VIDEO ARTICLE

The difference between night and day: antipredator behavior in birds

Jessica L. Yorzinski · Michael L. Platt

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Abstract Animals have evolved sophisticated strategies for avoiding predators during the day. These strategies can vary depending on the type of predator and level of threat. Although nocturnal predation is a major cause of animal mortality, antipredator behavior at night is poorly understood. To investigate how diurnal animals adjust their antipredator behavior during these different conditions, peahens (Pavo cristatus) were exposed to a taxidermy raccoon during the daytime and nighttime. During the day, the peahens emitted loud antipredator calls, extended their necks upward, adopted a preflight posture, and approached the predator; at night, the peahens emitted soft hissing calls, remained stationary, piloerected their feathers, and raised their tails. The results demonstrate that birds adopt radically different antipredator behavior depending on whether the threat occurs in the daytime or nighttime. These different tactics could result from limitations in sensory abilities. Videos showing nocturnal and diurnal antipredator behavior of peafowl are available online (http://www.momo-p.com/showdetail-e. php?movieid=momo111110pc01a and http://www.momop.com/showdetail-e.php?movieid=momo111110pc02a).

J. L. Yorzinski (🖂)

Animal Behavior Graduate Group and Department of Evolution and Ecology, University of California, Davis, CA 95616, USA e-mail: jyorzinski@ucdavis.edu

J. L. Yorzinski · M. L. Platt Center for Cognitive Neuroscience, Duke University, Durham, NC 27710, USA

M. L. Platt

Department of Neurobiology, Duke University Medical Center, Durham, NC 27710, USA

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Introduction

Animals exhibit sophisticated antipredator behavior in the daytime. They emit specific vocalizations that convey information about the type of predator and level of danger associated with it (Owings and Hennessy 1984; Fichtel and Kappeler 2002; Griesser 2008). They can approach predators by mobbing them (Yorzinski and Vehrencamp 2009) or flee from them (Lima 1994). In contrast, antipredator behavior in the nighttime is less often studied (Lima et al. 2005) even though the incidence of nocturnal predation can be especially high (Isbell 1990; Isbell and Young 1993; Reidy et al. 2009).

Animals can selectively choose their sleeping sites and alter their vigilance levels to reduce their chances of being predated at night. Many animals strategically sleep in places that are difficult for predators to access, such as at the tips of tree branches or above dense undergrowth (Busse 1980; Trivedi and Johnsingh 1996). Competition for these preferred sleeping sites can be intense (Tenaza and Tilson 1985). Animals can also alter their vigilance levels at night by remaining awake (Lendrem 1984; Rattenborg et al. 1999; Revell and Hayes 2009). Because of the difficultly of observing nocturnal predation (Isbell 1990; Isbell and Young 1993), we know virtually nothing about how diurnal animals directly respond to nocturnal threats (Lima et al. 2005).

Anecdotal reports indicate that diurnal primates and birds sometimes emit vocalizations in response to nocturnal threats but do not seem to mob the predators (Vessey 1973; Busse 1980; reviewed by Southern et al. 1982;



Shealer and Kress 1991; Carter et al. 2007). For example, ring-billed gulls emitted alarm calls when they were disturbed at night and fled from the area (Emlen et al. 1966; Southern et al. 1982). In contrast, Franklin's gulls did not exhibit any overt antipredator behavior in response to a nocturnal threat (Burger 1974). Only one study has experimentally exposed diurnal birds to predators at night; the birds flushed and emitted calls (Tillmann 2009).

In this study, the antipredator behavior of peahens (*Pavo cristatus*) was systematically investigated to learn how animals respond to nocturnal predation attempts. Peahens are a suitable species in which to study antipredator behavior because they are vulnerable to predation and exhibit antipredator responses (Kannan and James 1998). Their antipredator behavior at night was directly compared with that during the day to assess how they responded to the same threat at different times. The threat used to elicit antipredator behavior was a taxidermy raccoon (*Procyon lotor*); raccoons are known predators of adult peafowl in North America (Seideman 1993) that can be active during the day or night (Ellis 1964) and they are present at the study site.

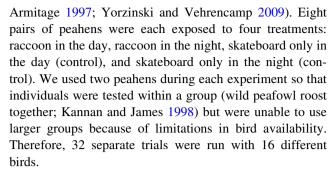
Materials and methods

Animals and housing

Antipredator behavior during the daytime and nighttime was investigated in a captive population of adult peafowl in Durham, NC, USA (36.01°N, 79.02°W) from September through November 2010. The birds were housed in a large outdoor enclosure (92 m perimeter) within a forest where they likely saw predators (including raccoons) outside their enclosure. Eight of the birds were originally captured from free-ranging populations in California and another eight of the birds were captured from free-ranging populations in Florida within 2 years of the start of this study, and they were therefore regularly exposed to natural predators for most of their lives; they remained in captivity after this study was completed. They were marked with a combination of metal and white plastic leg bands and were given food and water ad libitum. The testing cage $(8.4 \times 6.2 \text{ m})$ was along the edge of the large enclosure and its perimeter was surrounded by black plastic to prevent birds from the large enclosure from seeing into the testing cage.

Experimental design

The predator treatment was a taxidermy raccoon mounted on a skateboard and the control treatment was just the skateboard. Taxidermy models of predators are frequently used to elicit antipredator behavior (Blumstein and



For each set of trials, two females from the large enclosure were randomly selected and were housed together in the testing cage. We only tested females because we did not have access to additional males. The daytime trials were conducted in the morning between 8:00 and 11:00 EST (at least 30 min after sunrise; 15.2 ± 1.7 °C); the nighttime trials were conducted after it was completely dark between 19:30 and 22:30 (at least 1 h after sunset; 17.1 ± 1.5 °C). Although the moon phase varied from a full to crescent moon across trials, the amount of light reaching the ground through the canopy was minimal (between 0.01 and 0.02 lux; Extech EasyView 31 light meter) and was therefore unlikely to be driving their behavior (Mougeot and Bretagnolle 2000); furthermore, because each pair of birds was tested within 4 days, the moon phase was similar for each set of trials. The skateboard (and raccoon in predator treatments) were concealed underneath a large container that had a cloth covering one of the sides. The researcher revealed them by pulling on a fishing line that was attached to the front of the skateboard and pulled them out of the container (approximately 0.20 m/s) through the side with the cloth (they were revealed at least 5 min after the researcher began observing). In the daytime trials, the skateboard was pulled to the middle of the cage because the birds moved around the enclosure during these trials; in the nighttime trials, the skateboard was pulled directly in front of where the birds were sleeping because the birds were stationary during these trials (see "Results"). After 10 min, the researcher pulled the skateboard forward another 1-2 m. After another 20 min, the skateboard was pulled out of the testing cage. At night, the distance between the skateboard (and predator) and birds was approximately 1.5-2 m. During the day, the distance between the skateboard (and predator) and birds frequently changed as the birds repeatedly approached and retreated from the stimulus; the birds in the daytime trials often approached the stimulus so that they were within 1 m of it.

The order of treatments was randomized and each pair of birds was exposed to all four treatments within 4 days. The researcher (JLY) remained hidden during the entire trial while recording the daytime trials (Sony Handycam DCR-SR68; M-audio Microtrack II connected to a Sennheiser K6 microphones with ME62 omnidirectional



capsule) and nighttime trials (Sony Handycam HDR-HC1 and LT Security DVC-CMR601-CM night vision camcorder multiplexed with a Swann DVR4-Net-Plus). The amplitudes of the different call types were estimated when the researcher elicited the calls in peahens and recorded their amplitude (ExTech 407730 Digital Sound Level Meter); all amplitude values are dBA SPL re 20 μPa and were measured 1 m from the source.

At night, females in the testing enclosure were facing in

the direction of the stimulus, sitting, and were within 1 m of each other for every trial (Fig. 1a; http://www.momo-p.com/showdetail-e.php?movieid=momo111110pc01a). However, one bird in one of the pairs slept out of view behind a tree in both of her nighttime trials and was therefore excluded from the nighttime analyses. Peahens in this study slept near the ground because their enclosure prevented them from flying high into the trees. Wild peahens usually roost in tall trees at night (Kannan and James 1998) but sleep on the ground when they are incubating their eggs. In most of the night trials (over 80%), the birds roosted on a large log and were therefore slightly elevated off the ground (Fig. 1a), which resembles the manner in

which they would roost in the wild except that the log was

close to the ground rather than high up in the trees.





Fig. 1 During the nighttime (**a**), peahens lifted their tails while remaining stationary and either continued sitting or stood up (http://www.momo-p.com/showdetail-e.php?movieid=momo111110pc01a); during the daytime (**b**), peahens extended their neck upwards and approached the predator (http://www.momo-p.com/showdetail-e.php?movieid=momo111110pc02a)

Measurements and statistical analysis

The total number of antipredator vocalizations ("bu" and "bu-girk;" Takahashi and Hasegawa 2008) and hiss vocalizations (Fig. 2) emitted within 20 min after the stimulus was revealed was recorded for each trial (calls from both individuals within each pair were summed). The hiss vocalizations were so soft that the audio recorder did not record them; however, when birds hissed, their throat inflated and the number of times their throats inflated was counted. No antipredator vocalizations were emitted before (at least 5 min) the trial began. The amount of time birds were vigilant (scanning or moving) or non-vigilant (preening, foraging, and sleeping) was recorded during the first and fifth minute after the stimulus was revealed. The change in vigilance (during the trial) was calculated by subtracting the amount of time spent vigilant during the first minute from the fifth minute and then dividing by the amount of time spent vigilant during the first minute; thus, if the birds spent 60% of their time vigilant during the first minute and only 40% of their time vigilant during the fifth minute, the change in vigilance would be negative [(0.40 - 0.60)/0.60 = -0.33) and indicate that the birds became less vigilant over time. At night, birds were scored as scanning when one of their eyes was open; because of equipment limitations, only one eye of each bird could be recorded, and given the position where the birds roosted relative to the video camera, their right eye was always the eye that was being monitored. It is therefore possible that we underestimated the scanning rate because the right eye of the bird could have been closed while the left eye was scanning the environment (Rattenborg et al. 1999).

The occurrence of piloerection (either the neck feathers or feathers along the top of the shoulders) was recorded if it occurred within 20 min after the stimulus was revealed (at least one bird within a pair needed to piloerect her feathers). The duration of piloerection and the latency to the first occurrence of piloerection was measured. The occurrence of piloerection during the times when the stimulus was moving (1st and 10th minute) and not moving (2nd-9th and 11th-19th minute) were compared. The vertical extension of the birds' necks was scored every 5 s for 1 min after the stimulus was revealed and the mean value was then taken for each bird. This neck extension was calculated by obtaining the screen coordinates of a given frame for the top of the bird's head, the top of the bird's shoulder, and the bottom of the bird's body. The distance between the top of the head and the shoulders was divided by the distance between the shoulders and the bottom of the body; this proportion ensured that the values were consistent irrespective of the distance between the birds and the video camera. Last, we recorded whether or not at least one bird within a pair approached the stimulus within 1 min of



Fig. 2 Antipredator calls emitted during the day (a "bu", b "bu-girk", c "khok") and night (d hiss)

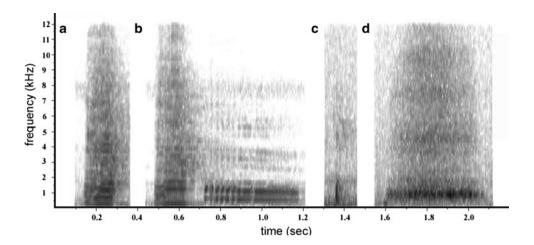


Table 1 Summary statistics

	Daytime predator	Daytime control	Nighttime predator	Nighttime control
Vocalizations				
"bu" (# of calls)	3.3 (1.8)	0	0	0
"bu-girk" (# of calls)	10.9 (6.2)	0	0	0
Latency to emit "bu" or "bu-girk" (min)	4.5 (2.1)	_	_	_
"hiss" (# of calls)	0	0	1.88 (1.39)	2.0 (1.59)
Latency to emit "hiss" (s)	_	_	18 (14)	2.11 (1.12)
Piloerection				
Occurrence (# of trials)				
Overall	0	0	6	4
When predator moving	0	0	6	4
When predator stationary	0	0	1	0
Duration (s)	_	_	43.8 (12.9)	38.9 (13.9)
Latency (s)	_	_	15.56 (3.57)	10.21 (5.03)
Approach (# of trials)	7	8	0	0

Means and SE (in parentheses) are reported

the stimulus being revealed for all four treatment types and then compared the number of approaches with that for the daytime trials.

Nonparametric data were analyzed with Friedman's nonparametric repeated-measures comparison and post-hoc comparisons were made with Wilcoxon signed-rank tests and Wilcoxon sign tests (reported with T or X^2 test statistics); parametric data were analyzed using mixed models with repeated measures or t tests (reported with F or t test statistics). Unless otherwise noted above, measurements for each individual of a pair were averaged and this average was used in the analyses; each pair of birds was used as a sampling unit, rather than each individual bird, because the birds within each pair were likely to be influenced by each other and their behavior was therefore not independent. Pairs were included as the repeated measure. When multiple comparisons were made in the vigilance and neck extension analysis, significant differences were concluded

when the P value fell below our Bonferroni adjusted P value of 0.008 (0.05/6 comparisons). All behavior was analyzed from the video recordings and the statistical tests were conducted with SAS version 9.2 (SAS Institute 2002). Means \pm SE are provided to illustrate effect sizes.

Results

Vocalizations and vigilance

Peahens did not emit "bu" (Fig. 2a; 95 dBA) and "bugirk" (Fig. 2b; 95 dBA) vocalizations in similar numbers across treatments ($X^2 = 15$, df = 3, P = 0.0018); they only emitted these vocalizations in response to the predator during the day and emitted them after a relatively long latency once the predator was revealed (Table 1). They also only emitted "khok" vocalizations (Takahashi and



Hasegawa 2008; Fig. 2c; less than 50 dBA) in response to the daytime predator but many of these calls were so soft relative to the background noise that it was not possible to reliably count them.

The birds only hissed (Fig. 2d; less than 50 dBA) during the nighttime treatments and not the daytime treatments, though this effect was not quite significant ($X^2 = 6.56$, df = 3, P = 0.088). They hissed at similar rates in response to the nighttime predator and nighttime control (T = 3, df = 7, P = 0.50). They primarily hissed within 1 min of the nighttime stimulus moving (77% of hisses were emitted during this period) and first hissed after the stimulus was shown (Table 1).

Peahens' change in vigilance varied depending on the treatment type ($X^2 = 10.58$, df = 3, P = 0.014; Fig. 3). During the first minute of the trial, the birds were vigilant during most of the time (predator day: $98.1 \pm 1.2\%$; control day: $94.3 \pm 3.8\%$; predator night: $99.9 \pm 0.13\%$; control night: $99.0 \pm 0.76\%$). They became less vigilant in the fifth minute of the trial compared with the first minute (more preening, foraging, and sleeping; less scanning and moving) after seeing the daytime control compared with the daytime predator (t = 3.71, df = 7, P = 0.0076); they

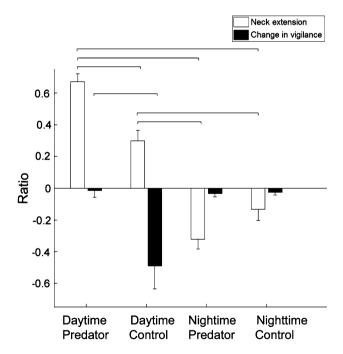


Fig. 3 Change in vigilance and neck extension with regard to treatment type. Neck extension is reported as a ratio such that a large *positive value* indicates that the neck was extended far above the shoulder line and a large *negative value* indicates that the neck was extended far below the shoulder line; change in vigilance is reported as differences in ratios such that a large *positive value* indicates that birds increased their vigilance and a large *negative value* indicates that the birds decreased their vigilance within 5 min of seeing the stimulus (see Materials and methods). Statistically significant results are connected by *lines*

also tended to become less vigilant after seeing the daytime control compared with the nighttime predator (t=3.38, df=7, P=0.012) and the nighttime control (t=2.82, df=7, P=0.039). However, their change in vigilance did not differ between the nighttime predator and the nighttime control (T=3.5, df=7, P=0.44), the nighttime predator and daytime predator (T=1, df=7, P=0.94), or the daytime predator and the nighttime control trials (T=7, df=7, P=0.30; Fig. 3).

Piloerection, postures, and movement

The occurrence of piloerection depended on the treatment type $(X^2 = 13.5, df = 3, P = 0.0037)$: peahens only piloerected their feathers in response to the nighttime treatments. At night, they piloerected their feathers more often when the stimulus was moving (T = 22.5, df = 15,P = 0.0039); in fact, only one individual piloerected their feathers during times when the stimulus was not moving. When the birds piloerected their feathers at night they either remained sitting (n = 4 raccoon trials; n = 3 control trials) or stood up (n = 2 raccoon trials; n = 1 control trials); when they piloerected their feathers, some raised their tail (n = 3 raccoon trials; n = 1 board trial)(Fig. 1a) whereas others did not (n = 3 raccoon trials; n = 3 board trials).The first time they piloerected their feathers after seeing the stimulus, they did so with a similar latency and for a similar duration in both nighttime treatments (latency: $F_{1,2} = 0.00$, P = 0.98; duration: $F_{1,2} = 0.37$, P = 0.61; Table 1).

Peahens extended their necks by different amounts depending on the treatment type ($F_{3,21} = 30.59, P < 0.0001$; Fig. 3). They extended their necks higher in daytime treatments than in nighttime treatments (daytime predator vs. nighttime predator: t = 8.70, df = 21, P < 0.0001; daytime predator vs. nighttime control: t = 7.11, df = 21, P < 0.0001; nighttime predator vs. daytime control: t = 5.42, df = 21, P < 0.0001; daytime control vs. nighttime control: t = 3.83, df = 21, P = 0.001). During the day, they extended their necks higher in response to the predator than in response to the control (t = 3.28, df = 21, P = 0.0035); during the night there was no significant difference between neck extension in the predator and control trials (t = 1.59, df = 21, P = 0.13; Fig. 3). During the day, peahens extended their necks above their shoulder line (test of whether the mean height at which they held their heads was greater or less than zero; raccoon: t = 8.34, df = 21, P < 0.0001; control: t = 3.69, df = 21, P = 0.0013); during the night, peahens' necks tended to be below their shoulder line (raccoon: t = 3.97, df = 21, P = 0.0007; control: t = 1.72, df = 21, P = 0.10).

Peahens only approached the stimulus in the daytime $(X^2 = 21.97, df = 3, P < 0.0001;$ Fig. 1b; http://www.momo-p.com/showdetail-e.php?movieid=momo111110pc02a) and approached both predator and control in similar



numbers of trials (T = 0.5, df = 7, P = 1.00). They also only bent down in a preflight posture (but did not actually take flight) after seeing the predator in the daytime (n = 4 individuals in 4 separate trials). At night, the birds never moved to a different location from where they were originally sleeping after seeing the stimulus (though they did sometimes stand up in a vigilant posture; see above).

Discussion

This is the first study to directly compare avian diurnal and nocturnal antipredator behavior. The antipredator behavior of the peahens was very different during these two conditions. During the night, peahens emitted soft hissing calls, remained stationary, piloerected their feathers, and raised their tails. Some of this behavior (hissing and raising their tails) has hitherto not been documented in this species. During the day, peahens emitted loud antipredator calls, extended their necks upward, adopted a preflight posture, and approached the predator.

This behavior is similar to anecdotal reports of behavior exhibited by free-ranging peafowl. During the day, we exposed two different flocks of free-ranging peafowl in North Carolina (one flock contained 18 birds of both sexes and the other flock contained two adult males) to the taxidermy raccoon. They approached the predator and did not fly away; they emitted "bu", "bu-girk", and "khok" calls and extended their necks in an alert posture (JLY, personal observation). Free-ranging peafowl also exhibit similar behavior in response to live predators by approaching threats (such as dogs) and emitting "bu" and "bu-girk" calls (Bill Poulos, personal communication).

At night, the captive peahens behaved similarly to their free-ranging counterparts in many respects. One nocturnal attempt at predation was witnessed in Florida and involved a large cat (probably a Florida panther) stalking a group of roosting peafowl at night (they were roosting in high trees); the peafowl did not take flight (they either remained stationary or walked around on the larger branches of the trees) but did emit "bu" and "bu-girk" vocalizations (Bill Poulos, personal communication). The free-ranging birds may have emitted loud antipredator calls because they were under greater threat than birds in the captive experiments. Two of the captive peahens used in this study (sleeping on the ground) were once observed when responding to a live raccoon at night and they exhibited behavior similar to that observed in response to the taxidermy raccoon (hissing calls, remaining stationary, and piloerecting while standing and lifting their tails); the raccoon initially approached the birds to within 2 m but retreated within 10 s of the birds exhibiting antipredator behavior (JLY, personal observation). Further studies exploring peafowl nocturnal behavior in the wild would be informative but are difficult because the birds roost in tall trees.

When peahens encounter predators during the night, piloerecting their feathers and raising their tails could make them appear larger to predators and potentially dissuade the predators from attacking (Wemmer and Wilson 1983). The hissing sound is so quiet that the predator would probably need to be directly beside the bird in order to hear it; because the birds may rely on camouflage at night to protect themselves, emitting a quiet call would not advertise their location to distant predators but could thwart imminent attack or warn nearby conspecifics of danger. It is possible that the hissing also mimics the hissing of a snake (Sibley 1955; Rowe et al. 1986). In contrast, when birds encounter predators during the day, their loud antipredator calls likely advertise their location to predators and alert nearby conspecifics. Compared with hiss vocalizations, the acoustic structure of these loud antipredator calls may also facilitate localization (Yorzinski and Patricelli 2010). By mobbing the predator (rather than relying on camouflage or fleeing), they may persuade the predator to leave the area during the day because the predator has been detected (Curio 1978). The birds also remained vigilant in response to the daytime predator and would therefore be able to monitor the predator's movements; the birds became less vigilant in response to the control but this could, in part, have been because the control stimulus was smaller than the predator stimulus. If the control stimulus was an innocuous animal (rather than just the skateboard), the birds may have remained vigilant in response to the control.

Peahens treated the predator and control similarly at night. They hissed, remained stationary, piloerected their feathers, and crouched down in response to both treatments. Peahens probably do not see well in low-light conditions. The F-number² (posterior nodal distance divided by entrance pupil diameter)² provides a rough indication of how well animals can see in the dark; diurnal animals have relatively high F-numbers² and therefore do not see as well as many nocturnal animals (Martin 1993). The F-number² of peacocks is approximately 2.10 ((11.6 mm PND/8.0 mm pupil diameter)²; Hart 2002) and this value falls within the range of F-numbers² (2–4) for other diurnal birds with similar axial lengths (distance between the anterior and posterior poles of the eye). Because of this relatively poor night vision, peafowl may be able to easily navigate their environment and identify threats during the day but have a reduced ability to do so at night (Martin 1993); they may have been unable to distinguish the predator from the control at night. Rather than responding to the type of stimulus, they seemed to respond to the movement of the stimulus (or the sound produced by the moving stimulus),



because they primarily hissed and piloerected their feathers when the stimulus was moving. Therefore, at night, the birds were able to detect changes in their environment and they treated them as potential threats; however, they seemed unable to accurately assess whether these changes represented real danger.

Even though visual capabilities may be shaping peahen antipredator strategies, other factors could also explain why the birds have different antipredator strategies in the night and day. In particular, they could be specifically employing one strategy in response to diurnal predators and another strategy in response to nocturnal predators. Different hunting techniques of diurnal and nocturnal predators could be driving different antipredator strategies during the day and night. Because animals can use different antipredator tactics, depending on predator type, level of risk, and group size (Blumstein and Armitage 1997; Arroyo et al. 2001; Fichtel and Kappeler 2002), they could likewise have alternative antipredator tactics (which are independent of predator type) depending on whether it is daytime or nighttime.

Despite the high risk of nocturnal predation (Isbell 1990; Stake and Cimprich 2003; Carter et al. 2007; Reidy et al. 2009), animals must find a balance between vigilance and sleep (Lima et al. 2005) and this balance is likely to affect their antipredator behavior. During sleep, animals can still be responsive to potential dangers but this depends on their sleep state and the type of danger (Velluti 1997; Coenen and Drinkenburg 2002). Birds are able to sleep with only one eye closed (Rattenborg et al. 1999) and this is likely to aid them in detecting potential threats while simultaneously allowing them to benefit from the restorative effects of sleep (Siegel 2003). Even though the peahens were sleeping at night, they periodically opened their eyes ("peeks;" Lendrem 1984) to scan the environment; because they were less alert during the nighttime (only "peeking") compared with the daytime (fully awake), these different states of alertness could have affected their subsequent responses to the predators. Furthermore, the eye (left or right) with which the predator was detected could have affected the peahens' initial responses. Additional studies that examine nocturnal antipredator behavior would help us better understand how animals avoid predation under different conditions.

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