending for each additional hour were considered an additional visit. This decision was based on the amount of time that known, collared groups spent activating the cameras during each visit, which was at maximum 60 minutes and more commonly between 10 and 30 minutes.

Analyses

To determine whether predator risk shaped lemur use of waterholes, we tested whether the number of visits to waterholes by predators predicted lemur groups' use of waterholes each week. We used generalized linear mixed models ("glmer.nb" function in the *lme4* R package; R Development Core Team, 2011; Bates *et al.*, 2015) to test for a relationship between predator visits and lemur group visits to each monitored waterhole in a given week. We investigated whether lemur visits were a function of fossa visits and harrier hawk visits in two separate statistical models. Waterhole identity was included as a random intercept effect in both models. Because our dependent variable was measured as count data and contained a large number of zeroes, we modeled the data using a negative binomial distribution. We also examined the counts of visits by lemurs and both predators to each waterhole summed across the entire study period, to see whether lemurs generally avoided waterholes that were most frequently used by predators, outside the relatively arbitrary binning of visits by week. We included log-transformed counts of lemur visits as a function of log-transformed counts of visits by each predator in a linear model (lm function in R).

To examine the timing of lemurs' waterhole use relative to that of predators, we estimated the coefficient of overlap, Δ , between camera activations by lemurs and by each of

their predators at the waterholes (using the “overlapEst” function in the *overlap* R package; Meredith & Ridout, 2016). The value of Δ can range from 0, representing no overlap to 1, complete overlap. We chose the Δ_4 estimator of overlap, which compares kernel densities estimated at the times of the observations, and is recommended by the package developers for minimum sample sizes exceeding 75 observations, based on their simulations (Linkie and Ridout 2011; Rowcliffe et al. 2014; Meredith and Ridout 2016). We also bootstrapped this estimate by resampling one thousand times from a kernel density fitted to the original data, and calculated the bootstrap mean, Δ_{4B} (using the “bootEst” function in *overlap*). To test for differences between the distributions of camera activations between lemurs and two of their predator species across the 24-hour cycle, we performed Watson’s two-sample test of homogeneity, which returns the test statistic U^2 . This is a test for circular data, such as time, and thus appropriate for our temporal data.

RESULTS

Overall, our camera traps recorded 142 videos of fossa, 144 of Madagascar harrier hawks, and 3728 videos of red-fronted lemurs at waterholes (Fig. 1). Multiple videos typically comprised each visit by a group of red-fronted lemurs or predator; thus, the videos corresponded to 683 visits by red-fronted lemurs to the waterholes (245 of which were by identifiable collared groups), 46 visits by fossa, and 39 visits by Madagascar harrier hawks. We found considerable co-occurrence of red-fronted lemur groups at waterholes, with 33.9% of the first camera activations by collared groups (which could be definitively identified) occurring within an hour of another group’s first camera activation at the same waterhole.

----- FIG. 1 HERE -----

We found no statistical support for the prediction that lemur groups avoided using waterholes that were more frequently visited by predators (Fig. 2). Neither the count of fossa nor Madagascar harrier hawk visits to waterholes was a significant predictor of lemur visits, and counter to expectations, both had small positive coefficients (Table 1). Predators exhibited considerable heterogeneity from week to week in their waterhole use. An extreme example of this was a waterhole with seven visits by Madagascar harrier hawks in one week, and zero visits the following week. When we combined all visits to each waterholes across the study period, we found a similar result: neither the count of fossa nor harrier hawk visits was a significant predictor of lemur visits, and both had positive coefficients (fossa: $\beta=0.50$, $SE=0.32$, $t=1.57$, $P>0.05$; harrier hawk: $\beta=-.54$, $SE=0.29$, $t=1.89$, $P>0.05$).

----- FIG. 2 HERE -----

In contrast, we found some support for the second prediction. Lemurs were relatively unlikely to overlap with predators in the timing of their waterhole use generally (Fig. 3). Lemurs activated the waterhole cameras at two peak times: one in the morning at around 09:30h, and another in the evening at 17:45h. These peaks fell on either side of the most frequent camera activations by the Madagascar harrier hawk, which tended to occur at midday. Fossa activated the waterhole cameras more consistently throughout the 24-h period, with slightly higher frequencies at night than during the day, especially between the hours of 18:00h and 02:00h. Consistent with the hypothesis that lemurs avoided predators, we recorded only one instance of a lemur group's first camera activation occurring within an hour of a fossa's first camera activation (0.3% of all lemur visits) and only two instances within an hour of a Madagascar harrier hawk's first camera activation (0.6% of lemur visits) at the same waterhole.

----- FIG. 3 HERE -----

When we examined the overall timing of each species' waterhole use (i.e. with times of use from across the study period lumped together), we found evidence of avoidance in the timing of waterhole use. We calculated a low coefficient of overlap between red-fronted lemurs and Madagascar harrier hawks ($\Delta_4 = 0.396$; $\Delta_{4B} = 0.439$, 95% *CI*: 0.38-0.50). The distribution of camera trap activations by lemurs was statistically significantly different from that of harrier hawks ($U^2 = 5.92$; $P < 0.001$). For red-fronted lemurs and fossa, we also calculated a low coefficient of overlap ($\Delta_4 = 0.328$; $\Delta_{4B} = 0.403$, 95% *CI*: 0.34-0.47). The distributions of camera trap activations by lemurs and fossa were also found to be statistically significantly different from one another ($U^2 = 4.65$; $P < 0.001$).

DISCUSSION

In this arid system featuring a shared waterhole, we found modest support for red-fronted lemurs avoiding waterholes at times that fossa and Madagascar harrier hawks were commonly present. Our results suggest that lemurs can reduce predation risk by these two complementary predators by visiting waterholes in the mid-morning and evening. In the case of harrier hawks, lemurs can reduce the likelihood of an encounter by avoiding waterholes during the middle of the day when harrier hawks are present. On the other hand, because fossa visit waterholes flexibly throughout the diel cycle, lemurs may avoid waterholes at night when fossa are generally more active, and/or use alternative strategies like heightened vigilance to adequately avoid fossa. The pattern of waterhole use by lemurs may thus represent a balance between the predictable harrier hawk and the unpredictable fossa, similar to patterns of space use and predator avoidance observed in other systems (Sokol-Hessner and Schmitz 2002; Thaker et al. 2011). Although our results are consistent with the hypothesis of lemurs avoiding predators at waterholes, we do not know the

mechanisms that have resulted in the observed temporal patterns. Lemurs may avoid waterholes at specific times of day, or they may be sensitive to the presence of predators in the surrounding habitat in their decisions about whether to visit waterholes.

We report a very low co-occurrence of lemurs with both predators (once between lemurs and fossa, twice between lemurs and harrier hawks) within an hour of each other at the same site. This low frequency of overlap (<1% of all lemur visits, collectively) suggests that in addition to temporal patterning, lemurs are detecting and avoiding direct cues of the predators. Red-fronted lemurs may be an especially relevant species for investigating temporal adjustments to predation, given their cathemerality, an activity pattern that peaks flexibly throughout the 24-hour cycle. More broadly, the distinctive pattern of non-overlap among red-fronted lemurs and their predators at waterholes aligns with previous evidence of anti-predator behavior by prey at waterholes in other biological systems (Valeix et al. 2009; Valeix 2011; Crosmar et al. 2012; Edwards et al. 2015).

The infrequent co-occurrence between lemurs and predators at the same site within an hour of each other suggests that heightened vigilance and other antipredator strategies by red-fronted lemurs at waterholes are effective, and that these behaviors make it difficult for predators to target red-fronted lemurs at waterholes. For example, we report a high rate of overlap with other groups at waterholes (33.9%), which would increase the number of individuals present and could reduce the costs of vigilance and increase drinking time for individuals. Such an effect has been demonstrated for larger groups at waterholes in other species, including coatis (*Nasua narica*) and white-faced capuchins (*Cebus capucinus*) (Burger, 2001; Burger & Gochfeld, 1992; Valenzuela & Ceballos, 2000). However, overlap among groups may also be accompanied by increased risk of intergroup aggression or competition, as has been reported for patas monkeys

(*Erythrocebus patas*) (Struhsaker and Gartlan 1970). How animals balance the potential aggressive costs and predation risk benefits of group encounters at waterholes is an open question for future research.

We did not find evidence that red-fronted lemurs avoided waterholes commonly visited by predators within the same week, perhaps because predators were not consistently observed at particular waterholes. Although we did not detect a relationship between lemur and predator visits to waterholes, the coefficients were positive, contrary to our prediction of avoidance. A positive relationship between red-fronted lemurs' waterhole use and that of the two predator species may reflect predators' attraction to waterholes commonly visited by lemurs. It is worth noting, however, that the timescale we quantified waterhole use was potentially too coarse to detect patterns of spatial avoidance of predators at waterholes, especially because predators were flexible in their waterhole use from week to week. Additional research is needed to understand the drivers of predator drinking patterns, and to what degree waterholes are used to meet the thermoregulatory and hydration needs of predators, versus as an opportunity to encounter prey.

Why predators did not appear to use the regularity of red-fronted lemurs' visits to the waterholes to their hunting advantage is an unanswered question. Whether predators seek out other prey at waterholes remains unknown. In this study, we did not account for the temporal patterns of waterhole use by other species, especially small mammals such as a variety of tenrec and rodent species (Ganzhorn et al. 1996), that might also serve as prey for the two predators. Future research should investigate a wider breadth of species involved in predator-prey dynamics in this ecosystem.

Alternatively, the temporal pattern of waterhole use by red-fronted lemurs observed in this study could simply reflect lemurs' activity patterns, in general, rather than an antipredator

strategy. Indeed, red-fronted lemurs frequently demonstrate a bimodal pattern of activity, with their primary periods of foraging and social activity in the early-midmorning and early-midafternoon, punctuated by a mid-day rest period, presumably to avoid thermoregulatory costs during the hottest period of the day (Kappeler and Erkert 2003). The lemurs may primarily seek out water sources in mid-late morning and mid-late afternoon following periods of active foraging, and their infrequency of waterhole use during dark hours and midday may reflect their general inactivity (i.e. resting state) during these periods. This study cannot rule out such an explanation, but this alternative would still likely reduce the risk of predation for lemurs at waterholes, and perhaps during their active periods more generally. More broadly, the cathemerality of lemurs could be the consequence of many interacting factors, not limited to foraging opportunities, interspecific competition, predator avoidance, and thermoregulation (Kappeler and Erkert 2003; Colquhoun 2006; Donati and Borgognini-Tarli 2006), and future research should examine overlaps in activity between red-fronted lemurs and their predators in a broader set of habitat types, beyond waterholes.

We found evidence of temporal avoidance of two predator species by red-fronted lemurs, corroborating previous evidence of temporal differentiation by predators and prey at waterholes in other systems (Valeix 2011; Crosmar et al. 2012; Sirot et al. 2016). However, we failed to find support for our prediction that red-fronted lemurs would avoid waterholes visited more by predators; lemurs were no more or less likely to use waterholes that predators also used. Our study highlights a unique characteristic of water resources: unlike food resources, waterholes attract species from a broad range of ecological guilds, including prey species and their predators. For this reason, the timing of prey's waterhole use may be under pressure to avoid overlapping with predators' visits to waterholes (Edwards et al., 2017). Species with flexible

320 activity patterns, such as the red-fronted lemur, may be less constrained in their response to the
321 temporal pressures of predation, and represent a useful system for exploration of these questions.
322 Future work should expand the investigation of temporal differentiation between predators and
323 prey at water sources into additional dry ecosystems to better understand the effects of limited
324 water resources on interspecific interactions.
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For Review Only

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FIGURE LEGENDS

Figure 1. Still photos of animals taken from videos recorded by the motion-activated camera traps at waterholes in Kirindy Forest, Madagascar in July 2017. a: red-fronted lemurs (*Eulemur rufifrons*); b: Madagascar harrier hawk (*Polyboroides radiatus*); c: fossa (*Cryptoprocta ferox*).

Figure 2. Counts of red-fronted lemur (*Eulemur rufifrons*) group visits to a single waterhole in Kirindy Forest, Madagascar during one week plotted against the number of visits to the same waterhole in the same week by each predator species. a: fossa (*Cryptoprocta ferox*), b: Madagascar harrier hawk (*Polyboroides radiatus*). Counts of predator visits are scaled by z-score.

Figure 3. Kernel density of activity throughout the 24-hour cycle by red-fronted lemurs (*Eulemur rufifrons*), Madagascar harrier hawk (*Polyboroides radiatus*), and fossa (*Cryptoprocta ferox*) at waterholes in Kirindy Forest, Madagascar as estimated by camera trap activations. Gray shading on either side of the plot represents that the x-axis is circular.

TABLES

Table 1: Results of generalized linear mixed models of visits to waterholes by red-fronted lemurs (*Eulemur rufifrons*) as a function of frequency of use by fossa (*Cryptoprocta ferox*) and harrier hawks (*Polyboroides radiatus*) in Kirindy Forest, Madagascar. For both models, n=61 for number of observations (i.e. waterhole-weeks). Predator visits are scaled by z-score. Waterhole identity is included as a random intercept effect in both models (fossa model: $SD=1.51$; harrier hawk model: $SD=1.34$).

Model	Fixed effects	β (SE)	z	P
Lemur visits ~ fossa visits	Intercept	-0.12 (0.28)	-0.43	0.67
	Fossa visits	0.15 (0.08)	1.79	0.07
Lemur visits ~ hawk visits	Intercept	0.33 (0.33)	1.01	0.31
	Hawk visits	0.02 (0.14)	0.16	0.87





