RESEARCH ARTICLE

BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology

Navigating new threats: Prey naïveté in native mammals

Rebecca K. McKee[1,2] | Kristen M. Hart[3] | Spencer Zeitoune[2] |
Robert A. McCleery[2]

[1]Department of Biology, Mercer University, Macon, Georgia, USA

[2]University of Florida, Department of Wildlife Ecology and Conservation, Gainesville, Florida, USA

[3]Wetland and Aquatic Research Center, U.S. Geological Survey, Davie, Florida, USA

Correspondence
Rebecca K. McKee
Email: mckee_rk@mercer.edu

Abstract

1. Invasive predators pose a substantial threat to global biodiversity. Native prey species frequently exhibit naïveté to the cues of invasive predators, and this phenomenon may contribute to the disproportionate impact of invasive predators on prey populations. However, not all species exhibit naïveté, which has led to the generation of many hypotheses to explain patterns in prey responses. These hypotheses primarily fall into two categories: system-centric hypotheses related to biogeographic isolation (BIH) and species-centric hypotheses, like the archetype similarity hypothesis (ASH).

2. We tested the predictions of these hypotheses by assessing the response of the common raccoon (*Procyon lotor*) and hispid cotton rat (*Sigmodon hispidus*), two native mammal species with divergent snake predation histories, to the cues of the invasive Burmese python (*Python bivittatus*) in the Florida Everglades (USA). Using giving-up densities (GUDs), we assessed the responses of both cotton rats and raccoons to life-size replicas of Burmese pythons and two North American predators—eastern diamondback rattlesnakes (*Crotalus adamanteus*) and coyotes (*Canis latrans*).

3. Although cotton rats increased their GUD in the presence of all three predators relative to the novel-object control, raccoons only increased their GUD in coyote treatments.

4. These results align with the predictions of the ASH but not the BIH, and mirror observed patterns of population declines in invaded areas of the Florida Everglades.

5. More broadly, our findings suggest that naïveté may contribute to the vulnerability of some species to invasive predators even in large continental systems.

KEYWORDS
Burmese python, cotton rat, Everglades, giving-up density, invasive species, predator archetype, raccoon, rodent

1 | INTRODUCTION

The introduction of invasive predators into novel systems poses a growing threat to biodiversity and has already contributed to the endangerment of over 700 vertebrate species globally (Doherty et al., 2016). Native prey often lack the necessary behavioural and morphological traits to avoid consumption by introduced predators because of their lack of shared evolutionary history (Banks & Dickman, 2007; Cox & Lima, 2006). This phenomenon, known as prey naïveté, may explain the dramatic declines of native species following the introduction of an invasive predator (Sih et al., 2010). In the most extreme form of prey naïveté (e.g. level 1), prey completely fail to recognize the predator as a threat (Banks & Dickman, 2007). When this scenario occurs, impacts of the invasive predator are usually severe (Carthey & Banks, 2014).

However, not all species exhibit naïveté when confronted with an invasive predator (Banks et al., 2018), and multiple hypotheses have been posited to explain and predict patterns in prey response (Anton et al., 2020; Carthey & Blumstein, 2018). Fundamentally, such predictions can be subdivided into two categories—those that emphasize characteristics of the system and those that emphasize characteristics of the species (Carthey et al., 2017; Carthey & Blumstein, 2018; Cox & Lima, 2006; Salo et al., 2007). Examples of system-centric hypotheses include the insularity hypothesis, which predicts that island prey species exhibit a higher degree of naïveté towards novel predators than prey species in mainland systems, and the related system type hypothesis, which predicts that insular freshwater systems will also exhibit high degrees of naïveté due to similar patterns of biogeographic isolation (Anton et al., 2020; Blackburn et al., 2014; Cox & Lima, 2006). Collectively, we refer to these hypotheses as the biogeographic isolation hypotheses (BIH). A prominent example of a hypothesis that emphasizes species-level characteristics is the archetype similarity hypothesis (ASH), which suggests that species facing predation pressure from a similar native predator archetype may be less likely to be naïve (Carthey & Blumstein, 2018; Cox & Lima, 2006; Ricciardi & Atkinson, 2004). Predator archetypes are defined as predators sharing similar morphological and behavioural traits to obtain prey (Cox & Lima, 2006). Similarities in predator characteristics create overlapping cues between native and invasive predators, enhancing prey's ability to recognize and respond to invasive predators (Carthey et al., 2017).

Although system-centric and species-centric hypotheses are theoretically distinct, many practical aspects of these hypotheses overlap, making it difficult to discern if naïveté is driven primarily by system or species-level characteristics. For instance, insular species inherently face fewer predator archetypes. Moreover, because many examples of prey naïveté have been documented in insular and isolated systems with few predator archetypes (Anton et al., 2020; Cox & Lima, 2006; Stockwell et al., 2022), it has been challenging to separate system-level and species-level factors that drive prey naïveté. However, the invasion of Burmese pythons (*Python bivittatus*) in the Greater Everglades Ecosystem (Florida, USA) provides a rare opportunity to assess prey naïveté in a large, continental system.

Burmese pythons are large constrictors native to Southeast Asia that were introduced to Florida via the pet trade (Willson et al., 2011). The establishment of Burmese pythons in the Everglades has had wide-ranging effects on native fauna and ecological function (Guzy et al., 2023). Most notably, native mammal populations have declined dramatically since pythons first became established in the 1980s (Dorcas et al., 2012; McCleery et al., 2015; Taillie et al., 2021). Many medium-sized mammal species (mesomammals) such as common raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), bobcats (*Lynx rufus*) and foxes (*Vulpes vulpes*; *Urocyon cinereoargenteus*) appear more vulnerable to the impacts of pythons than rodents such as the hispid cotton rat (*Sigmodon hispidus*). Although pythons consume cotton rats and other rodents (Guzy et al., 2023; McCampbell et al., 2023), their population sizes do not appear to be declining in peninsular Florida (Burkett-Cadena et al., 2021; McCampbell et al., 2023). However, we note recent research implicating pythons in the decline of some rodent species, such as the Key Largo woodrat (*Neotoma floridana smalli*), in the Florida Keys (Cove et al., 2019; U.S. Fish & Wildlife Service, 2008; Redinger et al., 2024).

In addition to a growing number of invasive reptiles, the Everglades is home to 23 native snake species (Meshaka et al., 2000). Although pythons are in different families than native snakes, they share many similar morphological and behavioural traits (Ernst & Ernst, 2011). Native snakes regularly prey upon rodents and account for a meaningful proportion of cotton rat mortalities (Conner et al., 2011; Larsen et al., 2016; McCampbell et al., 2023). Conversely, depredation of even juvenile raccoons by native snakes is rare and has not been identified as a cause of mortality in survival studies (Chamberlain et al., 1999; Gehrt & Fritzell, 1999; Judson et al., 1994).

Our objective for this study was to assess the ability of system-specific and species-specific hypotheses to predict prey response to this invasive predator. To do this, we experimentally assessed naïveté in raccoons and cotton rats, two model species with divergent predation histories and population responses to pythons. We also experimentally assessed the responses of both species to two North American predators—eastern diamondback rattlesnakes (*Crotalus adamanteus*) and coyotes (*Canis latrans*)—to evaluate their reactions to native predators with differing archetypes.

Because this invasion occurred in a large continental system, the BIH predicts that both raccoons and cotton rats should not exhibit naïveté to pythons. Conversely, the ASH predicts that raccoons and cotton rats should exhibit divergent responses to python cues based on their species-specific predation histories. Specifically, the ASH predicts that raccoons will exhibit naïveté towards the cues of invasive pythons, whereas cotton rats would recognize the cues of invasive pythons and exhibit a similar level of response to both native snakes and invasive pythons. Finally, regardless of which hypothesis was supported, we predicted that both model species would exhibit an anti-predator response to native species only if they represented a predation risk. Specifically,

we predicted that cotton rats would respond to the cues of both native snakes and native canids, whereas raccoons would respond only to the native canid cues.

2 | MATERIALS AND METHODS

2.1 | Study site

To measure innate responses of model species, we sought experimental mammal populations that were in similar ecological contexts to the Everglades but were outside the python invasion zone. This ensured that mammal responses in our experiments were not influenced by learning or prior selection pressure from pythons, thus recreating conditions of the initial python establishment. Specifically, we conducted our experiments at Paynes Prairie Preserve State Park (hereafter Paynes Prairie), an 8900-ha protected area in north-central Florida. At the time of our experiments, Paynes Prairie was located over 300 km north of the python invasion front (Guzy et al., 2023). Like the Everglades (Gunderson, 1994), Paynes Prairie features a mosaic of freshwater marshes, wet prairies and hardwood hammocks (Patton & Judd, 1986). The park is home to many native snake species also found in the Everglades, including rat snakes (*Pantherophis* spp.), water snakes (*Nerodia* spp.) and eastern diamondback rattlesnakes (Dalrymple et al., 1991; Smith & Dodd, 2003). Common mammalian predators in Paynes Prairie include bobcats and coyotes.

2.2 | Field experiments

To determine if cotton rats and raccoons exhibited behavioural naïveté to Burmese pythons, we conducted foraging experiments using giving-up densities (GUDs; Brown, 1988) from February 2022—December 2022. Giving-up densities measure the perceived risk of animals by providing consistent foraging stations and measuring the food remaining (Schmidt et al., 2008). The GUD marks the point when the benefits of additional foraging are outweighed by the perceived risk (Brown, 1988; Potash et al., 2019). As animals perceive higher levels of risk in the environment, the amount of food remaining (i.e. the GUD) increases. Originally an experimental approach developed for small mammals (Brown, 1988; McCleery et al., 2022), GUDs have since been adapted to measure the perceived risk in varied taxa, including mesocarnivores (Rodriguez Curras et al., 2021; Welch et al., 2017). Across all taxa, foraging stations are created by uniformly mixing a specific amount of food with inedible substrate, such that the foraging difficulty increases as the food depletes (Figure 1).

2.3 | Treatments

We quantified the perceived risk of raccoons and cotton rats to the visual cues of Burmese pythons (invasive snake), eastern diamondback rattlesnakes (North American snake) and coyotes (North American canid), versus a novel object control (45.7-cm orange traffic cone). Because both cotton rats and raccoons are prey for coyotes (Hayward et al., 2023; Watine & Giuliano, 2017), the coyote treatment provided a positive control for both species. To test whether the model species responded to a native species resembling pythons in predator archetype, we included a treatment with a replica of an eastern diamondback rattlesnake—a known predator of cotton rats (Timmerman, 1995), but not raccoos.

In addition to predator cues, many factors such as moon cycles, cloud cover and vegetation structure affect an animal's predation risk and therefore influence GUDs (Kotler et al., 1993;

FIGURE 1 Species-specific foraging stations for (a) cotton rats (*Sigmodon hispidus*) and (b) raccoons (*Procyon lotor*) used to measure the giving-up density, or amount of food remaining, in the control and predator treatments. Cotton rat foraging stations were baited with hulled millet uniformly mixed with sand. Raccoon foraging stations were baited with cat food uniformly mixed with pine pellets.

Loggins et al., 2019). Therefore, to reduce the influence of habitat and other environmental conditions on our experiments, we clustered stations into blocks of four and calculated a relative GUD by subtracting the baseline GUD for a given station from the treatment GUD. Using a relative GUD for each station helped control the individual variation in vegetation at the station level while the random variable of block allowed us to account for factors such as weather conditions that affected each station within this area (Supplement 1). Within each block we randomly assigned a treatment (python, coyote, rattlesnake or cone control) to each station and placed either a life-size replica of a predator or a traffic cone 0.5 m from the foraging station (Figure 2). To confirm the presence of target species and ensure non-target species were not influencing our results, we placed a Spartan SR2 motion-activated game camera (Spartan Camera, Duluth, GA) at each station. Experimental methods were conducted in accordance with the University of Florida's Institutional Animal Care and Use Committee (Permit #202111381). The Florida Department of Environmental Protection provided approval for our research at Paynes Prairie Preserve State Park (Permit #05052212A).

2.4 | Cotton rats

To measure GUDs of cotton rats, we created uniform foraging stations from 35.6-cm plastic plant saucers and clear lids (Darracq et al., 2016; McCleery et al., 2022). We placed foraging stations in clusters of four, with each treatment represented at each sampling location. Within each cluster, stations were located within 8–50 m from each other. We placed clusters at least 100 m apart, a distance that exceeds the diameter of a cotton rat home range, to ensure independence (Cameron & Spencer, 1985). We filled trays with 25 mL of hulled millet uniformly mixed with 1.5 L of sifted sand (Figure 1a). To ensure cotton rats were reliably feeding from each location and

FIGURE 2 Life-size replicas of an eastern diamondback rattlesnake (*Crotalus adamanteus*), the invasive Burmese python (*Python bivittatus*) and a coyote (*Canis latrans*) deployed as visual cues in foraging experiments. A 45.7-cm traffic cone (not pictured) was also used in the novel object control.

were acclimated to the foraging stations, we pre-baited the stations for 3 days and confirmed their presence on cameras before recording a baseline GUD measurement (Darracq et al., 2016). We repeated predator treatments for three nights, resulting in three treatment GUD measurements for each station. We monitored foraging stations daily, sifting sand to record the amount of millet remaining and resetting the station with the appropriate level of food and substrate. To minimize the influence of other rodents on GUDs, we placed stations in grassy environments preferred by cotton rats (Kincaid & Cameron, 1985). Songbirds occasionally visited cotton rat GUDs but had minimal impact, consuming less than 0.5 mL of millet during preliminary testing. Additionally, because stations were grouped in clusters, the effect of birds was likely similar across all stations within a cluster.

2.5 | Raccoons

To measure the GUDs of raccoons, we constructed foraging stations from 10.16-cm diameter PVC pipe with five 2.54-cm diameter holes (Figure 1b). We placed stations in clusters of 4, with each station located within 12–60 m of each other. We placed clusters ≥500 m apart, a distance that reflects the core home range diameter for this species (Beasley et al., 2007) to ensure independence. We placed 100 pieces of cat food with 1 L of pine pellets. We pre-baited stations for two nights before collecting a baseline measurement. Because raccoons appeared to habituate quickly in preliminary testing of stations, we recorded data for only one treatment night. We checked raccoon foraging stations daily to separate and count the cat food remaining at the end of each trial, before resetting the station to its original amount.

We reviewed photos from camera at stations to confirm raccoon activity in pre-baiting and during experiments. The unique design of foraging stations largely prevented non-target species (e.g. opossums, skunks, rodents) from consuming cat food within the PVC pipe. In rare cases, however, American black bears (*Ursus americanus*) approached and consumed food from raccoon foraging stations during the pre-baiting period, but never during baseline or treatment nights. Because black bears damage the stations and introduce additional predator cues, we did not continue GUD experiments in locations where bear activity was observed and instead began pre-baiting at alternative sites within the park. No other predators (e.g. coyotes, bobcats) were observed at raccoon foraging stations.

2.6 | Analysis

To determine if predator treatments were significantly different from the control, we used linear mixed models with relative GUD as the response variable. We included predator treatment as a fixed effect and cluster as a random effect. Because we had multiple treatment days at the same station during cotton rat trials, we also included station ID as a random effect in our analysis of cotton

rat data. We used packages lme4 (Bates et al., 2015) and car (Fox & Weisberg, 2019) in program R (version 4.3.1; R Core Team 2023) to run all models. We then conducted post hoc pairwise comparisons between each predator treatment and the control using the multcomp package (Hothorn et al., 2008). We considered there to be an anti-predator response if the comparison between the predator and cone was significantly different at the alpha = 0.05 level using a two-tailed test. To determine if cotton rats and raccoons exhibited naïveté, we specifically considered the comparison between the python cue and the cone control. To account for multiple comparisons, we employed a Hochberg adjustment (Hochberg, 1988). Based on the Bonferroni correction, the Hochberg adjustment is a stepwise process that reduces family-wise error. We also conducted a pairwise comparison approach in Supplement 2.

3 | RESULTS

3.1 | Cotton rats

We completed trials at 12 clusters with four stations at each location (Hart et al., 2024). Because we repeated treatments for three nights, our experiments yielded 144 individual observations. Relative GUD significantly varied by predator treatment ($\chi^2 = 9.49$, $p = 0.02$). For the cone treatment, the average relative GUD across clusters was -0.63 ± 1.91 mL ($\bar{x} \pm$ SE), with the negative value indicating a very slight increase in millet consumption between the baseline and the treatment night (i.e. less millet was left). Average relative GUDs were 4.40 ± 1.44 mL for coyote treatments, 4.93 ± 1.17 mL for python treatments and 4.01 ± 1.44 mL for rattlesnake treatments, with positive values indicating that more millet was left on treatment nights versus the baseline night. Pairwise comparisons were consistent with the predictions of the ASH, with cotton rats significantly increasing their GUD in python treatments and both native predator treatments (Table 1; Figure 3a).

TABLE 1 Pairwise differences of marginal means between three predator treatments—life size replicas of coyotes (*Canis latrans*), Burmese pythons (*Python bivittatus*), and eastern diamondback rattlesnakes (*Crotalus adamanteus*) versus a novel object control (45.7-cm orange traffic cone)—in giving-up-density foraging experiments for raccoons and cotton rats (Hart et al., 2024).

Species	Treatment	Estimate	z-value	p-value
Cotton rat	Cone: Coyote	−5.03	−2.58	0.02[a]
	Cone: Python	−5.56	−2.85	0.01[a]
	Cone: Rattlesnake	−4.64	−2.37	0.02[a]
Raccoon	Cone: Coyote	−34.91	−3.26	<0.01[a]
	Cone: Python	−17.36	−1.62	0.21
	Cone: Rattlesnake	−6.64	−0.62	0.54

Note: Hochberg adjusted p-values are reported to account for multiple comparisons.

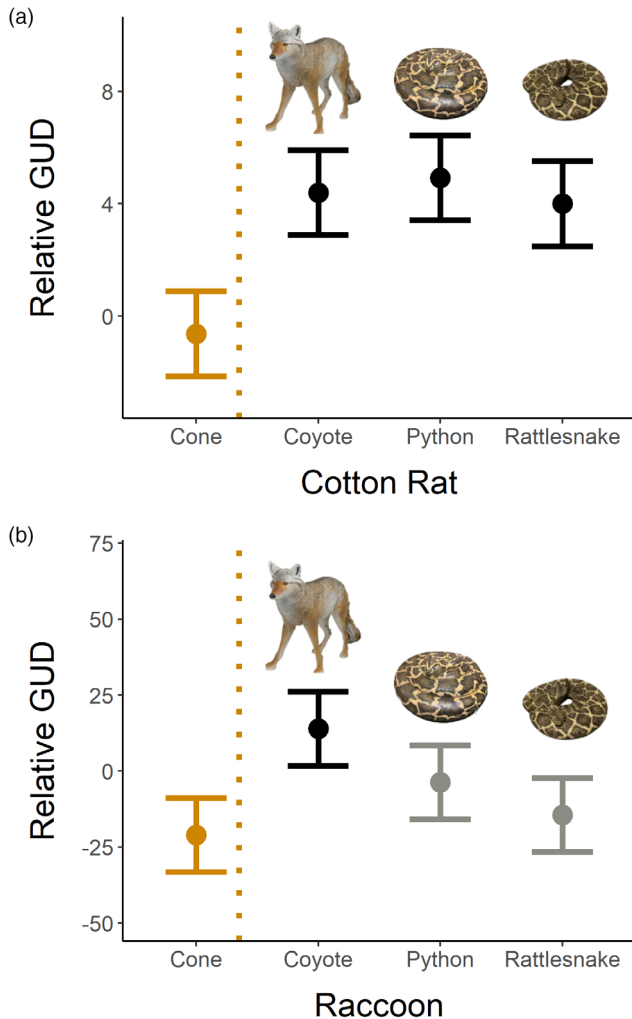[a]Indicates a significant difference between treatments.

FIGURE 3 Model estimated relative giving-up densities (GUD) of cotton rats (*Sigmodon hispidus*; a) and raccoons (*Procyon lotor*; b) to a cone control and three predator treatments, a coyote (*Canis latrans*), a Burmese python (*Python bivittatus*), and an eastern diamondback rattlesnake (*Crotalus adamanteus*). For cotton rats, GUDs were measured in mL of millet, with negative values indicating less millet remaining on treatment relative to the baseline. Raccoon GUDs were measured in pieces of cat food remaining. Treatments significantly different from the control are indicated in black, whereas treatments that did not differ are depicted in grey. Error bars represent standard error.

3.2 | Raccoons

We completed trials at 11 clusters with four stations at each location, yielding 44 observations (Hart et al., 2024). Relative GUD significantly varied by predator treatment ($\chi^2 = 12.15$, $p = 0.007$). On average raccoons decreased their GUD (i.e. they left less food) relative to the baseline of the cone for python and rattlesnake treatments. The average relative GUD was -21.00 ± 7.87 pieces ($\bar{x} \pm SE$) for the cone control, -3.64 ± 11.93 pieces for python treatment and -14.36 ± 13.48 for the rattlesnake treatment. Conversely, raccoons left 13.91 ± 14.38 more pieces of food when the coyote replica was present relative to the baseline night, indicating a 13.9% increase in

GUD when the coyote treatment was present. Pairwise comparisons revealed that only the coyote treatment significantly differed from the novel object control (Table 1; Figure 3b).

4 | DISCUSSION

Collectively, the results from the raccoon and cotton rat experiments provide support for the ASH and suggest that predation pressure from similar native species can lead to recognition of invasive predators (Cox & Lima, 2006). Despite having no history of python exposure, cotton rats responded similarly to cues of pythons and known native predators (Figure 3a). This pattern likely indicates cotton rats recognize python cues as threats (Beckmann et al., 2021) and do not exhibit extreme naïveté to this invader (Banks & Dickman, 2007). Alternatively, raccoons only significantly reduced their foraging activity during coyote treatments, suggesting they may exhibit naïveté to Burmese pythons. The evidence of naïveté of raccoons in a large continental system appears to contradict the predictions of BIH.

Support for the ASH has been observed in insular and freshwater systems (Anton et al., 2020), but to our knowledge, our study is the first to observe support for this hypothesis in a functional continental terrestrial ecosystem. Although there has been some support for the ASH in Australia (Banks et al., 2018), due to its isolation and high degree of biological endemism, Australia is often considered more analogous to insular systems (Ward et al., 2021; Woinarski et al., 2015). We acknowledge that our experiments were conducted in Peninsular Florida, which may not be fully representative of North America due to its unique geologic and climatic history, as well as its biodiversity patterns (Means & Simberloff, 1987; Soltis et al., 2006). However, because the species in our studies are not endemic to Florida and are instead widespread across much of the continent (Bradley et al., 2008; Cullingham et al., 2008), we anticipate that studies on raccoons and cotton rats conducted elsewhere within their range would yield similar results. Importantly, our findings indicate that naïveté may still be relevant for larger continental systems where prey species lack consistent predation risk from similar native archetypes. Moreover, the divergent responses of species impacted by the same invasive predator emphasizes the importance of considering species-specific predation histories when making predictions about naïveté.

Additional lines of evidence suggest that cotton rats avoid both native and invasive snake cues. A recent study working on cotton rats north of the invasion front showed reduced cotton rat captures in traps treated with either rattlesnake or python excrement (Beckmann et al., 2021). Accordingly, cotton rats innately recognize and avoid both the visual and olfactory cues of pythons without prior experience. This suggests they were likely pre-adapted to the python invasion with this behavioural response. Recognition of python cues by other native small mammal species with regular snake predation would further strengthen support for the ASH. Because pythons are expanding their range and may impact a growing

number of vulnerable rodent species (Redinger et al., 2024), it is especially important to understand how other small mammals respond to python cues.

Our foraging experiments revealed that raccoons foraged less when coyote cues were present, indicating that raccoons altered their behaviour in response to canid predators. This finding is consistent with previous research demonstrating that cues from canid predators, such as audio playbacks of domestic dog (*Canis lupus familiaris*) barks, decreased raccoon foraging activity (Suraci et al., 2016). However, other studies using olfactory cues (e.g. coyote urine, faeces) have failed to document similar effects on raccoon foraging behaviour (Etheredge, 2013; Gehrt & Prange, 2007). Visual and auditory cues of predators likely provide more precise information regarding the current location and behaviour of a predator than olfactory cues, which persist even after a predator may no longer pose an imminent threat (Bytheway et al., 2013; Jones et al., 2024). Possibly for this reason, a recent meta-analysis revealed that visual cues, such as those deployed in our study, elicit a stronger response than cues of other modalities (Jones et al., 2024). Although raccoons also do not appear to alter their spatial or temporal activity patterns in response to coyote occurrence more broadly (Chitwood et al., 2020; Cove et al., 2012; Gehrt & Prange, 2007), our results indicate that raccoons may alter their behaviour when the threat is more imminent—that is when a coyote is close enough to be detected visually.

Despite the presence of numerous native snakes in the Everglades, mesomammals in this ecosystem have evolved without predation pressure from a large constrictor (>2.4 m) in the last 16 million years (Dorcas et al., 2012). Based on our experiments, raccoons appear to lack the innate recognition of pythons and rattlesnakes as threatening, suggesting that they do not perceive snakes—even dangerous species like pythons—to be a threat. This lack of recognition is considered the most severe form of naïveté (Banks & Dickman, 2007) and is thought to correlate with severe declines in prey populations (Anton et al., 2020; Berger et al., 2001). Because python populations are expanding their range (Guzy et al., 2023), understanding patterns of naïveté in native mammals, and how these patterns relate to declines, is increasingly important. Our results indicate that raccoons, and possibly other vertebrate species lacking historical predation pressure from snakes, are likely to exhibit naïveté to pythons in these newly colonized areas, making them particularly vulnerable to this introduced predator.

Importantly, many animals that originally exhibit naïveté, learn to recognize and avoid invasive or historically absent predators (Berger et al., 2001; Carthey & Banks, 2016; Polo-Cavia et al., 2023; Robbins & Langkilde, 2021; Steindler & Letnic, 2021). Numerous studies have quantified the behavioural plasticity and learning behaviour of raccoons as it relates to puzzle solving and resource acquisition (Stanton et al., 2021, 2022), but fewer studies have documented learning as it relates to predator avoidance. Because of the potential lethal nature of predator encounters, it remains unclear if raccoons will be able to persist long enough to develop anti-predator reactions to pythons, and whether any such responses would extend to other snake species. Considering the Everglades' designation as a hotspot for invasive reptiles (Capinha et al., 2017)—a phenomenon potentially intensified by climate change (Howell et al., 2021)—developing proficiency in recognizing and avoiding potential dangers posed by snake predators is likely crucial for the survival of raccoons and other mesomammals inhabiting this area.

It is widely theorized that prey naïveté plays a significant role in the destructive impact of invasive predators (Cox & Lima, 2006; Paolucci et al., 2013; Stockwell et al., 2022). The contrasting responses we observed between these two model species in naïveté experiments is consistent with documented patterns in population resilience and declines (Guzy et al., 2023). Numerous factors, such as species body size and fecundity, are likely to influence population resilience (Soto-Shoender et al., 2020). However, our experimental results suggest that prey naïveté may indeed influence the susceptibility of certain species to python-related impacts. Furthermore, our findings imply that prey naïveté may warrant consideration as a potential contributing factor to the disproportionate impact of invasive predators beyond this specific ecosystem.

Early recognition of naïveté in prey species can lead to proactive management. For example, controlled exposure to predator cues can condition prey to avoid predators, reducing naïveté and improving prey survival (Ross et al., 2019). Similar exposure methods have been suggested for captive breeding and species reintroduction efforts (Griffin et al., 2000; Webb, 2020), particularly for long-lived species. Such efforts may be especially important if an invasive predator is contributing to declines. In the Everglades, management efforts have primarily focused on removing pythons (Guzy et al., 2023; Mazzotti et al., 2016; McCampbell et al., 2024). However, given the extensive spread of pythons (Taillie et al., 2021), complete removal or even population reductions of this apex predator appear unlikely and could be prohibitively expensive (Doherty & Ritchie, 2017). Consequently, alternative approaches such as predator training (Ross et al., 2019) or rapid selection (Moseby et al., 2016) from encounters may be useful tools in assisting prey in overcoming naïveté.

AUTHOR CONTRIBUTIONS

Rebecca K. McKee and Robert A. McCleery developed the concepts and methodology for the project. Rebecca K. McKee conducted the fieldwork for the project with assistance from Spencer Zeitoune. Kristen M. Hart and Robert A. McCleery secured the funding necessary for research. Rebecca K. McKee drafted the initial manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

reviewing earlier versions of this manuscript and providing guidance on the project's implementation.

ORCID

Rebecca K. McKee https://orcid.org/0000-0001-8364-3658
Kristen M. Hart https://orcid.org/0000-0002-5257-7974
Spencer Zeitoune https://orcid.org/0009-0005-1206-0435
Robert A. McCleery https://orcid.org/0000-0001-7018-005X

REFERENCES

Anton, A., Geraldi, N. R., Ricciardi, A., & Dick, J. T. A. (2020). Global determinants of prey naiveté to exotic predators. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1928), 20192978. https://doi.org/10.1098/rspb.2019.2978

Banks, P. B., Carthey, A. J. R., & Bytheway, J. P. (2018). Australian native mammals recognize and respond to alien predators: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1885), 20180857. https://doi.org/10.1098/rspb.2018.0857

Banks, P. B., & Dickman, C. R. (2007). Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology & Evolution*, *22*(5), 229–230. https://doi.org/10.1016/j.tree.2007.02.006

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Beasley, J. C., Devault, T. L., & Rhodes, O. E. (2007). Home-range attributes of raccoons in a fragmented agricultural region of northern Indiana. *Journal of Wildlife Management*, *71*(3), 844–850. https://doi.org/10.2193/2006-022

Beckmann, S., Avila, P., & Farrell, T. (2021). Effect of native and non-native snake scents on foraging activity of native rodents in Florida. *Journal of Mammalogy*, *103*, gyab124. https://doi.org/10.1093/jmammal/gyab124

Berger, J., Swenson, J. E., & Persson, I.-L. (2001). Recolonizing carnivores and naïve prey: Conservation lessons from Pleistocene extinctions. *Science*, *291*(5506), 1036–1039. https://doi.org/10.1126/science.1056466

Blackburn, T. M., Essl, F., Evans, T., Hulme, P. E., Jeschke, J. M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Wilson, J. R. U., Winter, M., … Bacher, S. (2014). A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biology*, *12*(5), e1001850. https://doi.org/10.1371/journal.pbio.1001850

Bradley, R. D., Henson, D. D., & Durish, N. D. (2008). Re-evaluation of the geographic distribution and phylogeography of the *Sigmodon hispidus* complex based on mitochondrial DNA sequences. *The Southwestern Naturalist*, *53*(3), 301–310. https://doi.org/10.1894/MRD-03.1

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, *22*(1), 37–47. https://doi.org/10.1007/BF00395696

Burkett-Cadena, N. D., Blosser, E. M., Loggins, A. A., Valente, M. C., Long, M. T., Campbell, L. P., Reeves, L. E., Bargielowski, I., & McCleery, R. A. (2021). Invasive Burmese pythons alter host use and virus infection in the vector of a zoonotic virus. *Communications Biology*, *4*(1), 1–11. https://doi.org/10.1038/s42003-021-02347-z

Bytheway, J. P., Carthey, A. J. R., & Banks, P. B. (2013). Risk vs. reward: How predators and prey respond to aging olfactory cues. *Behavioral Ecology and Sociobiology*, *67*(5), 715–725. https://doi.org/10.1007/s00265-013-1494-9

Cameron, G. N., & Spencer, S. R. (1985). Assessment of space-use patterns in the hispid cotton rat (*Sigmodon hispidus*). *Oecologia*, *68*(1), 133–139.

Capinha, C., Seebens, H., Cassey, P., García-Díaz, P., Lenzner, B., Mang, T., Moser, D., Pyšek, P., Rödder, D., Scalera, R., Winter, M., Dullinger, S., & Essl, F. (2017). Diversity, biogeography and the global flows of alien amphibians and reptiles. *Diversity and Distributions*, *23*(11), 1313–1322. https://doi.org/10.1111/ddi.12617

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews*, *89*(4), 932–949. https://doi.org/10.1111/brv.12087

Carthey, A. J. R., & Banks, P. B. (2016). Naiveté is not forever: Responses of a vulnerable native rodent to its long term alien predators. *Oikos*, *125*(7), 918–926. https://doi.org/10.1111/oik.02723

Carthey, A. J. R., & Blumstein, D. T. (2018). Predicting predator recognition in a changing world. *Trends in Ecology & Evolution*, *33*(2), 106–115. https://doi.org/10.1016/j.tree.2017.10.009

Carthey, A. J. R., Bucknall, M. P., Wierucka, K., & Banks, P. B. (2017). Novel predators emit novel cues: A mechanism for prey naivety towards alien predators. *Scientific Reports*, *7*(1), Article 1. https://doi.org/10.1038/s41598-017-16656-z

Chamberlain, M. J., Hodges, K. M., Leopold, B. D., & Wilson, T. S. (1999). Survival and cause-specific mortality of adult raccoons in central Mississippi. *The Journal of Wildlife Management*, *63*(3), 880–888. https://doi.org/10.2307/3802801

Chitwood, M. C., Lashley, M. A., Higdon, S. D., DePerno, C. S., & Moorman, C. E. (2020). Raccoon vigilance and activity patterns when sympatric with coyotes. *Diversity*, *12*(9), Article 9. https://doi.org/10.3390/d12090341

Conner, L. M., Castleberry, S. B., & Derrick, A. M. (2011). Effects of mesopredators and prescribed fire on hispid cotton rat survival and cause-specific mortality. *The Journal of Wildlife Management*, *75*(4), 938–944. https://doi.org/10.1002/jwmg.110

Cove, M. V., Jones, B. M., Bossert, A. J., Clever, D. R., Dunwoody, R. K., White, B. C., & Jackson, V. L. (2012). Use of camera traps to examine the mesopredator release hypothesis in a fragmented midwestern landscape. *The American Midland Naturalist*, *168*(2), 456–465. https://doi.org/10.1674/0003-0031-168.2.456

Cove, M. V., Simons, T. R., Gardner, B., & O'Connell, A. F. (2019). Towards recovery of an endangered Island endemic: Distributional and behavioral responses of key largo woodrats associated with exotic predator removal. *Biological Conservation*, *237*, 423–429. https://doi.org/10.1016/j.biocon.2019.07.032

Cox, J. G., & Lima, S. L. (2006). Naiveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution*, *21*(12), 674–680. https://doi.org/10.1016/j.tree.2006.07.011

Cullingham, C. I., Kyle, C. J., Pond, B. A., & White, B. N. (2008). Genetic structure of raccoons in eastern North America based on mtDNA: Implications for subspecies designation and rabies disease dynamics. *Canadian Journal of Zoology*, *86*(9), 947–958. https://doi.org/10.1139/Z08-072

Dalrymple, G. H., Bernardino, F. S., Steiner, T. M., & Nodell, R. J. (1991). Patterns of species diversity of snake community assemblages, with data on two everglades snake assemblages. *Copeia*, *1991*(2), 517–521. https://doi.org/10.2307/1446600

Darracq, A. K., Conner, L. M., Brown, J. S., & McCleery, R. A. (2016). Cotton rats alter foraging in response to an invasive ant. *PLoS One*, *11*(9), e0163220. https://doi.org/10.1371/journal.pone.0163220

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(40), 11261–11265. https://doi.org/10.1073/pnas.1602480113

Doherty, T. S., & Ritchie, E. G. (2017). Stop jumping the gun: A call for evidence-based invasive predator management. *Conservation Letters*, *10*(1), 15–22. https://doi.org/10.1111/conl.12251

Dorcas, M. E., Willson, J. D., Reed, R. N., Snow, R. W., Rochford, M. R., Miller, M. A., Meshaka, W. E., Andreadis, P. T., Mazzotti, F. J., Romagosa, C. M., & Hart, K. M. (2012). Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(7), 2418–2422. https://doi.org/10.1073/pnas.1115226109

Ernst, C. H., & Ernst, E. M. (2011). *Venomous reptiles of the United States, Canada, and Northern Mexico: Crotalus*. JHU Press.

Etheredge, C. (2013). Ecology and impacts of coyotes (*Canis latrans*) in the southeastern United States. *All Dissertations*. https://open.clemson.edu/all_dissertations/1221

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Gehrt, S. D., & Fritzell, E. K. (1999). Survivorship of a nonharvested raccoon population in South Texas. *The Journal of Wildlife Management*, *63*(3), 889–894. https://doi.org/10.2307/3802802

Gehrt, S. D., & Prange, S. (2007). Interference competition between coyotes and raccoons: A test of the mesopredator release hypothesis. *Behavioral Ecology*, *18*(1), 204–214. https://doi.org/10.1093/beheco/arl075

Griffin, A. S., Blumstein, D. T., & Evans, C. S. (2000). Training captive-bred or translocated animals to avoid predators. *Conservation Biology*, *14*(5), 1317–1326. https://doi.org/10.1046/j.1523-1739.2000.99326.x

Gunderson, L. H. (1994). Vegetation of the Everglades: Determinants of community composition. In S. Davis & J. C. Ogden (Eds.), *Everglades: The ecosystem and its restoration* (pp. 323–340). CRC Press.

Guzy, J. C., Falk, B. G., Smith, B. J., Willson, J. D., Reed, R. N., Aumen, N. G., Avery, M. L., Bartoszek, I. A., Campbell, E., Cherkiss, M. S., Claunch, N. M., Currylow, A. F., Dean, T., Dixon, J., Engeman, R., Funck, S., Gibble, R., Hengstebeck, K. C., Humphrey, J. S., ... Hart, K. M. (2023). Burmese pythons in Florida: A synthesis of biology, impacts, and management tools. *NeoBiota*, *80*, 1–119. https://doi.org/10.3897/neobiota.80.90439

Hart, K. M., McKee, R. K., & McCleery, R. A. (2024). Giving-up density experiments for two species of mammals in Florida, 2022. [dataset]. 10.5066. https://doi.org/10.5066/P1CXIQNI

Hayward, M. W., Mitchell, C. D., Kamler, J. F., Rippon, P., Heit, D. R., Nams, V., & Montgomery, R. A. (2023). Diet selection in the Coyote Canis latrans. *Journal of Mammalogy*, *104*(6), 1338–1352. https://doi.org/10.1093/jmammal/gyad094

Hochberg, Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. *Biometrika*, *75*(4), 800–802. https://doi.org/10.1093/biomet/75.4.800

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Howell, H. J., Delgado, G. L., Wood, A. C., Thompson, L. M., Cline, E. A., & Searcy, C. A. (2021). A dry future for the Everglades favors invasive herpetofauna. *Biological Invasions*, *23*(10), 3119–3133. https://doi.org/10.1007/s10530-021-02562-z

Jones, M. M., Fletcher, R. J., Jr., Potash, A. D., Sibiya, M., & McCleery, R. A. (2024). Prey responses to direct and indirect predation risk cues reveal the importance of multiple information sources. *Journal of Animal Ecology*, *93*, 1983–1995. https://doi.org/10.1111/1365-2656.14209

Judson, J., Clark, W., & Andrews, R. (1994). Post-natal survival of raccoons in relation to female age and denning behavior. *Journal of the Iowa Academy of Science*, *101*(1), 24–27. https://scholarworks.uni.edu/jias/vol101/iss1/7

Kincaid, W. B., & Cameron, G. N. (1985). Interactions of cotton rats with a patchy environment: Dietary responses and habitat selection. *Ecology*, *66*(6), 1769–1783. https://doi.org/10.2307/2937373

Kotler, B. P., Brown, J. S., & Mitchell, W. A. (1993). Environmental factors affecting patch use in two species of gerbilline rodents. *Journal of Mammalogy*, *74*(3), 614–620. https://doi.org/10.2307/1382281

Larsen, A. L., Homyack, J. A., Wigley, T. B., Miller, D. A., & Kalcounis-Rueppell, M. C. (2016). Effects of habitat modification on cotton rat population dynamics and rodent community structure. *Forest Ecology and Management*, *376*, 238–246. https://doi.org/10.1016/j.foreco.2016.06.018

Loggins, A. A., Shrader, A. M., Monadjem, A., & McCleery, R. A. (2019). Shrub cover homogenizes small mammals' activity and perceived predation risk. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-53071-y

Mazzotti, F. J., Rochford, M., Vinci, J., Jeffery, B. M., Eckles, J. K., Dove, C., & Sommers, K. P. (2016). Implications of the 2013 python challenge® for ecology and management of *Python molorus* bivittatus (Burmese python) in Florida. *Southeastern Naturalist*, *15*(sp8), 63–74. https://doi.org/10.1656/058.015.sp807

McCampbell, M. E., Hunter, M. E., Stechly, J. V., Leist, K. N., Hart, K., & McCleery, R. A. (2023). Compensatory mortality explains rodent resilience to an invasive predator. *Journal of Mammalogy*, *104*(5), 967–978. https://doi.org/10.1093/jmammal/gyad043

McCampbell, M. E., Spencer, M., Hart, K., Link, G., Watson, A., & McCleery, R. (2024). Mammalian lures monitored with time-lapse cameras increase detection of pythons and other snakes. *PeerJ*, *12*, e17577. https://doi.org/10.7717/peerj.17577

McCleery, R. A., Monadjem, A., Conner, L. M., Austin, J. D., & Taylor, P. J. (2022). *Methods for ecological research on terrestrial small mammals*. JHU Press.

McCleery, R. A., Sovie, A., Reed, R. N., Cunningham, M. W., Hunter, M. E., & Hart, K. M. (2015). Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1805), 20150120. https://doi.org/10.1098/rspb.2015.0120

Means, D. B., & Simberloff, D. (1987). The peninsula effect: Habitat-correlated species decline in Florida's herpetofauna. *Journal of Biogeography*, *14*(6), 551–568. https://doi.org/10.2307/2844880

Meshaka, W. E., Loftus, W. F., & Steiner, T. (2000). The herpetofauna of Everglades National Park. *Florida Scientist*, *63*(2), 84–103. https://www.jstor.org/stable/24321071

Moseby, K. E., Blumstein, D. T., & Letnic, M. (2016). Harnessing natural selection to tackle the problem of prey naïveté. *Evolutionary Applications*, *9*(2), 334–343. https://doi.org/10.1111/eva.12332

Paolucci, E. M., MacIsaac, H. J., & Ricciardi, A. (2013). Origin matters: Alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions*, *19*(8), 988–995. https://doi.org/10.1111/ddi.12073

Patton, J. E., & Judd, W. S. (1986). Vascular flora of Paynes Prairie Basin and Alachua Sink Hammock, Alachua County, Florida. *Castanea*, *51*(2), 88–110. https://www.jstor.org/stable/4033357

Polo-Cavia, N., Arribas, R., Caballero-Díaz, C., Baltanás, Á., & Gomez-Mestre, I. (2023). Widespread learned predator recognition to an alien predator across populations in an amphibian species. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-41624-1

Potash, A. D., Conner, L. M., & McCleery, R. A. (2019). Vertical and horizontal vegetation cover synergistically shape prey behaviour. *Animal Behaviour*, *152*, 39–44. https://doi.org/10.1016/j.anbehav.2019.04.007

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Redinger, J., Lord, I., Dixon, J., & Cove, M. V. (2024). Mammal declines correspond with increasing prevalence of Burmese pythons at their southern invasion front in the Florida Keys. *Biological Invasions*, 26(3), 889–903. https://doi.org/10.1007/s10530-023-03217-x

Ricciardi, A., & Atkinson, S. K. (2004). Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters*, 7(9), 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x

Robbins, T. R., & Langkilde, T. (2021). One and done: A single encounter with an invasive predator determines subsequent antipredator behavior of naive juvenile lizards. *Climate Change Ecology*, 1, 100002. https://doi.org/10.1016/j.ecochg.2021.100002

Rodriguez Curras, M., Donadío, E., Middleton, A. D., & Pauli, J. N. (2021). Perceived risk structures the space use of competing carnivores. *Behavioral Ecology*, 32(6), 1380–1390. https://doi.org/10.1093/beheco/arab104

Ross, A. K., Letnic, M., Blumstein, D. T., & Moseby, K. E. (2019). Reversing the effects of evolutionary prey naiveté through controlled predator exposure. *Journal of Applied Ecology*, 56(7), 1761–1769. https://doi.org/10.1111/1365-2664.13406

Salo, P., Korpimäki, E., Banks, P. B., Nordström, M., & Dickman, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences*, 274(1615), 1237–1243. https://doi.org/10.1098/rspb.2006.0444

Schmidt, K. A., Lee, E., Ostfeld, R. S., & Sieving, K. (2008). Eastern chipmunks increase their perception of predation risk in response to titmouse alarm calls. *Behavioral Ecology*, 19(4), 759–763. https://doi.org/10.1093/beheco/arn034

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., Preisser, E., Rehage, J. S., & Vonesh, J. R. (2010). Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, 119(4), 610–621. https://doi.org/10.1111/j.1600-0706.2009.18039.x

Smith, L. L., & Dodd, C. K. (2003). Wildlife mortality on U.S. Highway 441 across Paynes prairie, Alachua County, Florida. *Florida Scientist*, 66(2), 128–140. https://www.jstor.org/stable/24321153

Soltis, D. E., Morris, A. B., McLACHLAN, J. S., Manos, P. S., & Soltis, P. S. (2006). Comparative phylogeography of unglaciated eastern North America. *Molecular Ecology*, 15(14), 4261–4293. https://doi.org/10.1111/j.1365-294X.2006.03061.x

Soto-Shoender, J. R., Gwinn, D. C., Sovie, A., & McCleery, R. A. (2020). Life-history traits moderate the susceptibility of native mammals to an invasive predator. *Biological Invasions*, 22(9), 2671–2684. https://doi.org/10.1007/s10530-020-02278-6

Stanton, L. A., Bridge, E. S., Huizinga, J., & Benson-Amram, S. (2022). Environmental, individual and social traits of free-ranging raccoons influence performance in cognitive testing. *Journal of Experimental Biology*, 225(18), jeb243726. https://doi.org/10.1242/jeb.243726

Stanton, L. A., Bridge, E. S., Huizinga, J., Johnson, S. R., Young, J. K., & Benson-Amram, S. (2021). Variation in reversal learning by three generalist mesocarnivores. *Animal Cognition*, 24(3), 555–568. https://doi.org/10.1007/s10071-020-01438-4

Steindler, L., & Letnic, M. (2021). Not so naïve: Endangered mammal responds to olfactory cues of an introduced predator after less than 150 years of coexistence. *Behavioral Ecology and Sociobiology*, 75(1), 8. https://doi.org/10.1007/s00265-020-02952-8

Stockwell, C. A., Schmelzer, M. R., Gillis, B. E., Anderson, C. M., & Wisenden, B. D. (2022). Ignorance is not bliss: Evolutionary naiveté in an endangered desert fish and implications for conservation. *Proceedings of the Royal Society B: Biological Sciences*, 289(1981), 20220752. https://doi.org/10.1098/rspb.2022.0752

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D., & Zanette, L. Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, 7(1), 10698. https://doi.org/10.1038/ncomms10698

Taillie, P. J., Hart, K. M., Sovie, A. R., & McCleery, R. A. (2021). Native mammals lack resilience to invasive generalist predator. *Biological Conservation*, 261, 109290. https://doi.org/10.1016/j.biocon.2021.109290

Timmerman, W. W. (1995). Home range, habitat use, and behavior of the eastern diamondback rattlesnake (*Crotalus adamanteus*) on the Ordway Preserve. *Bulletin of the Florida Museum of Natural History*, 3(13), 127–158. https://doi.org/10.58782/flmnh.tvem1511

U.S. Fish & Wildlife Service. (2008). *Key largo woodrat (Neotoma floridana smalli) 5-year review*. U.S. Fish and Wildlife Service. https://www.fws.gov/node/64901

Ward, M., Carwardine, J., Yong, C. J., Watson, J. E. M., Silcock, J., Taylor, G. S., Lintermans, M., Gillespie, G. R., Garnett, S. T., Woinarski, J., Tingley, R., Fensham, R. J., Hoskin, C. J., Hines, H. B., Roberts, J. D., Kennard, M. J., Harvey, M. S., Chapple, D. G., & Reside, A. E. (2021). A national-scale dataset for threats impacting Australia's imperiled flora and fauna. *Ecology and Evolution*, 11(17), 11749–11761. https://doi.org/10.1002/ece3.7920

Watine, L. N., & Giuliano, W. M. (2017). Factors determining coyote (*Canis latrans*) diets. *Open Journal of Ecology*, 7(13), Article 13. https://doi.org/10.4236/oje.2017.713045

Webb, J. (2020). Training animals in captivity or the wild, so they can return to the wild. In *Zoo animal learning and training* (pp. 289–308). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118968543.ch12

Welch, R. J., Périquet, S., Petelle, M. B., & le Roux, A. (2017). Hunter or hunted? Perceptions of risk and reward in a small mesopredator. *Journal of Mammalogy*, 98(6), 1531–1537. https://doi.org/10.1093/jmammal/gyx100

Willson, J. D., Dorcas, M. E., & Snow, R. W. (2011). Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in Southern Florida. *Biological Invasions*, 13(7), 1493–1504. https://doi.org/10.1007/s10530-010-9908-3

Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America*, 112(15), 4531–4540. https://doi.org/10.1073/pnas.1417301112

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplement 1. Additional details of experimental design in GUD experiments.

Figure S1. Diagram displaying experimental approach for predator giving-up density experiments in trials with raccoons and cotton rats.

Supplement 2. Alternative approach to multiple comparisons.

Table S1. Pairwise differences of marginal means between three predator treatments (life size replicas of coyotes, Burmese pythons, and eastern diamondback rattlesnakes) versus a novel object control (45.7-cm orange traffic cone) in giving-up-density foraging experiments for raccoons and cotton rats.