A REVIEW OF LIFE-STAGE-SPECIFIC PREDATORS OF FOUR ENDEMIC HAWAIIAN WATERBIRDS

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ABSTRACT: Hawaiian wetlands provide habitat for seven indigenous waterbirds. Of the six endemic to Hawai'i, the U.S. Fish and Wildlife Service has designated five as endangered and one as threatened; maintaining their populations requires control of introduced species of predators. Their susceptibility to depredation varies by life stage, and they should be managed strategically to offset vulnerabilities specific to each life stage. A review of the literature for life-stage-specific predators of the eggs, chicks, and adults of the endemic Hawaiian Duck (*Anas wyvilliana*, koloa maoli), Hawaiian Coot (*Fulica alai*, 'alae ke'oke'o), Hawaiian Gallinule (*Gallinula galeata sandvicensis*, 'alae 'ula), and Hawaiian Stilt (*Himantopus mexicanus knudseni*, ae'o) yielded 99 sources and identified 17 predators, encompassing birds, mammals, reptiles, amphibians, and fish. Eleven species of predators took eggs or chicks; only four took adults. Although some predators may have been reported taking only one of the waterbirds, it is likely they pose at least some risk to all four taxa. However, variation in behavior and habitat among the four waterbirds may lead to slightly different predation pressures. Aquatic predators likely have a propensity for the more aquatic duck, coot, and gallinule chicks. Managers of Hawaiian waterbirds will require many tools and resources to combat predators that occupy land, air, and water, but control should focus on the most devastating taxa—nonnative birds and mammals.

Before humans settled in Hawai'i, its wetlands provided habitat for at least 23 species of taxonomically described native waterbirds: 10 waterfowl, two ibis, nine rails, a shorebird, and a heron (Walther 2022). Currently, Hawai'i's wetlands support seven species of waterbirds, six representing endemic species—the Hawaiian Goose (*Branta sandvicensis*, nēnē), Laysan Duck (*Anas laysanensis*, koloa pōhaka), Hawaiian Duck (*A. wyvilliana*, koloa maoli), and Hawaiian Coot (*Fulica alai*, 'alae ke'oke'o)—or subspecies—the Hawaiian Gallinule (*Gallinula galeata sandvicensis*, 'alae 'ula) and Hawaiian Stilt (*Himantopus mexicanus knudseni*, ae'o)—as well as the nonendemic but naturally occurring Black-crowned Night Heron (*Nycticorax nycticorax hoactli*). Because of wetland loss, habitat degradation, and introduced predators, all Hawaiian waterbirds designated as endangered or threatened by federal or state agencies will require active management indefinitely (Reed et al. 2012, Underwood et al. 2013, Van Rees and Reed 2014). Hawaiian waterbirds are ground-nesters and are particularly vulnerable to nonnative mammals (Reed et al. 2012). Because of their adaptations to the absence of mammalian threats, Hawaiian waterbird populations have declined to the point that their survival relies upon the intervention of wetland managers to reduce those predators. Potential predators are diverse (Underwood et al. 2013), with some of them capable of preying only on specific life stages of certain endangered waterbirds. Understanding life-stage-specific vulnerabilities to predators could help wetland managers prioritize tactics targeting the most devastating taxa, according to whether the predator preys on eggs, chicks, and/or adults.

Introduced predators that might prey on eggs of Hawaiian waterbirds include rats (*Rattus* spp.), the cat (*Felis catus*), dog (*Canis lupus familiaris*), feral

pig (*Sus scrofa*), Small Indian Mongoose (*Urva auropunctata*), Western Cattle-Egret (*Ardea ibis*), and Common Myna (*Acridotheres tristis*). Also, the naturally occurring Ruddy Turnstone (*Arenaria interpres*), Black-crowned Night Heron, and migratory gulls (*Leucophaeus* spp. and *Larus* spp.) may take eggs (Crossin and Huber 1970, Byrd 1979, Donehower et al. 2007, Harmon et al. 2021, Works et al. 2024). Likely predators of Hawaiian waterbird chicks include the endemic Hawaiian Hawk (*Buteo solitarius*, ʻio) and Hawaiian Short-eared Owl (*Asio flammeus sandwichensis*, pueo), the naturally occurring night heron, migratory gulls, vagrant or overwintering raptors, the Great Frigatebird (*Fregata minor*), brackish-water fish like the Great Barracuda (*Sphyraena barracuda*), and the introduced cat, dog, pig, mongoose, cattle-egret, American Barn Owl (*Tyto furcata*), American Bullfrog (*Lithobates catesbeiana*), Cane Toad (*Rhinella marina*), Red-eared Slider (*Trachemys scripta elegans*), and freshwater fish like the Largemouth Bass (*Micropterus salmoides*) (see Swedberg 1967, Collins 1979, Byrd and Telfer 1980, Megyesi and Griffin 1996, Fraticelli and Rocchi 1999, Donehower et al. 2007, USFWS 2011, Reynolds et al. 2015). After fledging, Hawaiian waterbirds might be preyed on by the endemic hawk, Short-eared Owl, vagrant or overwintering raptors, and by the introduced cat, dog, and barn owl (Byrd and Telfer 1980, Clarkson and Laniawe 2000, Reynolds et al. 2015).

Depending on the waterbird's life stage, potential predators seem to decrease as the waterbird matures from the egg to the chick to the adult stage. Identifying life stage-specific predators of Hawaiian waterbirds could provide the framework for a hierarchical predator-control plan that prioritizes effort for the predators that endanger all three life stages, then the predators that threaten two, then one.

Here I synthesize the peer-reviewed articles, theses, dissertations, and agency reports that document predators of the eggs, chicks, and adults of the Hawaiian Duck, Hawaiian Gallinule, Hawaiian Coot, and Hawaiian Stilt, and identify predators with the greatest effect, in terms of life stages. The goal is to provide managers of Hawaiian waterbirds with a prioritized list of predators to consider targeting for control.

METHODS

I reviewed the literature through the Web of Science database (https://www.webofscience.com) by using "all databases" and "all" collections for "all fields." For each of the four species, my search criteria combined the species name and its synonyms in both English and Hawaiian with any word related to "predator," with "mortality," with "nest success," and with "survival." This search returned 43 peer-reviewed articles. To supplement my review, I included agency reports available to me (Eijzenga 2009, Works 2022, 2024, 2025), the journal ʻ*Elepaio* (searching volume indexes when available [volumes 1–55] or article titles [volumes 56–85]), the Cornell Lab of Ornithology's *Birds of the World* species accounts, and personal communications with federal and state Hawaiian waterbird managers. Within each source, I searched for any term related to the word "predator." Upon searching each document for key words, I added all cross-references to the list to investigate further. The cross-references added an additional 47 documents, yielding a total of 99 documents searched for terms related to "predator." With these I compiled

all recorded cases of predation of the Hawaiian duck, gallinule, coot, and stilt, whether confirmed by camera, direct observation, or forensic analysis, by life stage: egg, chick, or adult (defined as any age after fledging). Predators were categorized taxonomically as a bird, mammal, amphibian, reptile, or fish.

RESULTS

I found 2436 mentions of the word "predator" or its derivatives in 99 references (listed in Appendix 1 at https://archive.westernfieldornithologists.org/archive/V57/Work-Appendix1.pdf). Seventeen species of predators were identified from five taxonomic classes (Table 1). The Hawaiian Duck had eight different identified predators, the Hawaiian Coot had 10, the Hawaiian Gallinule had 11, and the Hawaiian Stilt had 14. I identified 11 different predators of eggs, 11 of chicks, and four of adults (Figure 1). The most common egg predators were other birds, but for the chick and adult stages, mammal and bird predators contributed equally (Figure 2). The avian egg predators were all native or migratory birds. In contrast, half of the avian predators of chicks and adults were nonnative, and half were native or naturally occurring species. All predators from the other four taxonomic classes were introduced species. The chick stage was associated with the broadest spectrum of predators and represented all five taxonomic groups.

Reptile predators included one not described previously but mentioned as a personal communication in Rodriguez's (2024) thesis. Tyler Bogardus from the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, observed a Red-eared Slider drowning a gallinule chick by grabbing its foot with its mandibles and pulling it underwater. Afterward, the slider consumed the freshly killed carcass. The captured slider regurgitated remains, which contained body parts from a gallinule and a hybrid Hawaiian Duck × Mallard (*Anas platyrhynchos*; Figure 3). Personal communications with Lisa Roerk, a graduate student studying coot movements on Oʻahu, revealed evidence of a cat preying on an adult Hawaiian Coot. Additionally, Bryn Webber, refuge biologist for the Kauaʻi National Wildlife Refuge Complex, contributed documentation of predators of chicks and adults of the Hawaiian Duck.

DISCUSSION

Identifying the most common predators of Hawaiʻi's endemic waterbirds is important in understanding their conservation and in devising effective management. This study revealed that the stilt is subject to a wider variety of egg predators than is the duck, gallinule, or coot. Since these endemic Hawaiian waterbirds share wetland space, an egg predator of one might well be a predator of the other three. Stilts nest on open mudflats with sparse vegetation, so their nests are more conspicuous than those of the other three, which build their nests amid taller vegetation, providing additional concealment (Malachowski et al. 2018, Works et al. 2024). Stilts nest in the dry season when mudflats tend to dominate in wetlands, perhaps giving land predators more accessible pathways to their nests (Works et al. 2024). This difference might explain the predators on stilt eggs additional to those identified on duck, gallinule, and coot eggs. The most surprising egg preda-

Table 1 Predators of Hawaiian Waterbirds by Life Stage, as Identified in the Literature

	Life stage taken[a]			
Predator species	Egg	Chick	Adult	References
Bird				
Hawaiian Gallinule	g, s			Harmon et al. (2021), Works et al. (2024)
Hawaiian Coot	c, g, s			Works et al. (2024), Works (2024)
Hawaiian Stilt	s			Works (2024)
Ruddy Turnstone	s			Works (2022)
Laughing Gull	s			Coleman (1981)
Black-crowned Night Heron	s	c, d, g, s		Andrews (1981), Berger (1981), Pyle (1985), Harmon et al. (2021), Webber (2022)
Western Cattle-Egret[b]		c, d, g, s		S. Pelizza in litt. in USFWS (2011).
American Barn Owl[b]		d, g, s	d, g, s	K. Viernes pers. comm. in USFWS (2011), Webber (2022), Works (2025), B. Webber (pers. comm.)
Hawaiian Short-eared Owl		s	c, s	Ueoka et al. (1976), Chang (1990), Garcia-Heras et al. (2024)
Mammal				
Black Rat[b]	c, s			Chang (1990), Christensen et al. (2021), Harmon et al. (2021), Works (2024)
Cat[b]	g, s	d, g, s	c, d, g, s	Byrd and Zeillemaker (1981), Gassmann-Duvall (1994), Eijzenga (2009), Christensen et al. (2021), Harmon et al. (2021), Malachowski et al. (2022), Walther (2022), Webber (2022), Works (2024), L. Roerk (pers. comm.), B. Webber (pers. comm.)
Dog[a]	c, g, s	d, s	c, d, g, s	Berger (1981), Byrd and Zeillemaker (1981), Ueoka et al. (1981), Chang (1990)
Feral pig[a]	g	g		Webber (2022)
Small Indian Mongoose[a]	c, g, s	c, g, s		Nagata (1983), Chang (1990), Harmon et al. (2021), Rodriguez (2024), Works et al. (2024)
Reptile				
Red-eared Slider[a]		d, g		T. Bogardus (pers. comm.)
Amphibian				
American Bullfrog[a]		c, d, g, s		Berger (1981), Viernes (1995), Eijzenga (2009), Rodriguez (2024)
Fish				
Largemouth Bass[a]		c , d		Swedberg (1967), Berger (1981)

[a]c, Hawaiian Coot; d, Hawaiian Duck; g, Hawaiian Gallinule; s, Hawaiian Stilt.
[b]Introduced.

tors of Hawaiian waterbird nests were other birds—including conspecifics, likely due to territoriality.

In the literature surveyed, chick predators of the four Hawaiian waterbird species have been identified inconsistently, although a chick predator of one suggests the same vulnerability for the other three. The four waterbirds likely share many of the same bird and mammal predators of chicks (e.g., barn owl, cattle-egret, pueo, cat, dog, pig, and mongoose). The night heron, cattle-egret,

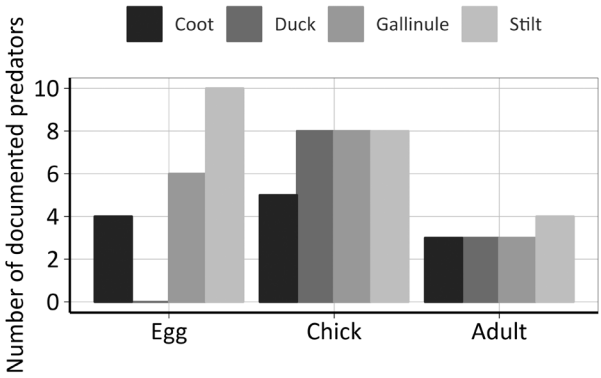

FIGURE 1. The number of documented predators of the Hawaiian Coot, Hawaiian Duck, Hawaiian Gallinule, and Hawaiian Stilt during three life stages—egg, chick, and adult (defined as any bird after fledging)—based on a literature review.

and mongoose have been documented as predators of gallinule, coot, and stilt chicks. The more aquatic duck, gallinule, and coot chicks are more susceptible to aquatic predators (e.g., bullfrog, slider, and bass). The bullfrog has been documented preying on chicks of all four species in this study, but it is an opportunistic carnivore capable of feeding both aquatically and terrestrially, so predation of stilt chicks is plausible. The slider and bass, however, have not been described as predators of the more terrestrial stilt chicks. In Hawai'i, the nonnative slider is an opportunistic feeder (Works and Olson 2018) and must consume prey underwater (Parmenter and Avery 1990). All described slider predation on wetland birds occurred in water deeper than stilt chicks use (Jensen et al. 2023). All reported slider predation on waterbirds involved the turtle's grabbing the bird's foot with its jaws and pulling the bird underwater until it

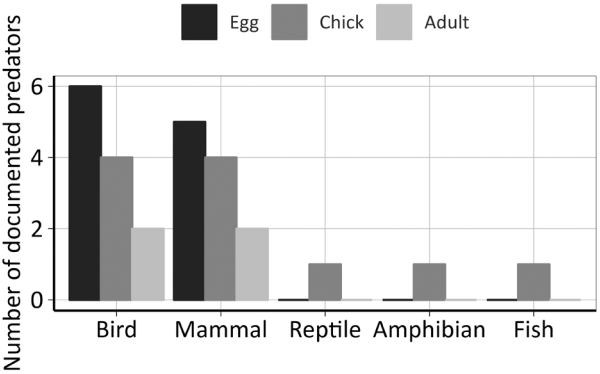

FIGURE 2. The number of identified predators of the Hawaiian Coot, Hawaiian Duck, Hawaiian Gallinule, and Hawaiian Stilt by taxonomic class (bird, mammal, reptile, amphibian, or fish) and life stage—egg, chick, or adult (defined as any bird after fledging)—based on a literature review.

FIGURE 3. A captured Red-eared Slider regurgitated remains of (A) a hybrid Hawaiian Duck × Mallard and (B) of a Hawaiian Gallinule. The slider was observed by Tyler Bogardus (U. S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services) at the O'ahu Club Pond, adjacent to Keawāwa Wetland, grabbing the chick's foot and pulling it underwater to drown it before consuming it.

Photo by Elizabeth Riley

drowned (Pritchard and Trebbau 1984, Fraticelli and Rocchi 1999, Salerno and van den Burg 2021, Glorioso et al. 2024). Likewise, it is not normal to observe stilt chicks in water deep enough to support bass large enough to swallow them.

The predators (e.g., barn and Short-eared owls, cat, dog) of the adults of all four Hawaiian waterbirds are likely the same. Only the cat and dog, however, have been documented taking all species of waterbird I investigated. Of the potential predators, the Hawaiian Hawk has not been documented in the literature as preying on adult waterbirds. Found only on the island of Hawai'i, it is large enough to take coots and stilts, the two waterbirds covered in this study that are present on that island. Clarkson and Laniawe (2000) reported that a stooping hawk contacted a flying adult Hawaiian Goose, but the attack was unsuccessful. Griffin et al. (1998) found nearly half of the diet items the hawk offers to its young to be birds, and nests have been found from sea level to 2600 m, surely overlapping with wetlands occupied by Hawaiian waterbirds.

The Great Frigatebird has not been identified as a predator of chicks of the four species I addressed, but I have observed this bird gliding over wetlands, presumably, to drink fresh water; Gauger Metz and Schreiber (2002) reported it to feed on seabird chicks, suggesting it could take waterbird chicks opportunistically. The Laughing Gull (*Leucophaeus atricilla*) is the only gull species documented as a predator of Hawaiian Stilt eggs, but it is capable of eating chicks too (Donehower et al. 2007). Other gulls visiting Hawai'i occasionally include the Glaucous-winged Gull (*Larus glaucescens*), which is capable of taking chicks, as well as adult waterbirds (Hayward and Verbeek 2008). Vagrant or overwinter-

ing raptors have the potential to prey on waterbird chicks and adults. Though such predation is likely rare, in the Northwestern Hawaiian Islands Reynolds et al. (2015) reported a Peregrine Falcon (*Falco peregrinus*) taking Laysan Ducks.

Identifying life-stage-specific predators of four endemic Hawaiian waterbirds highlights that each life stage of a Hawaiian waterbird is under constant predation pressure from ubiquitous predators, some life-stage-specific (e.g., bullfrog, slider, and largemouth bass), some nondiscriminatory (e.g., cat and dog). Waterbird managers must employ tools and resources to mitigate the effects of birds, mammals, frogs, turtles, and fish to provide complete predator control. The introduced predators should be the focus of management since four of the five taxonomic groups are made up entirely of introduced wildlife. For the avian category, control efforts need only to target the introduced American Barn Owl and Western Cattle-Egret.

The recent population declines of Hawaiian waterbirds, analyzed by Gorresen et al. (2024), suggest that current conservation strategies are not enough. This study provides managers of Hawaiian waterbirds a hierarchical list of the most serious predators, with those that prey on all three life stages (i.e., cat and dog) necessitating the most effort at control. However, the frequency with which predators prey on a single life stage must be considered. Works et al. (2024) found the mongoose to be the most important predator on the eggs of three Hawaiian waterbirds. Predator-control strategies for Hawaiian waterbird conservation must begin with the reduction of introduced predators that threaten two or three life stages (i.e., dog, cat, feral pig, mongoose, and barn owl).

Current control for Hawaiian waterbird predators relies principally on various types of traps. Control effort for predatory mammals in Hawai‘i has leaned heavily on kill and live traps (Roerk et al. 2022), to a lesser degree on mammal-exclusion fencing (Christensen et al. 2021). Mammal-exclusion fencing is expensive and not suitable for wetlands that frequently flood, but otherwise it is effective at excluding mammalian predators. In the future, toxicant bait that is geared for the mongoose rather than the black rat (*Rattus rattus*) may become available on the market (Antaky et al. 2023); Works et al. (2024) found that rats are not a significant predator of gallinule, coot, and stilt eggs. The barn owl and cattle-egret are challenging to control, and firearms are used most effectively; however, Nilsson and Watson (2025) designed a trap box for owls that could allow managers of Hawaiian waterbirds another tool to reduce barn owl populations safely in more urbanized wetlands. Turtles are not major predators of Hawaiian waterbirds, but if localized populations of turtles are problematic, Kuchling (2003) presented a simple and effective trap design. For bullfrog reduction in Hawaiian waterbird habitat, Underwood and Letchworth (2016) designed and tested a trap with limited success at reducing bullfrogs efficiently. Future development of new tools and technology that improve predator reduction in Hawaiian wetlands may provide the missing link to population recovery of these endangered, endemic waterbirds.

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