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Scavenging dynamics on Guam and implications for invasive species management

Jacob E. Hill · Kelsey L. Turner · Joshua B. Smith · Matthew T. Hamilton ·
Travis L. DeVault · William C. Pitt · James C. Beasley · Olin E. Rhodes Jr.

Abstract Deployment of mouse carcasses laced with acetaminophen has become a common management tool to control invasive brown tree snakes (*Boiga irregularis*; BTS) on Guam. Additionally, anticoagulant rodenticides may be used to control invasive rats (*Rattus* spp.) if their populations increase due to predator release in the wake of BTS eradication. However, there has been little research examining how scavengers on Guam could be incidentally exposed to toxicants by scavenging carcasses of animals that die from these population control strategies. Furthermore, there is a limited understanding of how the proliferation of invasive species on Guam has influenced the composition of the scavenger community. We investigated these topics by examining scavenger consumption of mouse, rat, and BTS carcasses on Guam in both a coastal and upland site during the wet (May–Aug 2016) and dry season (Jan–Apr 2017). We documented carcass consumption by 9 species, which scavenged 48% of carcasses. Interactions between season, habitat, and carcass type influenced probability of scavenging, and appeared to be driven by consumption by the two main scavenger species, BTS and cane toads (*Rhinella marina*), both of which are invasive on Guam. Baiting programs should consider the potential for toxin exposure to land crabs (*Coenobita* spp., *Birgus latro*), native species that scavenged at every combination of carcass type, habitat, and season. Overall, 60% of scavenging events were attributed to species considered pests that are recent introductions to Guam. Invasive species on Guam are the primary scavengers of small vertebrate carrion, suggesting a substantial role in trophic dynamics that extends beyond predation.

J. E. Hill (✉) · K. L. Turner · J. B. Smith ·
M. T. Hamilton · T. L. DeVault
Savannah River Ecology Laboratory, University of Georgia, Aiken, SC, USA
e-mail: jehill@uga.edu

W. C. Pitt
Smithsonian Conservation Biology Institute, Smithsonian Institution, Front Royal, VA, USA

J. C. Beasley
Savannah River Ecology Laboratory, Warnell School of Forestry and Natural Resources, University of Georgia, Aiken, SC, USA

O. E. Rhodes Jr.
Savannah River Ecology Laboratory, Odum School of Ecology, University of Georgia, Aiken, SC, USA

Introduction

Islands contain a disproportionate share of global biodiversity (Courchamp et al. 2014). Invasive species,

however, threaten the viability of island wildlife populations and constitute the primary cause of island vertebrate extinctions (Bellard et al. 2016; Doherty et al. 2016). In the years following World War II, ships salvaging war material from islands in the western Pacific inadvertently introduced brown tree snakes (*Boiga irregularis*; BTS) to Guam, the largest of the Mariana Islands (Richmond et al. 2015; Rodda et al. 1992). The dietary flexibility of BTS coupled with a lack of predators spawned dramatic population increases following their introduction (Savidge 1988). By 1970, BTS occurred across the entire island with densities reaching as high as 100 individuals per ha (Rodda et al. 1992). Today, BTS densities on Guam (8.3–22.4 snakes/ha) are among the highest recorded for any reptile worldwide (Smith et al. 2016).

The ecological consequences of BTS on Guam have been profound (Clark et al. 2017). Predation by BTS has reduced abundances of many vertebrates, resulting in the extinction or extirpation of 20 native bird species and several endemic lizard species (Wiles 1987; Wiles et al. 2003). As a result, there are currently portions of Guam that are largely devoid of native vertebrates (Rodda and Savidge 2007). Extirpations of these species have in turn suppressed key ecosystem functions such as pollination and seed dispersal with subsequent effects to plant community structure (Mortensen et al. 2008; Rodda and Savidge 2007). Additionally, the cost of repairing infrastructure damages caused by BTS on Guam and investment in eradication efforts collectively exceeds 4 million US dollars annually (Pimental 2007). Based on their biological and economic impact, BTS thus rank among the world's most damaging invasive species (Invasive Species Specialist Group 2021).

Despite their success at invading Guam and decimating native wildlife, BTS possess vulnerabilities that have been exploited in eradication efforts. Acetaminophen is toxic to BTS and an 80-mg dose is fatal to the majority of individuals (Siers et al. 2021). BTS readily scavenge mouse carcasses, and deployment of neonatal mouse carcasses laced with acetaminophen is an effective management tool, reducing the presence of BTS by 80–85% (Clark and Savarie 2012). By deploying baits aerially, BTS populations can be reduced over large inaccessible areas (Siers et al. 2019). Using oral toxicants is also more cost effective than other techniques such as trapping and has been determined to pose little risk to other wildlife (Clark

et al. 2012). As a result, control efforts implementing toxic baits are part of an integrated approach to BTS management on Guam (Engeman et al. 2018).

Although the ecological benefits can be immense, invasive species reduction can also have unpredictable negative consequences termed 'surprise effects' (Courchamp et al. 2003). In the case of predators such as BTS, a potential 'surprise effect' is an increase in other invasive species resulting from predator release (Courchamp et al. 2003). In New Zealand, for example, invasive Pacific rat (*Rattus exulans*) populations increased after feral cat (*Felis cattus*) removal, leading to greater native bird mortality as the result of greater rat predation (Rayner et al. 2007). Invasive Pacific rats and black rats (*Rattus rattus*) constitute important prey items for BTS on Guam, raising the potential for increased populations of these invasive rodents following BTS reduction (Fritts and Rodda 1998). Therefore, control efforts for BTS may in turn necessitate control of rats, which is often accomplished with baits containing anticoagulant rodenticides such as brodifacoum (Pitt et al. 2011).

In contrast to techniques such as trapping where the carcass is contained, broadcast applications of toxic baits can result in the diffusion of carcasses across the landscape. Such widespread carrion availability may have consequences for other wildlife because many vertebrates are facultative scavengers and invertebrates often scavenge as well (DeVault et al. 2003). Thus, there is the potential for incidental exposure of nontarget wildlife to toxicants as the result of their scavenging behavior. This may occur through primary ingestion when scavengers consume toxic baits intended for invasive species, or through secondary ingestion by scavenging carcasses of animals that have ingested toxic baits (Lujan et al. 2010). Although BTS are arboreal, their carcasses frequently come to rest on the ground after dying from toxicant ingestion, where they are potentially available to many vertebrate scavengers (Smith et al. 2016). There has been little research, however, into the extent to which invasive species management on Guam may expose scavengers to toxicants. Although many native vertebrates have been extirpated from the island, invertebrate scavengers such as hermit crabs are still abundant and could experience toxicant exposure. Understanding patterns in carcass consumption is important for predicting the risk of invasive species management programs to native fauna as the result of scavenging. Additionally, with many native animals

having been extirpated, investigating carrion consumption would provide insight into trophic interactions on an island where native animals have been largely replaced by invasive species (Abernethy et al. 2016).

Scavenging is widespread among vertebrates, but its prevalence is impacted by a variety of factors including climatic conditions, habitat type, location, and carcass species (Beasley et al. 2015; Olson et al. 2016; Smith et al. 2017; Turner et al. 2017). As such, consumption of toxic bait carcasses (defined as both baits laced with toxicants [i.e., mice] and animals dying from the consumption of toxic baits [i.e., rats and BTS]) may vary based on season, as well as the habitat where carcasses are located. During warmer seasons, vertebrate scavenging is often reduced because the rapid activity by microbes results in a narrow window during which carcasses are palatable (DeVault et al. 2004; Hill et al. 2018b; Turner et al. 2017). Habitats with less understory may also have greater scavenging activity due to increased visual detection and accessibility of carcasses by scavengers (Selva et al. 2005; Turner et al. 2017). Additionally, carcass type may influence scavenging patterns because some scavengers avoid particular species of carrion (Butler-Valverde et al. 2022; Moleón et al. 2017; Olson et al. 2016).

To investigate the potential for toxicant exposure to scavengers resulting from toxic bait carcass consumption and further understand scavenging dynamics on Guam, we experimentally placed mouse, rat, and BTS carcasses in two habitats (coastal and upland) in both wet and dry seasons. We tested the hypothesis that carcass type, habitat, and season influenced scavenging behavior. We predicted that carcasses would be consumed more quickly, and a greater proportion of carcasses would be scavenged in the coastal compared to the upland site due to less understory vegetation. We also predicted that more carcasses would be consumed in the dry season compared to the wet season due to lower temperatures prolonging the period of carcass availability.

Methods

Study site

We carried out this study on Guam, a 543 km^2 island in the western Pacific Ocean. Trials were conducted in two 0.25 km^2 research sites (coastal and upland) located ~3.2 km apart on Andersen Air Force Base (13.587° N, 144.924° E, Fig. 1). The coastal site was an old growth, historical coconut (*Cocos nucifera*) plantation with primarily coconut palms in the overstory and little understory vegetation. The site was located within 1 km of the ocean and elevation ranged from 22 to 41 m. The upland site was in a secondary mixed limestone forest-plateau approximately 150-m above sea-level. Vegetation was characterized by a dense forest of short trees with relatively open canopy that permitted extensive understory growth. Common plant species in the undergrowth included *Ficus prolixa*, *Guamia mariannae*, *Aglaia mariannensis* and *Vitex parviflora*. We carried out this study during both a wet season (May–August 2016) and a dry season (January–April 2017). Mean monthly temperature was 29.1 °C during the wet season and 27.8 °C during the dry season. Mean monthly precipitation during the wet season was 235.9 mm and during the dry season was 159.9 mm (NOAA 2021).

Experimental design

We carried out 1376 trials (i.e., unique carcasses monitored). Trials were run for 5 days because we estimated that all carcasses would be fully scavenged or decomposed (defined as the time when there appeared to be no edible flesh remaining) over this duration given the size of the carcasses and environmental conditions (Abernethy et al. 2016). In the dry season we performed 11 consecutive sessions of concurrent trials (60 trials/session), and during the wet season we performed 10 sessions (72 trials/session). During each session, trials were evenly divided among the three carcass types and both habitats. After each session, we moved the cameras and removed all traces of carcass remains to reduce the likelihood of scavengers becoming habituated to carcass locations. Following the 6th session in each season, there was a 7-day pause before beginning the 7th session to decrease the chances of scavengers becoming habituated to carcasses along transects (Abernethy et al. 2016).

In each habitat, we established 5 transects located 50-m inland from roads that measured 1 km in length and were spaced 0.1 km apart. Carcasses were placed in randomized sequences along each transect such that active cameras were buffered by 150 m from other

Fig. 1 Map of Guam with location of Andersen Air Force Base and boxes indicating locations of upland and coastal sites where scavenging trials were carried out during May–August 2016 and January–April 2017
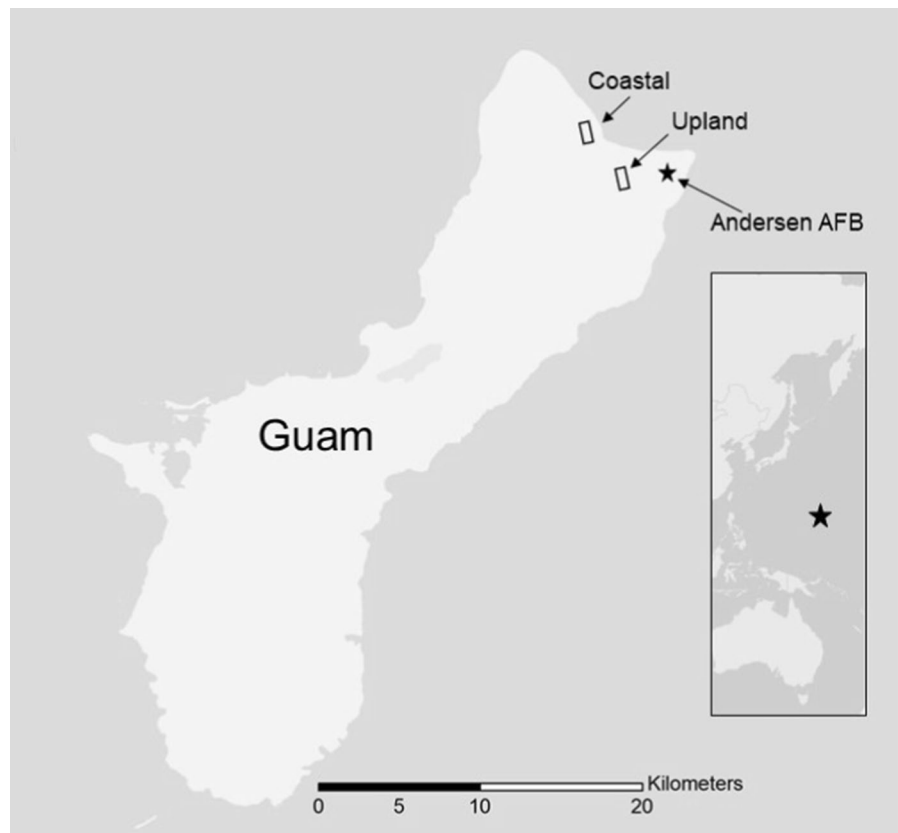
active cameras on a given transect and a minimum of 100 m from cameras on neighboring transects (Abernethy et al. 2016). These distances were based on spatial constrains within the focal habitats. For each trial, we baited the camera with either a mouse, rat, or BTS carcass. Mice were used to examine potential scavenging of acetaminophen-laced mouse carcasses by non-target animals. Rats were used to examine impacts on scavengers of potential rat increases following BTS eradication. BTS carcasses were used to examine scavenger consumption and subsequent toxin ingestion of these carcasses resulting from control efforts. Dark colored, frozen mice (13.0–18.0 g) and rats (40.0–165.0 g) were acquired from RodentPro. com (RodentPro.com, LLC, Inglefield, IN) and PerfectPrey.com (PerfectPrey.com LLC, Loxahatchee, FL), respectively. We acquired frozen BTS carcasses from lethal control operations on Guam conducted by the US Department of Agriculture. BTS carcasses varied in size (28.0–270.0 g) depending on availability of euthanized captures at the time of use. All carcasses were stored frozen and thawed to ambient

temperature prior to deployment. The masses of these carcasses were equivalent to what would be available to scavengers following BTS management efforts.

We manipulated carcass placement along transects to mimic the natural conditions where carcasses would be likely to occur, standardizing carcass placements across different canopy covers. Small mammal carcasses often are obstructed from view and are not visually conspicuous (DeVault and Rhodes Jr 2002; DeVault et al. 2003). Therefore, we placed half of the mouse and rat carcasses on the ground uncovered and the other half inside burrows. BTS carcasses were placed uncovered (92%), inside a burrow (4%), or approximately 1.5–2.0 m in a tree (4%) to imitate typical carcass locations of BTS that die from acetaminophen consumption (Smith et al. 2016). We constructed burrows above ground using available natural materials such as rocks, vegetation and sticks because site restrictions prevented us from digging burrows in the ground.

We set carcasses 0.3–1 m away from the camera lens and programmed cameras (Reconyx infrared

PC900 Hyperfire™ cameras, Reconyx, Inc., Holmen, WI) to record a single image every 6 min as well as a burst of 5 images when triggered by motion and/or by an external trigger. We equipped cameras paired with rodent carcasses with a water resistant, external trigger system (FB Engineering, Hilo, HI) constructed with a 0E2385HX-snap action switch (ZF Electronics Corporation, Pleasant Prairie, WI) and base, made from acrylic sheets, such that when the rodent was removed from the switch, the camera would be triggered (DeVault et al. 2004) (Fig S1). To prevent rodents from falling off external switches, we loosely tied them with thread as to not inhibit scavengers from taking carcasses. When we returned to carcass sites at the end of every trial, we estimated the percent of flesh that remained to determine whether the carcass had been fully scavenged. We analyzed camera images to document which scavengers consumed carcasses. We also determined the amount of time elapsed between carcass placement and when the carcass had been fully scavenged.

In addition to the scavenging trials, we conducted a series of decomposition trials to assess decomposition of carcasses in the absence of vertebrate scavenging. The goal of this was to understand how long carcasses would be available to vertebrate scavengers. In these trials, we placed a wire cage with 2.54 cm by 1.00 cm mesh over the carcass to prohibit access by vertebrates. There were 10 trials of each of the 3 carcass types per season per habitat for 120 total decomposition trials. We programed cameras to take a single picture every 15 min until decomposition occurred. Decomposition trials were conducted concurrently with scavenging trials but outside the standard spatial buffer of the scavenging trials so that they would remain independent of the scavenging experiments.

Statistical analysis

We performed all analyses in R version 4.0.4 (R Core Team 2022). Our scavenging models contained combinations of these three independent variables with the following levels: season (wet or dry); habitat (coastal or upland); and carcass type (mouse, rat, or BTS). We did not include carcass mass as a variable because each of the three carcass types differ in mass (mouse < rat < BTS), so carcass mass is already accounted for to some extent. Additionally, variation within carcass types is not

pertinent to our objectives as these carcasses are meant to represent types that would potentially be available as the result of BTS control efforts, and in reality there would be a range of weights within a carcass type as we have in our study.

We examined probability of carcasses being scavenged using a generalized linear model with binomial distribution with the response variable scavenged or not scavenged. We also examined consumption by the four most common scavengers: BTS, cane toads (*Rhinella marina*), monitor lizards (*Varanus indicus*), and hermit crabs (*Coenobita* spp.). Invertebrate scavengers included ants and flies, but we did not document them frequently enough to analyze their scavenging behavior. The response for each model was presence or absence of that species scavenging at each carcass. For the BTS model, we excluded BTS carcasses because they were only scavenged by BTS on one occasion. We assessed species richness of scavengers (i.e., number of species scavenging a carcass) using a generalized linear model with Poisson distribution, including only carcasses that were scavenged.

We analyzed time to carcass consumption using an accelerated failure time Weibull regression with the package 'survival' (Therneau et al. 2020), which is commonly used to study carcass persistence in scavenging studies (Bispo et al. 2013). Stratified Kaplan–Meier curves indicated that the model was appropriate for our data (Zhang 2016). Time to consumption was calculated as the time elapsed between carcass placement and complete consumption by scavengers. Carcasses that were not fully scavenged were right-censored at 5 days. We used the same model to assess time to decomposition for the decomposition trials.

For the overall probability of scavenging model, species richness model, and scavenging survival model, we considered the 3-way interaction and all possible two-way interactions. If the 3-way interaction was significant, we evaluated the 2-way interactions organized by the third factor (Abernethy et al. 2016; Turner et al. 2017). For the species-specific scavenging models, we examined main effects only due to the smaller frequency of scavenging across every treatment level. For the decomposition survival model, we included carcass type, season, and habitat as in the other models, but also incorporated the carcass weight. We also only assessed

main effects in this model due to the smaller sample sizes.

We ranked all possible model combinations using sample size corrected AIC$_c$, selecting that with the lowest AIC$_c$ as the best performing model and making inferences from this top model. When carcass type as a main effect or interactions were included in the top model, we assessed pairwise comparisons with α = 0.05 to determine differences using the package 'emmeans' (Lenth et al. 2019) for the generalized linear models and the package 'rarredd/rawr' for the survival models (Redd 2021).

Results

We determined carcass fate in 1305 of the trials (94%), of which 622 carcasses were scavenged (48%; Table 1). During the dry season, 46% of carcasses were scavenged, and 49% were scavenged during the wet season. Fifty twopercent of carcasses in coastal habitat were scavenged and 44% were scavenged in the upland site. Across carcass species, 63% of mouse, 49% of rat, and 30% of snake carcasses were scavenged. We were able to identify all scavengers in

580 (93%) of the trials. We observed scavenging by 9 species (Table 2), the most common of which were cane toads, documented at 217 carcasses (16.6% of all carcasses), followed by BTS (161 carcasses, 12.3%), monitor lizards (108 carcasses, 8.2%), and hermit crabs (100 carcasses, 7.6%). The remaining species were all documented at 1% or less of carcasses.

Our top model for probability of scavenging included all three main effects and the carcass × habitat and habitat × season interactions (AIC$_c$ = 1681.9, LL = −832.91, w_i = 0.68; Table S1). There was no difference in probability of scavenging between coastal and upland for mouse (adjusted p value = 0.139) or snake carcasses (adjusted p value = 0.349), but rat carcasses were approximately 20% more likely to be scavenged in coastal than upland habitat (adjusted p value < 0.0001, Fig. 2). In coastal habitat, there was no difference in probability of scavenging between seasons (adjusted p value = 0.335), but carcasses were 11% less likely to be scavenged in the dry season compared to the wet season in upland habitat (adjusted p value = 0.004, Fig. 2).

The top model for BTS scavenging included only habitat (AIC$_c$ = 741.8, LL = −368.89, w_i = 0.43;

Table 1 Proportion of mouse, rat, and brown tree snake carcasses scavenged in a coastal and upland site on Guam during the wet season (May–August 2016) and dry season (January–April 2017)

Season	Site	Carcass	Scavenged		Unscavenged	
			n	Proportion	n	Proportion
Dry	Coastal	Mouse	64	0.62	39	0.38
		Rat	70	0.62	43	0.38
		Snake	35	0.34	68	0.66
		Site total	169	0.53	150	0.47
	Upland	Mouse	61	0.59	42	0.41
		Rat	30	0.28	76	0.72
		Snake	26	0.27	72	0.73
		Site total	117	0.38	190	0.62
	Season total		286	0.46	340	0.54
Wet	Coastal	Mouse	67	0.58	48	0.42
		Rat	71	0.62	43	0.38
		Snake	36	0.31	81	0.69
		Site total	174	0.50	172	0.50
	Upland	Mouse	81	0.74	28	0.26
		Rat	49	0.41	70	0.59
		Snake	32	0.30	73	0.70
		Site total	162	0.49	171	0.51
	Season total		336	0.49	343	0.51
Overall total			622	0.48	683	0.52

Table 2 Species documented scavenging at mouse, rat, and brown tree snake carcasses placed in a coastal and upland site on Guam during the wet season (May–August 2016) and dry season (January–April 2017)

Scavenger species	Dry season						Wet season						Total
	Coastal			Upland			Coastal			Upland			
	Mouse	Rat	Snake	Mouse	Rat	Snake	Mouse	Rat	Snake	Mouse	Rat	Snake	
Cane toad (*Rhinella marina*)	10	3	4	33	9	14	16	9	4	60	29	26	217
Brown tree snake (*Boiga irregularis*)	35	30		5	2	1	26	44		9	9		161
Monitor lizard (*Varanus indicus*)	12	23	23	4	1		12	13	18		2		108
Hermit crab (*Coenobita* spp)	6	9	1	19	10	8	5	2	5	9	18	8	100
Wild pig (*Sus scrofa*)	1	3	1	1			4	2	1	1	1		15
Coconut crab (*Birgus latro*)	1	4		2	2		2		1		1	1	14
Domestic dog (*Canis lupus*)					5	2							7
Domestic cat (*Felis catus*)										1			1
Domestic chicken (*Gallus gallus*)										1			1
Unknown	1	3	7	4	3	3	5	4	8	1	1	2	42

Fig. 2 Panel **A** Predicted proportion of mouse, rat, and brown tree snake carcasses scavenged across a coastal and upland site in Guam (2016–2017). Panel **B** Predicted proportion of carcasses (mouse, rat and brown tree snake combined) scavenged in a coastal and upland site on Guam during the wet season (May–August 2016) and dry season (January–April 2017)
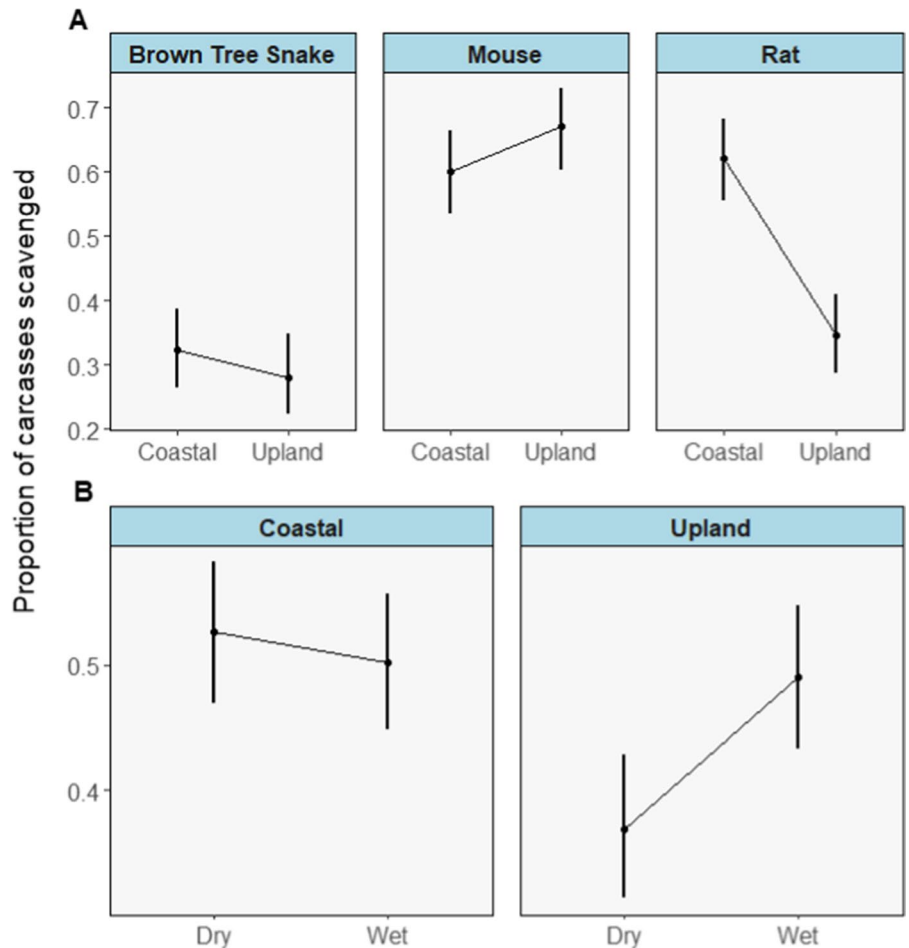
Table S2) and predicted a 25% increase in frequency of scavenging in the coastal compared to the upland site. The top model for cane toad scavenging included all three variables (AIC$_c$ = 1004.8, LL = −497.40, w_i = 1.00; Table S2). The model predicted a 12% increase in cane toad scavenging in wet season compared to dry season, and 18% increase in scavenging in the upland compared to the coastal site. Cane toads were more likely to consume mice than snakes or rats ($p < 0.001$ for both cases), but there was no difference in frequency of rat and snake consumption ($p = 0.959$).

For monitor lizards, the top model included habitat and season (AIC$_c$ = 644.3, LL = −319.112 w_i = 0.53; Table S2). It predicted a 17% increase in scavenging in upland compared to coastal habitat, and an increase of 6% in the dry season compared to the wet season. The top model for hermit crab scavenging included carcass and habitat (AIC$_c$ = 684.9, LL = −338.42, w_i = 0.42; Table S2) and predicted a 7% increase in scavenging by hermit crabs in the upland compared to the coastal site. Although the top model included carcass type, there was no difference in frequency of carcass consumption based on pairwise comparisons (p values: mouse–rat = 0.965; mouse–snake = 0.083; rat–snake = 0.133).

Mean species richness overall was 1.07; one scavenger species was documented at 580 carcasses, 2 species at 40 carcasses, and 3 species at 2 carcasses. The top model for species richness was the null

model (AIC$_c$ = 1305.6, LL = −651.79, w_i = 0.43; Table S3). For the scavenging survival analysis, the top model included all three independent variables as well as the carcass × habitat and habitat × season interactions (AIC$_c$ = 2691.0, LL = −1336.43, w_i = 0.57; Table S4). For mouse carcasses, there was no difference in time to carcass consumption between habitats ($p = 0.321$), but time to consumption was shorter in the coastal habitat compared to the upland habitat for snakes ($p = 0.029$) and rats ($p < 0.001$; Fig. 3). Although the habitat × season interaction was included in our top model, pairwise comparisons indicated no significant differences in time to consumption between seasons in the coastal ($p = 0.441$) or upland habitats ($p = 0.121$).

After removing 7 trials due to camera failure, our sample size for the decomposition analysis consisted of 113 trials. The median time to decomposition was 3.96 days (range 1.66–8.64 days; Fig. 4). The top model for the decomposition survival analysis included carcass type and season (AIC$_c$ = 1083.7, LL = −536.55, w_i = 0.42; Table S5). Predicted median time to decomposition was 3.67 ± 0.18 days for carcasses in the wet season compared to 4.48 ± 0.21 days for carcasses in the dry season (Fig. 5). There was no difference in time to decomposition between mouse and rat carcasses ($p = 0.118$), but both types decomposed more quickly than BTS carcasses ($p < 0.001$ both cases; Fig. 5).

Fig. 3 Predicted time to carcass removal of mouse, rat, and brown tree snake carcasses placed in a coastal and upland site on Guam (May 2016–April 2017)
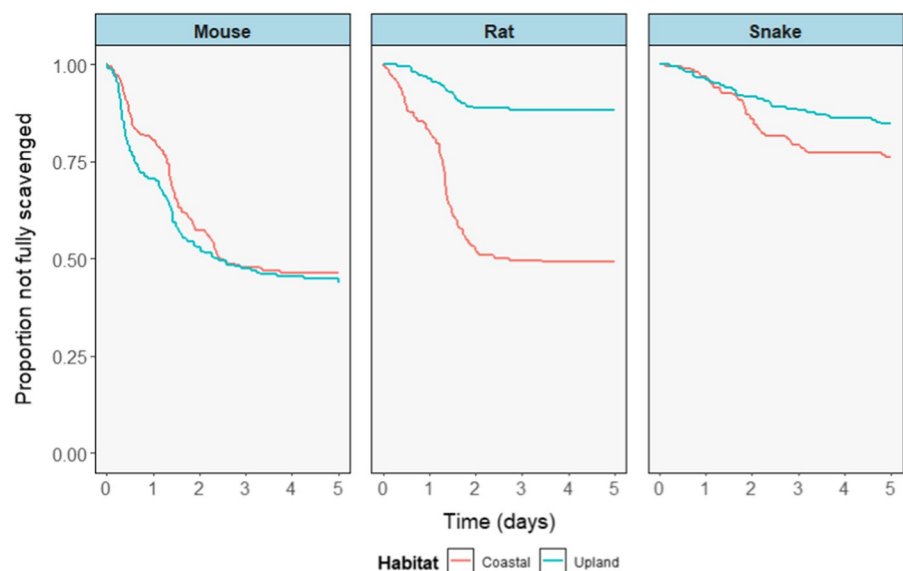
Fig. 4 Days to decomposition for rat, mouse and brown tree snake carcasses placed in a coastal and upland site on Guam (May 2016–April 2017)
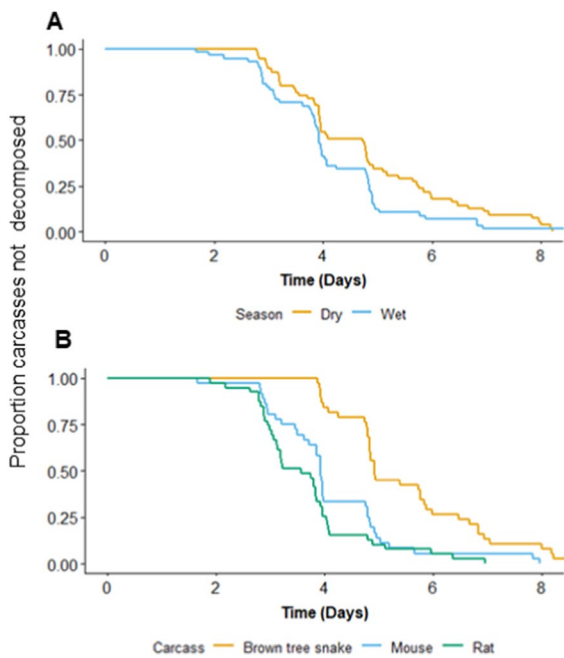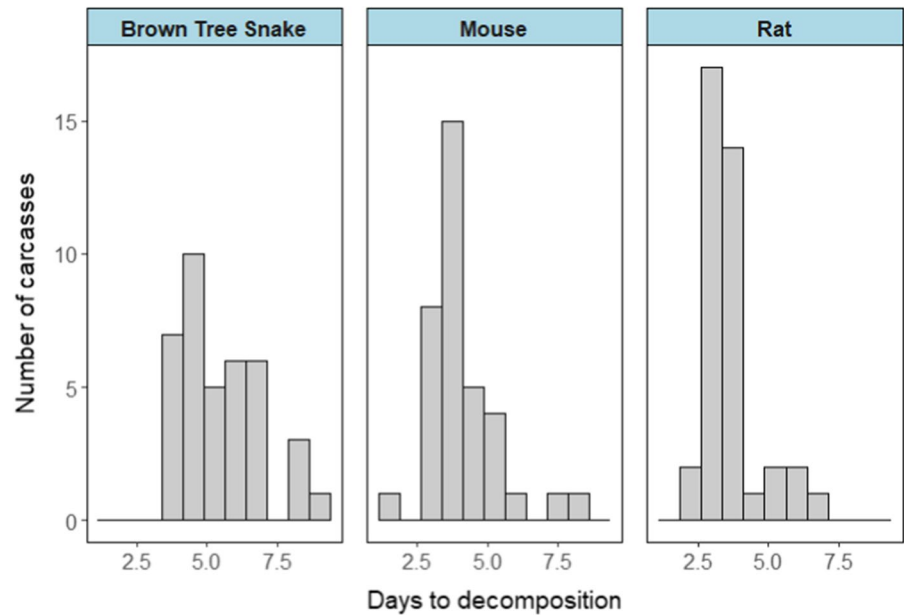

Fig. 5 Panel **A** Predicted time to carcass decomposition (mouse, rat and brown tree snake combined) on Guam during the wet season (May–August 2016) and dry season (January–April 2017). Panel **B** Predicted time to decomposition of mouse, rat and brown tree snake carcasses on Guam (May 2016–April 2017)

Discussion

Invasive species consume the majority of small vertebrate carrion on Guam. Similarly, invasive vertebrates were the primary scavengers of carcasses in Hawaii (Abernethy et al. 2016), and invasive red foxes on Australian beaches outcompeted native birds for carrion to become the dominant scavenger (Brown et al. 2015). Scavenging behavior can play an important role in vertebrate range expansions, possibly contributing to invasion success by increasing dietary niche breadth (Blázquez et al. 2016; Clergeau and Yésou 2006). Invasive species sometimes fail to establish because they are unable to exploit novel prey, but this pitfall may be somewhat circumvented by utilization of carrion in destination landscapes (Mack et al. 2000; Preiszner et al. 2020; Sih et al. 2010).

As they become the dominant scavengers, these invasive species likely have a substantial effect on the detrital pathway of food webs because more energy is transferred via scavenging links than predation links (Wilson and Wolkovich 2011). Invasive species can affect the rate of scavenging and competitively exclude native species from an important resource (Brown et al. 2015). Scavenging by invasive animals likely also influences the spatial distribution of nutrients across the landscape with subsequent effects to plant communities (Abernethy et al. 2016). Thus, the impacts of invasive species on food webs and

ecological functions may be much greater when their scavenging behavior is considered. On Guam, BTS and cane toads probably have such an effect considering they collectively were responsible for over half of all scavenging events. Furthermore, the dominance of scavenging by these invasive animals on Guam also raises the possibility of positive feedback loops contributing to invasion meltdown, wherein greater abundance of these species increases their carrying capacity via provisioning of resources in the form of carrion (Abernethy et al. 2016; Bump et al. 2009; Simberloff and Von Holle 1999).

Invasive species were largely responsible for the relationships between scavenging and habitat, carcass type and season on Guam. As a result, variation in scavenging by these species across treatments accounts for the lack of full support for our predictions. BTS, for example, are trapped in the upland site but not the coastal site, resulting in densities at the coastal site that are nearly three times higher (Smith et al. 2016). These differences in abundance of a major scavenger likely contributed to the interaction between habitat and carcass, with a pronounced decline in scavenging of rat carcasses, but not other carcass types, in the upland site. Cane toads, the other major scavenger, consumed rats less frequently and thus did not compensate for reduced scavenging of rats by BTS in the upland site. Additionally, reduced activity by BTS in the upland site may have led to scavenging by a greater variety of species due to reduced competition, as all three of the other major scavengers (i.e., cane toads, hermit crabs, and monitor lizards) individually consumed more carcasses in the upland than in the coastal site.

Cane toads were introduced to Guam in the 1930s to control agricultural pests (Rodda et al. 1991) and were the most common scavenger overall, documented at every combination of carcass type, habitat, and season. The interaction between habitat and season can be attributed to cane toads because their activity levels increase with greater amounts of rainfall, which led to increased scavenging during the wet season in the upland site (Muller et al. 2018; Schwarzkopf and Alford 2002). The lack of increase in scavenging in the coastal site by cane toads during the wet season adds further support for a dampening effect of BTS on activity by other scavengers in this habitat. More frequent consumption of mice compared to rats and BTS by cane

toads was likely the result of mouse carcasses sizes, which were more similar in size to cane toads' prey and likely easier to consume (Reed et al. 2007).

Scavenging behavior of BTS also influenced the lower overall consumption of BTS carcasses compared to rats and mice because BTS scavenged conspecifics on just one occasion. A review of scavenging by snakes found only one instance of scavenging a conspecific (DeVault and Krochmal 2002). Aversion to intraspecific scavenging (i.e., scavenging carrion of the same species) has also been reported for birds and mammals (Butler-Valverde et al. 2022; Muñoz-Lozano et al. 2019; Olson et al. 2016). This behavior may be adaptive as species that are more closely related are more likely to be affected by the same pathogens (Moleón et al. 2017). As such, the risk of contracting disease may outweigh the benefits of scavenging, particularly when other food sources are available (Moleón et al. 2017). The minimal potential for secondary ingestion of acetaminophen by BTS through scavenging indicates that toxic baiting programs must rely on primary bait consumption because scavenging of conspecifics is virtually nonexistent.

More frequent scavenging by monitor lizards during the dry season may reflect a seasonal increase in carrion consumption due to decreased availability of their major prey items such as gastropods and earthworms (Dryden 1965; Wikramanayake and Dryden 1988). Additionally, the slower decomposition times of carcasses in the dry season may have resulted in a larger window in which carcasses were palatable to monitor lizards. Consumption of mouse and BTS carcasses could pose a risk to monitor lizards because acetaminophen can kill juveniles of this species (Dorr et al. 2016). However, scavenging at these carcass types was relatively infrequent, documented at 6% of mouse and 9% of snake carcasses. The ecological consequences of potential monitor lizard mortality from toxic bait carcass consumption are unclear, as the status of the species as native or introduced has been debated, and they have been subject to various removal efforts on Guam (Weijola et al. 2020). Because there was no seasonal difference in carcass consumption by BTS, concentrating baiting efforts during the wet season may reduce the potential for nontarget mortality of monitor lizards without sacrificing the efficiency of control efforts.

Hermit crabs scavenged extensively and were the only species besides cane toads to scavenge at every treatment level. Hermit crabs can survive 80-mg doses of acetaminophen (Johnston et al. 2002), but thresholds for toxicity have not been established, nor have potential sublethal effects of acetaminophen exposure. Brodifacoum even at high doses is not toxic to crabs and is likely to pose little risk to invertebrates generally (Pain et al. 2000). Widespread scavenging by hermit crabs suggests the potential for substantial toxicant exposure, which warrants further study to understand their effects on hermit crabs, especially considering their important ecological role on Pacific islands (Nigro et al. 2017; Page and Willason 1983). Additionally, although they were less common scavengers, potential effects of carcass consumption on coconut crabs is also an area where additional research is needed, as coconut crabs are economically and culturally important on Guam.

Scavenging behavior of hermit crabs could expose other vertebrates to toxicants through trophic transfer. Birds in particular are susceptible to poisoning by brodifacoum and hermit crabs are consumed by some critically endangered species found on Guam, such as Mariana crows (*Corvus kubaryi*) (Faegre et al. 2020). Native avifauna could therefore be at risk of exposure to toxicants through predation of scavengers. Additionally, with more than half of carcasses not scavenged by vertebrates or crabs, there was likely considerable scavenging by insects, which can also store brodifacoum in their tissues and could serve as a pathway for toxicant exposure (Brooke et al. 2013). Indeed, we sometimes observed skinks consuming maggots that were present on carcasses. Brodifacoum does not generally persist in the environment or invertebrate tissues for long periods of time, so overall risk of secondary poisoning may be low (Brooke et al. 2013; Wegmann et al. 2019), but it has been implicated in the mortality of nestling birds (Masuda et al. 2014). The potential transfer of toxicants from scavengers to predators warrants further investigation to ensure toxic bait carcasses do not incidentally harm species that occupy higher trophic levels.

Scavenging activity at less than half of all carcasses was likely in part the result of the small carcass sizes and environmental conditions. Carcasses of larger species such as large ungulates compared to small birds or rodents are more likely to be detected and consumed as the result of increased visual and chemical cues (Moleón et al. 2015; Turner et al. 2017). Because carcass size is positively associated with scavenger species richness, the small vertebrate carcasses also resulted in low species richness, similar to other studies using small vertebrate carcasses (DeVault et al. 2011; Inger et al. 2016; Sebastián-González et al. 2020; Turner et al. 2017). The small carcass sizes we used also enabled scavengers to often consume the entire carcass at once, resulting in largely similar patterns between frequency of carcass consumption and time to carcass removal.

Additionally, the high temperatures of our study site led to rapid carcass decomposition, resulting in a narrow time frame in which carrion is palatable to most scavengers (DeVault et al. 2004; Hill et al. 2018a; Turner et al. 2017). Our decomposition trials indicated that on average, carcasses decomposed within 4 days, but in some cases as little as 1 day. For many facultative scavengers, carrion consumption is more prevalent when other resources are scarce, and alternative food availability may have led to low scavenging rates (Jędrzejewski and Jędrzejewska 1992; Jędrzejewski et al. 1993). Indeed, we captured images of wild pigs consuming coconuts in the background, but not scavenging the carcass. Rapid carcass decomposition coupled with availability of other food resources thus contributed to the observed consumption rates of small vertebrate carcasses on Guam.

Scavenging by invasive animals on Guam raises potential issues with invasive species control efforts. Toxic baiting programs could increase food availability to invasive vertebrates, but successful eradication efforts would produce a single pulse of carrion that may not benefit invasive species over the long term. However, if management practices result in reductions of BTS but not complete eradication, continued control efforts could provide a more long-term source of carrion for invasive species, albeit at a lower quantity. The dominance of cane toad scavenging in the site with lower BTS densities suggests that they would be the species most likely to benefit from increases in carrion availability resulting from BTS eradication. Thus, there is the potential for the elimination of one invasive species to benefit another via reduced competition for resources, another 'surprise effect' of invasive species eradication (Courchamp et al. 2003). However, since BTS are arboreal and cane toads are not, there is not complete trophic overlap because many BTS prey are inaccessible to cane

toads. As such, the functional response of cane toads due to BTS eradication is unclear. Nevertheless, an integrated approach to invasive species management on Guam will likely necessitate strategies to reduce cane toad abundances (e.g., Muller, Schwarzkopf 2018) to ensure that BTS eradication does not result in trading one invasive species for another.

Data availability The datasets generated during the current study are included in its supplementary information files.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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