



Seabird consumption on Kauaʻi: age-dependent risk from free-ranging cats (*Felis catus*) based on gut content analysis

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Abstract Free-ranging domestic cats (*Felis catus*) pose a significant threat to global biodiversity, especially for avifauna on islands. On Kauaʻi, Hawaiʻi, cats are responsible for 35.6% of predation events on endangered ʻuaʻu (*Pterodroma sandwichensis*) and ʻaʻo (*Puffinus newelli*) seabirds. Both species have experienced population declines on Kauaʻi in recent decades, with 78% of ʻuaʻu and 94% of ʻaʻo lost. Cats are the most destructive predator of these seabirds, yet there are few studies examining demographics, morphology, and diet of cats on Kauaʻi. This study aimed to identify demographic and morphometric characteristics associated with increased seabird consumption by free-ranging cats on Kauaʻi to inform adaptive management strategies. We described the age, sex, body mass and bite force of cats in three regions: upland remote, lowland remote, and lowland suburban. As hypothesized, cats in the region with access to anthropogenic food sources were larger; however,

bite force did not differ significantly between regions. Cats captured in seabird colonies had a more male-skewed sex ratio and were generally younger than cats in other regions, suggesting that these may be dispersing individuals. A logistic regression of gastro-intestinal content data for upland cats (n=113) revealed that seabird consumption probability is positively associated with age (Odds Ratio=1.414, 95% CI [1.074, 1.861]) but has little directional relationship with body mass (OR=1.002, 95% CI [1.000, 1.003]); bite force and sex were not retained. Model predictions indicated that body mass constrained consumption risk in younger individuals, while age alone predicted consumption in individuals older than our model-derived value of 5.8 years. However, while this estimate is modeled from observed data, it remains exploratory and not a demonstrated threshold for seabird consumption. Yet, the significance of age indicates consumption could be a learned behavior and highlights the temporal urgency of removing cats from seabird colonies. We recommend managers employ adaptive, diverse removal strategies that prioritize rapid removal of cats after detection in seabird colonies. Additionally, source populations of cats in lowland regions should be suppressed to limit dispersal into sensitive upland habitats.

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Introduction

Domestic cats (*Felis catus*) are successful predators that have been introduced globally by humans (Turner & Bateson 2013). Cats are at least partly responsible for 14% of global bird, mammal, and reptile extinctions, and have been listed as one of the world's 100 worst invasive species due to their serious impact on native biodiversity (GISD 2020; Lowe et al. 2000; Medina et al. 2011). Free-ranging cats are especially destructive on islands and in areas where wild-life has not evolved alongside mammalian predators (Philippe-Lesaffre et al. 2025; Nogales et al. 2013) and are considered the primary extinction driver for 33 species of endemic island vertebrates (Medina et al. 2011). In a review of cat diets on islands, 16% of 179 consumed vertebrate species were listed on the IUCN Red List of Threatened Species (Bonnaud et al. 2011). Additionally, cats act as reservoirs for multiple diseases, including serving as the definitive host for the parasite *Toxoplasma gondii*, which poses significant health risks to humans and has been identified as a substantial cause of mortality in some threatened wildlife populations (Harting et al. 2020; Kreuder et al. 2003; Work et al. 2000).

On islands, predation by cats poses significant risks to populations of vulnerable seabird species (Fitzgerald & Veitch 1985; Kirkpatrick & Rauzon 2009; Veitch 2001). Kaua'i serves as the breeding ground for a significant portion of the endangered 'ua'u (Hawaiian Petrel, *Pterodroma sandwichensis*) and 90% of the threatened 'a'o (Newell's Shearwater, *Puffinus newelli*) population, making the island critical to continued survival of these species (Ainley et al. 2019; U.S. Fish and Wildlife Service 1967, 1975, 2021). A combination of powerline collisions, light attraction, habitat modification, and introduced predators, such as cats, has resulted in sharp declines in populations of both species on Kaua'i in recent decades, with 78% of 'ua'u and 94% of 'a'o lost between 1993 and 2013 (Raine et al. 2017, 2020).

Both the 'a'o and 'ua'u evolved without terrestrial predators and thus display little anti-predator behavior (Carthey & Banks 2014; Warham 1996). Although other nonnative vertebrates, including black rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), the house mouse (*Mus musculus*), feral pigs (*Sus scrofa*), and Barn Owls (*Tyto alba*), prey on these seabirds, cats are the most destructive

predator at breeding grounds in the Hono O Nā Pali Natural Area Reserve (NAR) on Kaua'i as cats disproportionately target adult birds (Raine et al. 2020). Both the 'a'o and 'ua'u reach sexual maturity at five to seven years of age, nest in underground burrows accessible to terrestrial predators, and exhibit strong site and mate fidelity, meaning the loss of one adult to predation can disrupt breeding for multiple seasons (Ainley et al. 2001; Raine et al. 2020). Cats pose a major threat, not only at breeding colonies, but in rural, suburban, and urban areas across Kaua'i when seabirds become disoriented and grounded by artificial lights and are vulnerable to predation (Ainley et al. 2001; Friswold et al. 2020; Rodríguez et al. 2014; Telfer et al. 1987). To protect these seabird species, the free-ranging cat population must be managed (Raine et al. 2020). Because eradication of cats on Kaua'i is not currently feasible due to the island's rugged terrain, cat density, and continued reintroduction from the pet trade, management should focus on individuals that pose the greatest risk to native species (Bomford & O'Brien, 1995; Moseby et al. 2015; Nogales et al. 2004).

Understanding the demographics and morphology of invasive predators can provide valuable insights for management efforts. Cats are generalist predators that consume a wide range of prey species, and on islands in particular, prey selection is driven by local availability (Lepczyk et al. 2023). This suggests seabird predation may be driven less by active prey selection, but instead by whether cats are able to successfully capture these relatively large prey (418–433 g at fledging; Young et al. 2023). Age may influence prey choice, with evidence that individuals may learn the skills necessary to depredate certain species with repeated encounters (Dickman & Newsome 2015; Fleming et al. 2020; Hardman et al. 2016). Larger predators are able to exploit larger prey, as has been demonstrated within sexually dimorphic felid species, with larger males taking larger prey than their female counterparts (Litvaitis et al. 1986; Radloff & Du Toit 2004). Felids also characteristically kill prey through a bite to the head or neck (Leyhausen 1979). Greater jaw muscle area and mechanical advantage can increase the force delivered during a killing bite, suggesting more developed cat bite force musculature may be necessary to subdue larger prey. Therefore, age, body size, sex, and bite force may influence the

likelihood of successfully capturing and subduing seabird prey in Kauai's cats.

Evidence for prey specialization in free-ranging cats has led to a call for predator profiling techniques in wildlife protection programs to identify and remove individual cats that pose the greatest threat to focal wildlife species (Choeur et al. 2022; Dickman & Newsome 2015; Moseby et al. 2015). In Western Australia, leghold traps captured a higher proportion of adult cats, particularly males, while cage traps caught younger cats and those that scavenged for food (Short et al. 2002). There is also evidence that different scent lures and baits can be effective for attracting specific cats. Verbene & Ruardij (1982) observed that male cats responded more to the urine of oestrous females than anoestrous females, and Clapper-ton et al. (1994) found that extracts from two plants containing lactones were more effective in attracting captive cats and urban strays than social odors such as urine, anal-gland secretions, and commercial lures.

Investigating the demographic and morphological characteristics of cats known to consume seabirds can distinguish high-priority cats for removal through targeted management strategies and could be paramount toward preserving 'a'o and 'ua'u populations on Kauaʻi. Moreover, recognizing intraspecific variation and dietary specialization within this generalist carnivore population can inform managers in designing diverse and adaptive trapping programs to effectively target the full spectrum of predators on the landscape. While complete eradication of cats from sensitive habitats on Kauaʻi would provide the greatest benefit to native species, logistical, financial, and social constraints currently limit the feasibility of island-wide removal. Additionally, sustained control efforts can unintentionally select for individuals that avoid capture, resulting in a remaining population that is increasingly trap-recalcitrant and more difficult to capture over time (Johnstone et al. 2024). Therefore, management strategies that account for variation in predator demography, morphology, and prey selection may improve effectiveness by prioritizing individuals most likely to impact vulnerable species. However, there are few studies examining the demographic and morphometrics of free-ranging cat populations globally.

This study aims to identify which demographic and morphometric characteristics of cats on Kauaʻi are associated with higher seabird consumption to inform

management strategies by wildlife agencies. First, we hypothesized that the demographic and morphometric characteristics of captured cats would differ across regions of Kauaʻi due to differences in human presence influencing anthropogenic food availability. We predicted that regions with greater human influence would contain cats of older age and larger size distributions compared with remote regions. Second, we hypothesized that certain demographic and morphometric characteristics are associated with greater predation capacity and would increase the likelihood of seabird consumption history. We predicted that older, larger, male cats with higher bite force estimates would be more likely to have consumed seabirds, as determined by gastrointestinal (GI) content analysis.

Methods

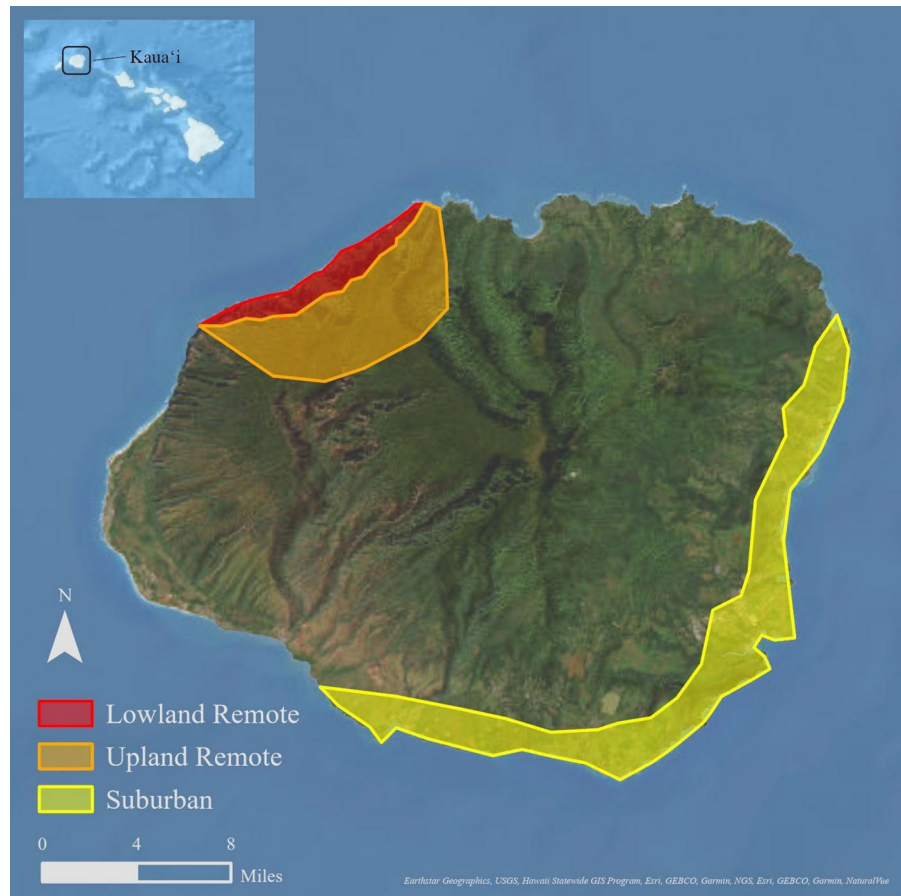
Data was collected from free-ranging cats removed from Kauaʻi, HI between 2015 and 2023 by Hallux Ecosystem Restoration LLC (HER) during management actions. HER is a wildlife management organization which oversees predator control for seabird protection through contracts with local, state, and federal government agencies and private entities on Kauaʻi. From collected cat necropsy data, we generated age distribution, sex ratio, body mass, bite force estimates, and seabird consumption rates to describe the island-wide cat population and inform wildlife managers for improved seabird conservation. The Bernice Pauahi Bishop Museum (Honolulu, HI) currently maintains a sizable collection of free-ranging cat skulls and associated data generated by HER (n=230). Additional data for 469 cats were provided by HER staff. All data and code are available on Figshare.

Study system

We divided the cat population into three regions based on capture location and level of human presence (Fig. 1).

- a. Upland Remote (UR): Free-ranging cats were collected from remote areas of mountainous, wet rainforest in the Hono O Nā Pali NAR on Kauaʻi from 2015–2023 at elevations ranging from 900–1200 m. This area contains critical popula-

Fig. 1 Map of the three study regions where free-ranging cats (*Felis catus*) were removed on Kaua'i from 2015 to 2023



tions of 'a'o and 'ua'u as well as other threatened and endangered species. Human presence at these sites is extremely low. As a result, cat populations are not supplemented by people and instead survive independently. Access into these sites often involves extensive effort via helicopter operations or intense hiking.

- b. Lowland Remote (LR): Free-ranging cats were collected from remote mesic valleys along the Nā Pali Coast of northwestern Kaua'i from 2017 to 2022 at elevations ranging from 0 to 180 m. There is no permanent human presence in this region; however, some areas are frequented by hikers and campers, and cats may have occasional access to anthropogenic food. Entry into these sites involves extensive effort via helicopter, hiking, or boating operations.
- c. Lowland Suburban (LS): Free-ranging cats were collected around areas of human habitation on the east, south, and west sides of Kaua'i

from 2020 to 2023 at elevations ranging from 0 to 75 m. Human presence is high at these sites, and cats are likely subsisting on human refuse, being directly fed by people, and catching live prey. Cats were from properties belonging to and managed by Kaua'i County as mandated by the Kaua'i County Seabird Habitat Conservation Plan (State of Hawai'i, Department of Land and Natural Resources, Division of Forestry and Wildlife, 2020).

Specimen acquisition and preparation

Walk-in cage traps (sizes 762–914 mm, Tomahawk Live Trap, Hazelhurst, WI, USA) were the primary trap type used to capture cats across all sites. Single-door cage traps were placed near trails and baited with cat food or scent lures to attract cats into the trap. Double-door cage traps were typically set unbaited

and camouflaged on trails, and captured individuals as they naturally moved through the landscape. Cage trap bases were further camouflaged with leaves and dirt to simulate the trail surface. Cage traps were checked and rebaited every 1–2 days and captured cats were humanely euthanized following the AVMA Guidelines on Euthanasia of companion animals S1.3.3 (American Veterinary Medical Association 2020). Spring-driven body-grip traps (sizes 220–330, Belisle Trap, Belisle Pieges, Canada) were used to lethally remove cats at remote sites not frequented by seabirds or during times of the year when seabirds were not present to prevent nontarget capture. Body-grip traps were either set with scent lures to attract cats, or camouflaged on trails to capture cats as they moved along the trail. Because of the potential harm to humans and pets, body-grip traps were not used in publicly accessible areas. After field collection, carcasses were refrigerated and necropsied within seven days or stored frozen until thawed and necropsied. Specimens were collected prior to South Dakota State University research involvement and analyses performed were on archived remains and associated data.

Demographic and morphometric data collection

Sex (male, female, unknown) was determined based on genital presentation during necropsy. Age class (juvenile, subadult, adult) was assigned based on body mass and dental eruption of each individual (Fleming et al. 2021). Juvenile cats were identified by the presence of deciduous teeth and/or lack of most permanent teeth. Subadult cats exhibited mixed dentition of deciduous and permanent teeth, consistent with individuals under 8 months of age. Adult cats were distinguished by the presence of fully erupted permanent dentition. To complement the assigned age class and obtain a more precise age estimate for each specimen, canine teeth ($n=244$) were sent to Matson Laboratories (Manhattan, MT; www.MatsonLab.com) for cementum annuli analysis, a technique with a demonstrated record of successfully aging felines (Danner et al. 2010; Fleming et al. 2021; Hiller et al. 2022). Canine teeth were isolated by soaking lower jaws in water at 130–140°F until the lower canines were easily removed following recommendations from Matson Laboratories. All samples received an estimated birth year based on incremental lines of the

canine cementum and/or degree of canine root closure as per published methods (Grue & Jensen 1979).

Body mass (g) was measured during necropsy using a Pesola 80,015 Macro-Line Spring Scale 5 kg×50 g (Pesola Präzisionswaagen AG, Chur, Switzerland). Each individual was weighed before and after removal of all internal organs (excluding the brain) to obtain full body mass and dressed carcass mass, respectively. Dressed carcass mass was used in all analyses to capture muscle and subcutaneous fat mass while eliminating the possibility of artificially inflated and variable body mass measures due to presence or absence of GI contents. The GI tract (stomach and intestine) contents were examined macroscopically during necropsy to document consumed contents, including ‘a’o and ‘ua’u seabird remains, other prey items, or anthropogenic sources of food. The presence or absence of seabirds as a diet item was determined by manually investigating necropsy notes for records of ‘a’o or ‘ua’u flesh, feathers, or bone. We use the term seabird ‘consumption’ rather than ‘predation’, as GI tract analysis cannot differentiate between active predation and potential scavenging.

Cranial measurements were obtained from skulls that had been dehydrated and cleaned using a dermestid beetle colony. Available crania ($n=349$) were photographed in standardized ventral, dorsal, and lateral views with the lower jaw removed using a digital camera on a tripod (Olympus Tough TG-6). Linear and areal dry skull measurements (mm) were collected from these photographs using ImageJ software following established methods (Damascono et al. 2013) (see Fleming et al. 2020, Fig. 1). Bite force (F , in Newtons) was calculated using the lever model method following a published formula (Forbes-Harper et al. 2017; Kiltie 1984; Thomason 1991), where:

$$F = 2 \times \frac{(dm \times m \times \sigma) + (dt \times t \times \sigma)}{c}$$

whereas, m and t are the cross-sectional areas of the masseter/pterygoid muscles and temporal muscle, respectively; dm and dt are the distances between the center of these muscle groups and the temporomandibular joint (TMJ); σ is the isometric muscle stress value of 0.3 Newtons • mm⁻² (Sakamoto et al. 2010); and c is the distance between the TMJ and base of the upper canines (mm).

Bite force was corrected using the formula below (F_{corr} ; N), as the dry skull method has been shown to underestimate bite force (Sakamoto et al. 2010).

$$F_{corr} = 10^{(0.859 \times \log F + 0.559)}$$

Statistical analyses

To compare if cat sex ratios differed between three study regions on Kaua'i, we used a Kruskal-Wallis test followed by Dunn's post-hoc test with a Bonferroni adjustment for pairwise comparisons (R Core Team 2024; Ogle et al. 2025). The rank-based Dunn's test was used to accommodate unequal sample sizes, with the Bonferroni adjustment applied to control the familywise error rate across pairwise contrasts. Age, dressed carcass mass, bite force, head length, and head-body length data violated the assumptions of normality. We performed a Kruskal-Wallis test to assess if these variables differed significantly between regions (R Core Team 2024). Only morphometric data (F_{corr} , head length, head-body length) from adult cats based on age class assignments were used for significance testing to prevent disproportionate age ratios from skewing regional averages. If the test indicated significant differences, Dunn's tests were conducted to identify which specific subpopulations differed (Ogle et al. 2025). Mann-Whitney U tests were performed using the *rstatix* package for all variables to identify adult differences between sexes (Kassambara 2023). The results of these comparisons were adjusted for multiple comparisons using the Bonferroni correction (R Core Team 2024). Additionally, the *rcompanion* package (Mangiafico 2024) was used to compute the Wilcoxon Z statistic for the pairwise Mann-Whitney U tests. Statistical significance was determined using an alpha value of $p < 0.05$.

To evaluate factors associated with seabird consumption by UR free-ranging cats, we fit a logistic regression model relating consumption history (coded as 1 for presence of seabird remains in the GI tract and 0 for no remains) to a set of predictor variables. Predictor variables included estimated bite force (F_{corr} ; Newtons), dressed carcass mass (grams), sex (numerically coded), and age (years) for cats captured during times of year when seabirds are present on the island ($n=113$). Variable selection was conducted using the LASSO approach implemented in the *lasso2*

package (Ahrens et al. 2020) in StataSE. Potential interactions were tested using the Chi-squared automated interaction detection (CHAID) algorithm in the *chaid* package (Luchman 2014). Model performance was evaluated using a goodness-of-fit for the logistic regression against the null model; we report McFadden's pseudo- R^2 (McFadden 1972).

To evaluate model performance and determine the predictive threshold for seabird consumption, we conducted Receiver Operating Characteristic (ROC) curve analysis. We identified the empirical optimal cutpoint of predicted probability using the Liu method (Liu 2012), which maximizes the product of sensitivity and specificity.

To translate this probability threshold into management-relevant metrics, we mapped the optimal cutpoint back into the parameter space to calculate a consumption capability threshold. This boundary represents the predicted body mass required to likely consume a seabird as a continuous function of age. We used the delta method to estimate 95% confidence intervals around this boundary. Finally, we calculated the theoretical age at which the mass threshold intersects zero—both for the mean boundary and the lower confidence limit—to identify when seabird consumption transitions from a mass-dependent constraint to a generalized, mass-independent capability. Logistic regression analyses were conducted using StataSE v.19.0 (StataCorp 2024, College Station, TX).

Results

We found significant differences in the proportion of sexes captured between the UR and both low-land regions (Fig. 2). A significant difference was observed between LR and UR, ($p \leq 0.05$; LR: 39% M; UR: 66% M) and between LS and UR, ($p \leq 0.001$, LS: 53% M; UR: 66% M), but not between LR and LS ($p=0.332$).

Significant regional and/or sex differences for adult cats were found in dressed carcass mass, age, bite force, head length, and head-body length (Table 1, 2). The average dressed carcass mass of LS cats was 48.8% heavier than the average body mass of cats from remote regions, while body mass differences between the two remote regions were not significant (Fig. 3, Table 2). Male cat dressed carcass mass was 24.5% higher on average than females, and

Fig. 2 Stacked bar plot of sex ratios of free-ranging cats (*Felis catus*) removed from three study regions on Kaua'i between 2015 to 2023

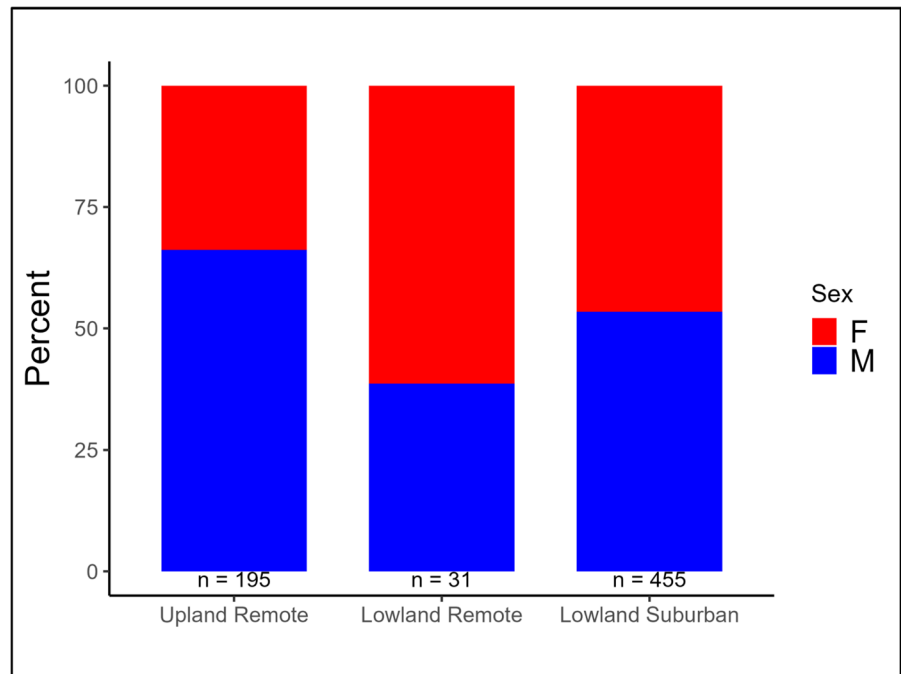


Table 1 Mann–Whitney U test summary statistics of the sexual demographics of free-ranging cats (*Felis catus*) collected on Kaua'i from 2015 to 2023. Comparisons between sexes are presented as Z-scores with corresponding *p*-values. Statistically significant comparisons ($p \leq 0.05$) are shown in bold

Sex	Median (IQR)	Mean $\pm$ SD	Sample Size	F
			<i>N</i>	<i>Z-score,</i> <i>p-value</i>
<i>Dressed Carcass Mass (g)</i>				
M	2350 (1119)	2472 $\pm$ 809	242	6.21, ≤ 0.001
F	1888 (800)	1999 $\pm$ 650	174	
<i>Age (years)</i>				
M	0.0 (1.0)	1.0 $\pm$ 1.8	105	-2.27, ≤ 0.05
F	1.0 (2.0)	1.8 $\pm$ 2.6	59	
<i>F_{corr} (N)</i>				
M	221 (47)	225 $\pm$ 43	78	4.17, ≤ 0.001
F	189 (32)	193 $\pm$ 29	44	
<i>Head Length (mm)</i>				
M	94 (12)	94 $\pm$ 9	329	7.81, ≤ 0.001
F	88 (9)	88 $\pm$ 8	247	
<i>Head-Body Length (mm)</i>				
M	501 (73)	504 $\pm$ 73	324	7.06, ≤ 0.001
F	473 (56)	471 $\pm$ 45	246	

male cats were significantly younger (M: 0 [interquartile range (IQR)=1]; $n=105$, F: 1 [IQR=2]; $n=59$) (Table 1). UR cats were significantly younger (0 [IQR=1]; $n=137$) than LR cats (2 [IQR=4.75]; $n=18$) (Table 2). Some individuals greatly exceeded these averages, with maximum ages of 11 years (Fig. 4). Male cats had significantly longer head and head-body lengths than females, as did LS cats compared to remote regions (Table 1, 2). Male cats had significantly higher bite force values than females, but bite force was not significantly different between regions (Table 1, 2).

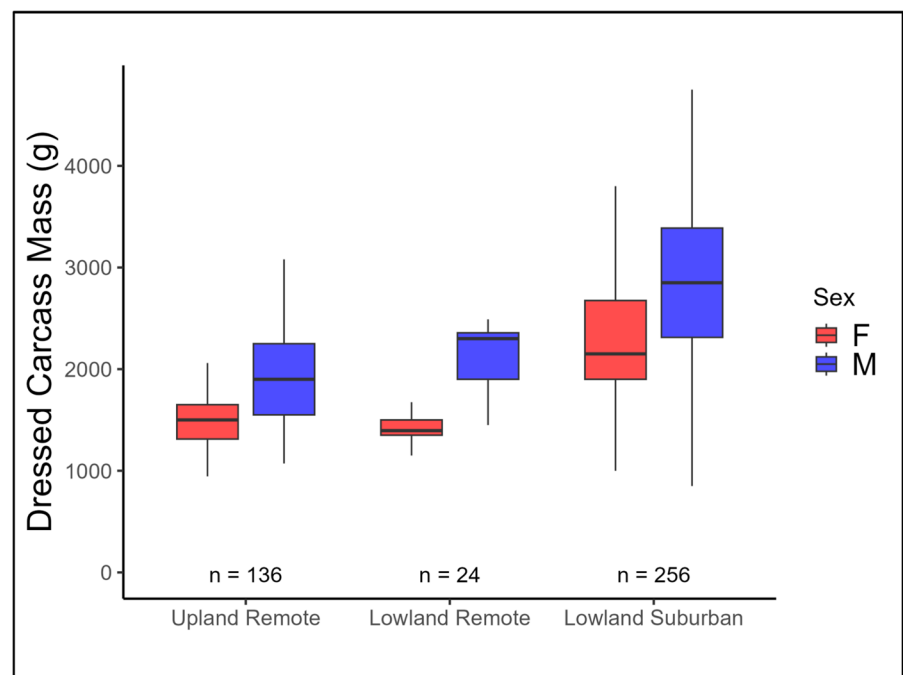
Necropsy data indicated that only cats captured from the UR region had seabirds present in their GI tract. Of the 26 UR cats positively identified with seabird remains (12.32% of region), 18 were male, five were female, and three were of unknown sex. From cementum results, the median age of cats that consumed seabirds was 1.5 [IQR=4.25] years, while those without seabird remains had a median age of 0 [IQR=1] years.

We evaluated corrected bite force as a potential predictor of seabird consumption alongside dressed carcass mass and age. Inclusion of bite force resulted in a small increase in explained variance but had a weak effect with marginal statistical support and a negative coefficient. Penalized

Table 2 Dunn's test summary statistics of the regional demographics and morphometrics of free-ranging cats (*Felis catus*) collected on Kaua'i from 2015 to 2023. Pairwise comparisons between regions are presented as Z-scores with corresponding *p*-values (Bonferroni corrected). Statistically significant comparisons ($p \leq 0.05$) are shown in bold

Region	Median (IQR)	Mean $\pm$ SD	Sample Size	LR	LS
			<i>n</i>	<i>Z</i> -score, <i>p</i> -value	<i>Z</i> -score, <i>p</i> -value
<i>Dressed Carcass Mass (g)</i>					
UR	1725 (600)	1793 $\pm$ 460	137	1.30, 0.59	-10.53, ≤ 0.001
LR	1442 (269)	1602 $\pm$ 406	24		
LS	2500 (1060)	2593 $\pm$ 773	256	6.36, ≤ 0.001	
<i>Age (years)</i>					
UR	0.0 (1.0)	1.0 $\pm$ 1.9	137	-2.62, ≤ 0.05	-1.97, 0.15
LR	2.0 (4.8)	2.7 $\pm$ 3.0	18		
LS	1.5 (2.0)	1.8 $\pm$ 2.4	16	-0.40, 1.00	
<i>Head Length (mm)</i>					
UR	86 (8)	86 $\pm$ 8	151	2.07, 0.12	-10.52, ≤ 0.001
LR	81 (7)	82 $\pm$ 6	26		
LS	93 (11)	94 $\pm$ 9	410	7.02, ≤ 0.001	
<i>Head-Body Length (mm)</i>					
UR	459 (58)	471 $\pm$ 88	141	1.49, 0.41	-7.07, ≤ 0.001
LR	451 (57)	448 $\pm$ 59	25		
LS	495 (63)	498 $\pm$ 52	407	4.80, ≤ 0.001	

Fig. 3 Bar-and-whisker plot of dressed carcass mass (g) of free-ranging cats (*Felis catus*) removed from three study regions on Kaua'i between 2015 and 2023

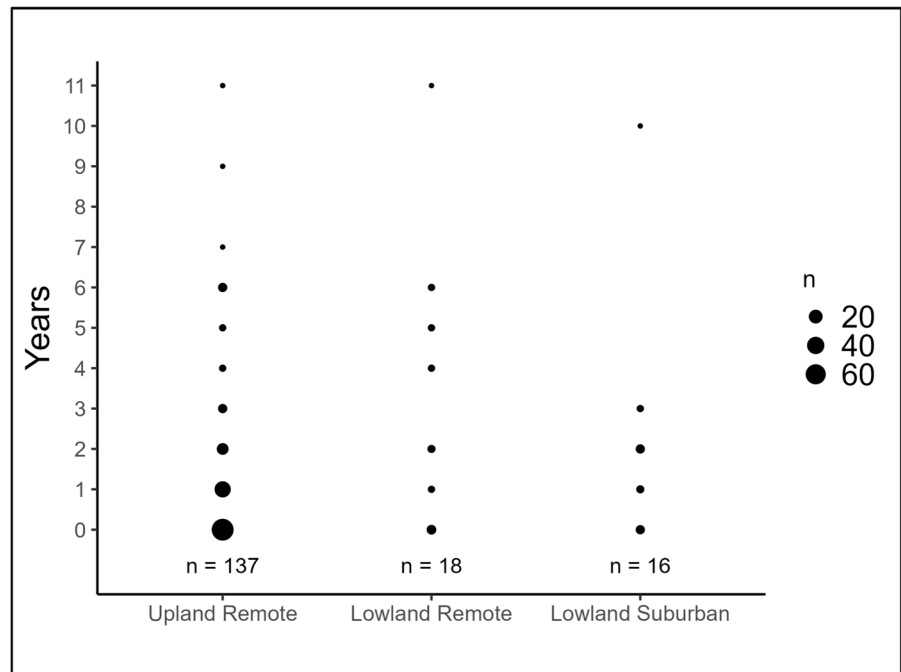


regression (adaptive LASSO with EBIC) excluded bite force, and effect sizes indicated that body mass and age accounted for the majority of explained variation. These results suggest that bite force does not contribute independent functional information

beyond body size and experience; therefore we have excluded bite force from further analyses.

A logistic regression of gut content data for all UR cats ($n=113$), including individuals with and without seabird remains, revealed

Fig. 4 Scatter plot of age (years) of free-ranging cats (*Felis catus*) removed from three study regions on Kaua'i between 2015 and 2023 determined by cementum age analysis



that seabird consumption probability is positively associated with age (Odds Ratio=1.414, 95% CI [1.074, 1.861]) but has almost no directional relationship with dressed carcass mass (OR=1.002, 95% CI [1.000, 1.003]); bite force and sex were dropped during initial variable selection by adaptive LASSO.

The final logistic regression model explained 20.8% of the variance in seabird consumption (pseudo- $R^2=0.208$), and the likelihood ratio test indicated that the inclusion of predictors significantly improved model fit ($\chi^2=14.23$, $p \leq 0.001$). The estimated log-odds of seabird consumption can be calculated as follows,

$$\text{logit}(P) = -6.265 + 0.0018 \times (\text{mass}) + 0.3462 \times (\text{age})$$

where, mass is dressed body mass in grams, and age is estimated age in years. This main-effects model was retained as the most parsimonious and predictive framework for subsequent threshold calculations.

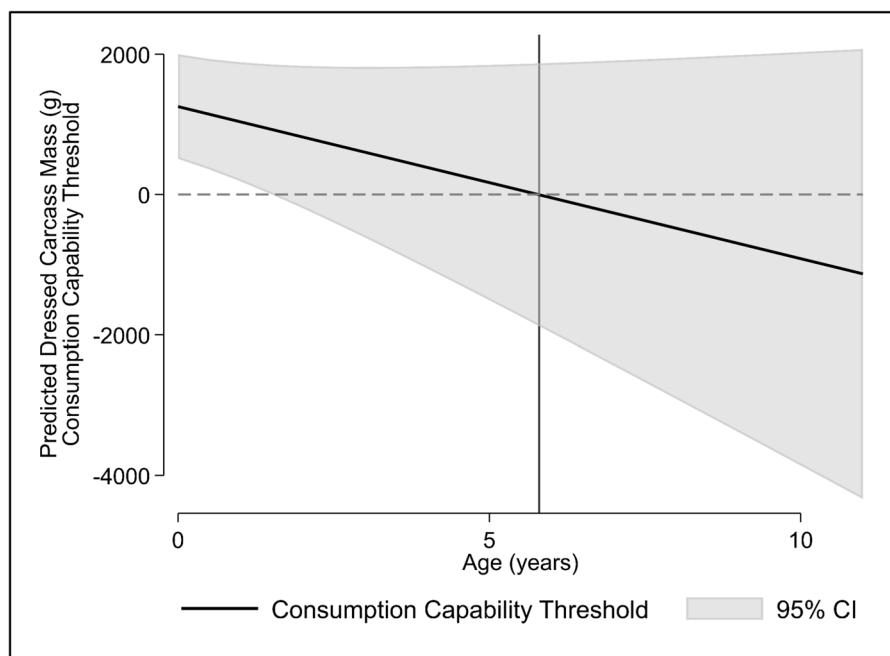
Utilizing this model, ROC analysis identified an empirical optimal probability cutpoint of 0.107 (Liu method; sensitivity=0.80, specificity=0.78, AUC=0.79). By projecting this probability threshold back into the biological parameter space, we established a model-derived consumption capability

threshold defining the required dressed carcass mass for likely seabird consumption across ages (Fig. 5). This boundary revealed an inverse relationship: younger cats require substantially greater mass than the observed minimum for that age class to exceed the consumption threshold (e.g., a required mass of 2162 g at 1 year, which is 1090 g beyond the observed minimum versus a required mass of 2223 g at 2 years, which is 873 g beyond the observed minimum). The mean predictive boundary intersected zero body mass at 5.78 years, indicating that age increasingly contributed to predicted consumption probability as body mass approached zero. However, delta-method standard errors demonstrated that the lower bound of the 95% confidence interval intersects the zero-mass threshold much earlier, at approximately 1.5 years. These model-derived values of 1.5 and 5.8 years are exploratory and should not be interpreted as biological thresholds.

Discussion

Cats from the Lowland Suburban (LS), Lowland Remote (LR), and Upland Remote (UR) regions demonstrated significant differences in sex ratios, body

Fig. 5 Predicted cat dressed carcass mass (g) threshold for likely seabird consumption as a function of age (years). The solid black line represents the predicted mean consumption capability threshold for cats to consume seabirds in relation to mass and age. The shaded gray region denotes the 95% confidence interval and the vertical black solid line indicates ~ 5.8y of age at which the estimated consumption threshold intersects zero dressed carcass mass



size, body mass, and age measures. LS cats were larger and heavier than cats from remote regions, while UR cats had a more male-skewed sex ratio and were generally younger. While cats with a higher body mass were generally associated with higher bite force (Supp. Figure 1), age was the largest predictor of seabird consumption, with older cats more likely to be identified as having consumed seabirds from GI tract analysis.

Male cats generally exhibited higher bite force values than females, reflecting their larger body sizes and more robust masseter musculature (Table 1). However, while cats from the LS region were significantly heavier and larger than cats from either of the remote regions (Table 2), they did not display significantly higher bite force values. Other studies have documented differences in skull shape between wild and captive carnivores as a result of captive diet (Antonelli et al. 2022; Cooper et al. 2023; Hartstone-Rose et al. 2014; Siciliano-Martina et al. 2021). Although all cats in this system were free-ranging, cats from the LS region were in closer proximity to anthropogenic food sources, which likely require less jaw strength to process than live prey. Differences in resource use could therefore contribute to variation in bite force independent of body size, though this mechanism was not tested in the present study.

Age emerged as the primary explanatory variable of consumption probability, as older cats are modeled to be more likely to have consumed seabirds, supporting previously documented increases in prey size as felids age (Elbroch & Quigley 2019; Fleming et al. 2020). While other variables such as sex and bite force were dropped during initial variable selection, our consumption capability threshold analysis revealed a nuanced relationship between age and body mass. Rather than acting as a simple linear predictor, body mass appears to place a greater constraint on predicted consumption capability at younger ages, with this constraint relaxing as age increases. Younger cats, particularly those over 1.5 years that have consequently achieved mature size (Supp. Figure 2), require substantially greater body mass to exceed the estimated consumption threshold, whereas the model-derived boundary approaches zero body mass at approximately 5.8 years. While these thresholds should be interpreted as model-derived exploratory values, this shifting relationship between age and body mass suggests that seabird consumption may reflect cumulative experience and learned behavior rather than physical attributes alone. Cats are generalist predators that exploit a wide range of available prey, with prey use largely driven by local availability (Lepczyk et al. 2023). While most cats in this system

are likely capable of exploiting seabirds as a food source, 'a'o and 'ua'u seabirds are seasonally present on Kaua'i, and breeding colonies are restricted to relatively small geographic areas. Therefore, repeated opportunistic encounters with seabirds may reinforce behavior as cats recognize seabirds as high-calorie prey that exhibit minimal predator defense behaviors. Previous studies have suggested individual cats may 'prey-switch' when discovering a new abundant prey type (Dowding & Murphy 1993; Hardman et al. 2016; Murdoch & Oaten 1975). Here, the higher occurrence of seabird in the GI tract of older cats could reflect greater cumulative exposure to seabird colonies over time, increasing opportunities to encounter and repeatedly consume this resource.

Limitations

This study is based on data collected from cats that were successfully trapped, and several factors may influence the results. A male bias has been reported in other trapping studies and is hypothesized to be due to sexual differences affecting behavior, such as a larger home range and increased encounters with traps, rather than a disproportionate sex ratio (Kay et al. 2000; Liberg et al. 2000; Molsher 2001). We reported a male skewed ratio in the UR region; however, similar trapping methods were employed in other regions that produced a more even or female-biased sex ratio, suggesting this male bias may be representative of the regional population. In remote areas, body-grip traps are used for lethal removal of cats and are not monitored as frequently as live traps. As a result, specimens from body-grip traps may be retrieved days or weeks after capture and may be unsuitable for determining sex, age, body mass, or bite force. Therefore, UR and LR cats that were caught in body-grip trap types may be underrepresented in this study. Additionally, some cats in this study may have been capable of consuming seabirds but were removed before having the opportunity to engage in this behavior because HER staff often target cats along ingress routes into seabird nesting areas or immediately after detection. Finally, while some morphometric measures were well represented across regions, age estimates were disproportionately limited in some areas due to time constraints associated with tooth extraction and laboratory processing.

GI contents provide a temporally limited snapshot of dietary intake and thus are limited in assessing long-term depredation. Additionally, seabird consumption history was derived by manually verifying previously recorded necropsy notes. Records indicating unidentified feathers, flesh, or bone fragments were assessed to determine whether they were likely from 'ua'u, 'a'o, or other prey species, using knowledge of prey densities in the habitat where each cat was captured. This method may underestimate seabird consumption in cats from lowland areas, where the prey availability of non-seabird bird species, such as free-ranging chickens, is high. Interestingly, unpublished game camera evidence indicates that cats from lowland areas also prey on seabirds. These cats may not consume much of their prey when well-fed (Cecchetti et al. 2021; Loyd et al. 2013), meaning remains may be less evident in the GI tract. Stable isotope analysis could address GI limitations, as seabirds represent a marine diet item that can be distinguished from terrestrial dietary sources of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Harper 2007; Pascoe et al. 2022).

Management implications

Our findings have implications for removal strategies because the predicted lower confidence interval of the model-derived consumption capability threshold suggests that the stochastic onset of predicted seabird consumption may begin at younger ages among larger individuals. Given the potential for consumption risk to increase with age and body mass, earlier removal could be a critical preventative measure to effectively remove cats from the landscape before they have the cumulative age, size, and exposure to establish seabird hunting behaviors. Intensive use of cage traps in the UR region is recommended to catch young cats before they engage with seabirds and to avoid negative impacts of trapping on seabird populations. However, although the UR region consisted of a younger average age due to a higher proportion of young individuals, age classes extended up to 11 years, indicating that older, experienced cats are also present. Therefore, managers should use an adaptive removal strategy that targets cats quickly after detection to limit seabird predation.

Early detection of cats within seabird colonies is critical to allow managers to respond before hunting behavior is established. Cellular game cameras, which

transmit images electronically, can be used within and around seabird colonies to alert managers in real-time to cat detections, enabling rapid response to ingress events. Cameras spaced 500 m apart, with additional units at trail junctions, have proven effective in assisting HER managers with early cat detections.

Once cats are detected, an adaptive trapping strategy that utilizes a variety of trap types, set configurations, and attractants can further improve removal success. Body-grip traps should be used where appropriate to target older, experienced seabird predators and individuals that display trap-recalcitrant behavior. Although foothold traps were impractical at many sites in this study, they may also be effective for capturing experienced adults (Short et al. 2002). Both double-door cage traps and body-grip traps can be set with attractants or deployed unbaited along trails to capture cats as they naturally move through the landscape. Camouflaging traps along trails may further improve capture of experienced or trap-shy individuals. Lures that mimic familiar prey can serve as effective attractants to predators (Hughes et al. 2010); seabird guano or nesting material placed in the back of traps may improve capture success of known seabird predators. Finally, because cats are more receptive to baits as prey availability decreases (Algar et al. 2007; Short et al. 2002), baited traps may be particularly effective during times of year when seabirds are not seasonally present.

While cats in the UR region pose the most direct threat to remnant seabird colonies, cats in lowland regions of the island must be managed due to the potential for seabird light-pollution fallout and to limit cat dispersal into breeding areas. Cats are highly mobile, and regional differences in sex and age further support the need for landscape-scale suppression on Kauaʻi. Research on Hawaiʻi Island has supported male-biased dispersal and female philopatry using genetic structure and relatedness estimates of free-ranging cats (Hansen et al. 2007), whereas work on an urban population of cats in France found high philopatry in both sexes and female-biased dispersal (Devillard et al. 2003). Here, the UR region's younger and male-dominated population may indicate it serves as a dispersal sink, while the female-skewed LR population and urban LS population could indicate greater philopatry of females and increased breeding potential (Table 2). The geographic proximity of the UR region to LR and LS regions reinforces the need

for island-wide cat suppression to reduce cat dispersal into seabird breeding colonies (Fig. 1).

Free-ranging cats are a major driver of global biodiversity loss and are especially harmful in insular systems (Lowe et al. 2000; Medina et al. 2011). On large islands (> 50km²) cat eradication programs are often impractical (Nogales et al. 2004). Kauaʻi is a large island (~1,456km²) with high levels of species endemism (Rønsted et al. 2022), and many species are threatened with extinction, including the 'a'o and 'ua'u (Raine et al. 2017). Predator control has contributed substantially to the conservation of 'a'o and 'ua'u on Kauaʻi, with both species experiencing significant increases in reproductive success with the initiation of control operations (Raine et al. 2020). Without this control, population modeling has indicated rapid population decline (Raine et al. 2020). The continued recovery of 'a'o and 'ua'u on Kauaʻi, along with seabird populations globally, will depend on cat management strategies that prioritize rapid removal of seabird specialists and aim for landscape-scale suppression of cats. Long-term management strategies should consider regional human and environmental factors influencing cat demographics and trapping success. Variables such as cat density, food availability, foraging strategy (hunting vs. scavenging), sex, age, and seabird presence can guide the selection of traps, baits, and lures for each region (Clapperton et al. 1994; Molsher 2001; Short et al. 2002). However, the lack of demographic predictors other than age highlights the broader threat all outdoor cats pose to seabirds on Kauaʻi, as individual cats can rapidly switch prey bases and become dietary specialists (Dickman 2009). These findings caution against a highly-targeted trapping operation or traps that lack sufficient variety to address the range of cats present at a given site, and wildlife professionals are strongly advised to employ a diverse array of trapping techniques across management sites to capture the full range of cats on the landscape.

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Data availability All datasets and R code are publicly available on Figshare at: https://figshare.com/projects/Gheida_et_al_Seabird_consumption_on_Kaua_i/259784.

Declarations

Competing interests Alex Dutcher and Kyle Pias are co-founders of Hallux Ecosystem Restoration. The authors declare that there is no conflict of interest regarding the publication of this article.

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