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Avian Conservation and Management

Nest predation and daily survival rates of three Hawaiian endemic species

Depredación de nidos y tasas de supervivencia diaria de tres especies endémicas de Hawái

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ABSTRACT. Specific State Wildlife Sanctuaries have been identified as core wetlands for the recovery of endangered waterbirds in Hawaiʻi. Hawaiian waterbirds require direct management of habitat and invasive predators for their survival. Therefore, it is crucial to identify seasonal nesting patterns and specific nest predators to improve nesting success. Hāmākua Marsh and Kawainui Marsh, two State Wildlife Sanctuaries, were surveyed weekly for Hawaiian Coot (*Fulica alai*), Hawaiian Common Gallinule (*Gallinula galeata sandvicensis*), and Hawaiian Stilt (*Himantopus mexicanus knudseni*) nests from 2020 through 2023. Some nests were monitored with passive infrared cameras ($n = 240$), and all nests were manually observed twice per week until the fate of the nest was determined. Nest phenology was recorded for all nests, and predation events were determined through camera photos or predator forensics. The seasonal nesting patterns for coots and gallinules showed weakly bimodal distributions, while stilt nesting was unimodal. A total of 395 nests were discovered (coot [$n = 115$], gallinule [$n = 164$], and stilt [$n = 116$]), out of which 59 had unknown fates, 156 failed (46%), and 180 were successful (54%). The daily nest survival rates at Hāmākua were higher for coots (0.975), gallinules (0.973), and stilts (0.972) compared with Kawainui (0.962, 0.942, and 0.969, respectively). Nest failure events documented with cameras were predominantly due to predators at Kawainui (58%) and abandonment at Hāmākua (51%). Nest predation events accounted for 43% (coots), 38% (gallinules), and 55% (stilts) of the confirmed nest failures. The small Indian mongoose (*Urva auropunctata*) was identified as the primary predator responsible for 76% of predator-caused nest failures at both marshes combined. The findings suggest that conservation efforts for Hawaiian waterbirds in Hawaiʻi should prioritize predator control, particularly focusing on the invasive mongoose, to enhance nest success.

RESUMEN. Se han identificado Santuarios Estatales de Vida Silvestre específicos como humedales clave para la recuperación de aves acuáticas en peligro en Hawái. Las aves acuáticas hawaianas requieren manejo directo de su hábitat y de depredadores invasores para su supervivencia. Por lo tanto, es crucial identificar patrones de anidación estacionales y los depredadores específicos de los nidos para mejorar el éxito reproductivo. Entre 2020 y 2023, se realizaron monitoreos semanales de nidos de *Fulica alai*, *Gallinula galeata sandvicensis* e *Himantopus mexicanus knudseni* en Hāmākua Marsh y Kawainui Marsh, dos Santuarios Estatales de Vida Silvestre. Algunos nidos fueron monitoreados con cámaras de infrarrojo pasivo (n = 240), y todos los nidos fueron visitados dos veces por semana hasta determinar su finalización. Se registró la fenología de todos los nidos y se determinaron los eventos de depredación mediante cámaras de fotos o análisis forense de depredadores. Los patrones estacionales de anidación de *F. alai* y *G. g. sandvicensis* mostraron distribuciones débilmente bimodales, mientras que *H. m. knudseni* presentó un patrón unimodal. En total, se encontraron 395 nidos (*F. alai* [n = 115], *G. g. sandvicensis* [n = 164] y *H. m. knudseni* [n = 116]). De estos, 59 tuvieron un destino desconocido, 156 fracasaron (46 %) y 180 tuvieron éxito (54 %). Las tasas de supervivencia diaria de los nidos fueron más altas en Hāmākua para *F. alai* (0.975), *G. g. sandvicensis* (0.973) y *H. m. knudseni* (0.972) en comparación con Kawainui (0.962, 0.942 y 0.969, respectivamente). Los eventos de fracaso documentados con cámaras fueron principalmente causados por depredadores en Kawainui (58 %) y por abandono en Hāmākua (51 %). Los eventos de depredación representaron el 43 % (*F. alai*), 38 % (*G. g. sandvicensis*) y 55 % (*H. m. knudseni*) de los fracasos confirmados de los nidos. Urva auropunctata fue identificada como el principal depredador responsable del 76 % de los fracasos de los nidos causados por depredadores en los dos humedales combinados. Los hallazgos sugieren que los esfuerzos de conservación para las aves acuáticas en Hawái deberían priorizar el control de depredadores, enfocándose especialmente en la especie invasora U. auropunctata, para mejorar el éxito reproductivo de los nidos.

Key Words: *coot; gallinule; mongoose; nest phenology; nest predation; nest survival; stilt; waterbirds*

INTRODUCTION

Hawaiian waterbirds are considered "conservation-reliant," meaning that populations will require active management for the foreseeable future (Reed et al. 2012, Underwood et al. 2013, 2014, van Rees et al. 2022). Increases in Hawaiian waterbird populations have been attributed to the consistency of active management at National Wildlife Refuges and State Wildlife Sanctuaries; the federal and state wetlands contain the largest Hawaiian waterbird populations (Paxton et al. 2021). Federal and state wetland managers mitigate threats to Hawaiian waterbirds by controlling invasive plants and removing invasive predators. Monitoring the success of these strategies over time allows managers to adapt management actions to protect waterbirds most efficiently, given limited personnel and resources. Because nest and pre-fledging

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survival is low for these species (Byrd and Zeillemaker 1981, van Rees et al. 2018, 2024, Pratt and Brisbin 2020, Robinson et al. 2020), monitoring nests and chicks is essential to guide management decisions.

The U.S. Fish and Wildlife Service has identified Hāmākua Marsh State Wildlife Sanctuary and Kawainui Marsh State Wildlife Sanctuary as "core" wetlands for the recovery of three endemic and endangered waterbirds: the Hawaiian Coot (*ʻalae keʻokeʻo*; *Fulica alai*), Hawaiian Common Gallinule (*ʻalae ʻula*; *Gallinula galeata sandvicensis*), and Hawaiian Stilt (*aeʻo*; *Himantopus mexicanus knudseni*; USFWS 2011). These State Wildlife Sanctuaries are managed to provide foraging and breeding habitat and to mitigate non-native predators of these endangered waterbird nests, chicks, and adults.

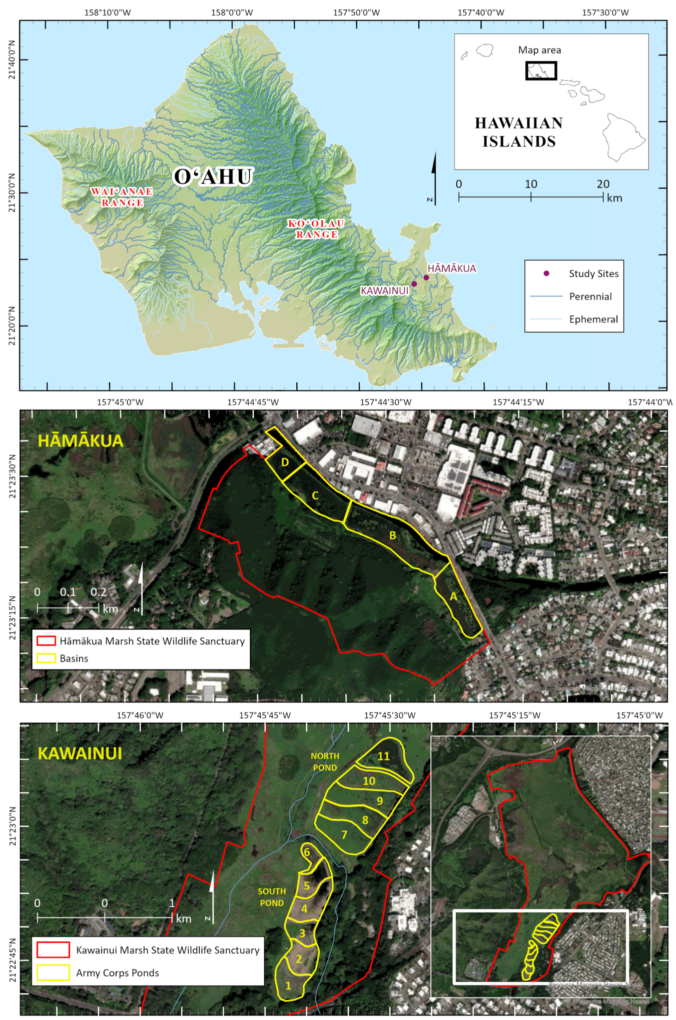
A major threat to the recovery of Hawaiʻi's endangered waterbirds is introduced non-native predators (USFWS 2011, Underwood et al. 2013). Potential egg predators include small Indian mongooses (*Urva auropunctata*), black rats (*Rattus rattus*), feral cats (*Felis catus*), feral dogs (*Canis familiaris*), wild pigs (*Sus scrofa*), and Common Mynah (*Acridotheres tristis*; Byrd and Zeillemaker 1981, Eijzenga 2009, USFWS 2011, Underwood et al. 2013, Robinson et al. 2020, Harmon et al. 2021, Webber 2022). Identification of nest predators, a potentially manageable threat, is an important objective in creating an appropriate predator control program for the recovery of Hawaiian waterbird populations. Predators of waterbird nests in Hawaiʻi have been anecdotally reported but seldom quantified through direct observations. Nest predators that have been documented are largely mammalian and avian (USFWS 2011), although unpublished reports document a broader range of predators. Eijzenga (2009) reported 10% of Hawaiian Stilt nests were depredated by avian or mammalian predators for two consecutive nesting seasons, and Harmon et al. (2021) found 17% of Hawaiian Stilt nests failed because of predation spanning three nesting seasons and seven Oʻahu wetland sites. Webber (2022) observed that 6% of Hawaiian Common Gallinule nests failed because of depredation by mammalian predators. No studies have quantified predators of Hawaiian Coot nests nor included these three species (Hawaiian Common Gallinule and Hawaiian Stilt) in a single study.

This study aimed to determine patterns in nest phenology, daily nest survival, the rate of nest depredations, and the predators responsible for depredating Hawaiian Coot, Hawaiian Common Gallinule, and Hawaiian Stilt nests at Hāmākua Marsh and Kawainui Marsh State Wildlife Sanctuaries on Oʻahu, Hawaiʻi. Our overarching goal was to determine patterns and causes of nest failures so that conservation managers could develop targeted actions to protect vulnerable Hawaiian waterbirds.

STUDY SITE

Hāmākua Marsh (37 ha) and Kawainui Marsh (336 ha) State Wildlife Sanctuaries (Kailua, Hawaiʻi) form a wetland and upland complex on the windward side of the Koʻolau Range on the island of Oʻahu (Fig. 1). The wetlands were historically connected prior to the construction of the Kawainui flood control levee in 1966. Today, Hāmākua Marsh is seasonally brackish, while Kawainui Marsh is palustrine, lending to differences in dominant vegetation between sites.

Fig. 1. Map of Hāmākua Marsh and Kawainui Marsh State Wildlife Sanctuaries on the island of Oʻahu in the Hawaiian Islands (inset map). The Hāmākua map pictures the State Wildlife Sanctuary boundary (red line) and the study site (yellow line) within Basins A, B, C, and D. The Kawainui map displays the State Wildlife Sanctuary boundary (inset map, red line) and the study site (yellow lines) in the South (cells 1–6) and North Ponds (cells 7–11).



The location of the study took place in the waterbird habitat at Hāmākua Marsh, which comprises the smaller 9.4-hectare wetland portion within the State Wildlife Sanctuary (21°23′23.3″ N 157°44′ 30.0″ W). The wetland is a series of four interconnected basins via the Kawainui Stream, and each basin is unique in topography, resulting in a spectrum of water depths (0–60 cm) through the dry and wet seasons. The wetland is fed from rainfall (82 cm mean annual precipitation) and runoff from the adjacent 27.5-hectare Puʻu o ʻEhu upland. Water from the adjoining Kawainui Stream will flood the interior of the wetland during the rainy season or when the sand berm at Kailua Beach Park is removed, and the ocean tides result in a net increase in water level. However, during those events, water levels usually drop. Managers do not have control over water input, so the basins tend to dehydrate during the dry season (May–Oct). The dominant vegetation within the wetland is non-native pickleweed (*Batis maritima*) and native saltmarsh bulrush (*kaluh*ā; *Bolboschoenus maritimus*). Pickleweed is managed through thinning using a disking attachment on an amphibious machine to replicate the structure native wetland vegetation would provide and to increase interspersion (the interface between water and vegetation); vegetation structure analogous to a native wetland should improve Hawaiian waterbird habitat (Bantilan-Smith et al. 2009, Reed et al. 2012, Underwood et al. 2013, van Rees et al. 2022).

The Kawainui Marsh portion of the study focused on excavated ponds in the southwestern portion of Kawainui Marsh State Wildlife Sanctuary (21°22′57.9″ N 157°45′37.4″ W). This site comprises two ponds (12.7 total ha) separated into 11 terraced cells (0.2–1.7 ha each) by low earthen berms. The ponds were excavated from pastureland by the Army Corps of Engineers (ACOE) in 2012. The pond complex is bisected by the Maunawili Stream, dividing the site into the North Pond (5 cells) and South Pond (6 cells), and the average depths range from 0 to 76 cm, with South Pond tending drier than the North Pond. The cells were constructed in an irregular mosaic pattern and are supplied with water through rainfall (82 cm mean annual precipitation) and periodic flooding of the Maunawili Stream. Because managers do not have control over water input, the ponds tend to dry out during the summer, complicating the management of invasive vegetation. The dominant vegetation at this site is invasive California grass (*Brachiaria mutica*), non-native barnyardgrass (*Echinochloa crus-galli*), invasive Mexican primrose willow (*Ludwigia octovalvis*), and native water hyssop (*ʻaeʻae*; *Bacopa monnieri*). The waterbird habitat at Kawainui is characterized by difficult-to-manage, tall, dense, and invasive vegetation (i.e., California grass) dominating the ponds, providing a low-quality habitat for Hawaiian waterbirds (Bantilan-Smith et al. 2009, Reed et al. 2012, Underwood et al. 2013, van Rees and Reed 2014, van Rees et al. 2022). This is contrasted by a wetland dominated by native vegetation (i.e., *B. maritimus*, *Cyperus* spp., and *Schoenoplectus tabernaemontani*), which provides less dense vegetation structure and more interspersion.

METHODS

Nest searching and monitoring

We located and monitored waterbird nests from January 2020 through December 2023. We located nests during routine weekly to monthly surveys designed to count adult waterbirds and during separate area-search nest surveys designed to locate nests in dense vegetation. We conducted waterbird count surveys utilizing a census technique to sum all waterbirds present using the direct count method. During our area-search surveys (37 mean surveys annually), a team of three to seven observers walked meandering transects with the goal of locating all nests in a given area. In Kawainui, we targeted pond cells 5, 6, 10, and 11 for area-search surveys because the thick vegetation in these pond cells made locating nests during routine surveys difficult. In Hāmākua, we searched Basins A through D because traversing the entirety of the wetland was manageable. Our focus at both sites, outside the stilt nesting season, was on searching coot and gallinule nest habitats. Nest phenology was calculated using the first discovery dates for each nest to compile a pool of nest discovery dates for each species of waterbird; both sites were combined for this analysis.

All nests were checked once or twice per week until hatching or failure. A subset of nests were monitored using SPYPOINT Solar Dark (GG Telecom, Victoriaville, Canada) passive infrared cameras (trigger speed: 0.07 s) placed about 1–3 m from the nest, mounted on a 7.6 cm wide metal post 1.8 m long, fixed with a fully adjustable camera mount that allows a camera angle of 0–90°. Cameras were programmed to take two images back-to-back immediately upon infrared motion activation. Cameras were programmed to take photos instantly for each activation (instant setting recovery speed: 0.3 s). Cameras were checked weekly for battery life and SD card data retrieval and removed immediately after a nest was confirmed failed or after a nest was confirmed successful.

Nest fate categories and determination

Nest fates were determined by observing the evidence surrounding the nest site from direct field observation or camera photos. A nest was considered successful if at least one egg hatched and was categorized as failed if the eggs disappeared before the expected hatch date or remained beyond it. Failed nests were classified as follows: predated (e.g., predator scat/tracks in the nest or destroyed eggs adjacent to the nest), flooded (e.g., intact eggs outside nest following an increase in water level or nest submerged under water), or abandoned (e.g., intact eggs were present beyond expected hatch date or eggs were cold on two subsequent visits and egg count was unchanged). In cases where nest fate could not be determined, the outcome was considered "unknown."

Statistical analyses

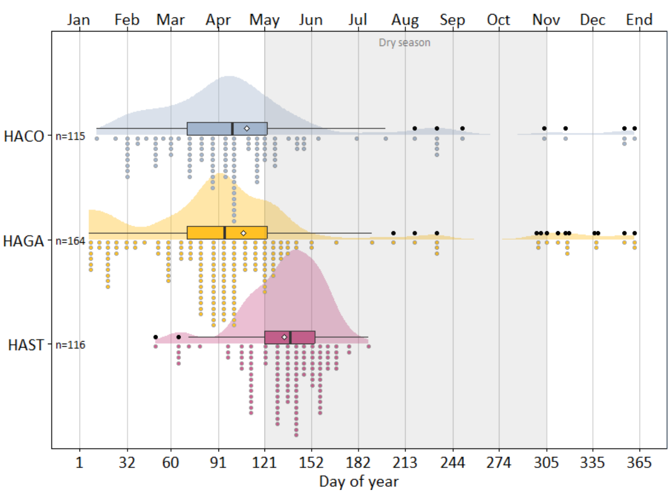
To identify differences in nest failure categories between sites, we calculated Fisher's exact test of independence for each nest failure category. Daily survival rates (DSR) for nests were estimated using the program MARK (version 10.1; White and Burnham 1999) and the nest survival model (Dinsmore et al. 2002, Dinsmore and Dinsmore 2007, Rotella 2021). Of the 395 nests found, 59 nests were excluded from the nest survival analysis because the outcomes were unknown. DSR estimates were derived from encounter histories using the following four variables: (a) the first day the nest was found, (b) the last day the nest was checked alive, (c) the last day the nest was visited (i.e., first chick's hatch date for successful nests), and (d) the fate of the nest (Dinsmore and Dinsmore 2007, Rotella 2021). Nest success was estimated using the constant DSR and incubation time (from the first egg to the first chick as estimated by this study [27.6, 25.4, and 27.3 d for coots, gallinules, and stilts, respectively]) as outlined by Mayfield (1975), exponentiating DSR to the incubation period. The constant DSR nest estimates were used for comparisons between sites, and a likelihood ratio test (LRT) was used for statistical comparisons. All other analyses were performed in R version 4.3.2 (R Core Team 2023). We used an α of 0.05 to indicate significance for all statistical analyses.

RESULTS

Nest phenology

We observed 395 nests at Hāmākua Marsh ($n = 276$) and Kawainui Marsh ($n = 119$) from January 2020 through December 2023 (Fig. 2). Coot (n = 115) and gallinule (n = 164) nests were largely observed from January through July, with a few nests (coot = 8%, n = 9; gallinule = 10%, n = 16) initiated from August through December. Stilt nests (n = 116) were largely observed from March

Fig. 2. Raincloud plot of nest discovery dates for Hawaiian Coot (HACO; *Fulica alai*), Hawaiian Common Gallinule (HAGA; *Gallinula galeata sandvicensis*), and Hawaiian Stilt (HAST; *Himantopus mexicanus knudseni*) at Hāmākua Marsh and Kawainui Marsh State Wildlife Sanctuaries from 2020 to 2023. The violin plots display the distribution and density of data, and the boxplots represent the summary of statistics like the medians (bold vertical lines) and means (white diamonds) within the rectangles (25th to 75th percentiles) attached to the whiskers (minimum and maximum); outliers are represented as black points. The dot plots represent the raw data (small points underneath the violin plots) that coincide with individual nest discovery days. The gray shading demarcates the dry season. All years and sites were combined to display long-term nest phenology. Nest surveys were conducted weekly until no nests were discovered for four consecutive weeks, then bi-weekly checks were initiated. Weekly checks were resumed once wetland water levels were significant enough to spur nest initiation.



through July, with 4% ($n = 5$) of nests initiated in February through early March, and no nests were observed between August and January. Coots and gallinules initiated 75% of their nests during the wet season (Nov–Apr), and stilts initiated 75% of their nests during the dry season (May–Oct).

Nest fates

Out of 395 nests discovered, 46% ($n = 180$) produced at least one chick, 17% ($n = 68$) failed due to predation, 13% ($n = 52$) failed due to abandonment, 6% ($n = 25$) failed due to flooding, 3% ($n = 11$) failed for unknown reasons, and 15% ($n = 59$) had unknown fates (Table 1).

Of the 116 coot nests, 47% ($n = 54$) produced at least one chick, 17% ($n = 20$) failed due to predation, 12% ($n = 14$) failed due to abandonment, 7% ($n = 8$) failed due to flooding, and 17% ($n = 20$) had unknown fates (Table 1).

Of the 164 gallinule nests, 46% ($n = 75$) produced at least one chick, 15% (n = 24) failed due to predation, 11% ($n = 18$) failed due to abandonment, 10% ($n = 17$) failed due to flooding, 3% ($n = 5$) failed for unknown reasons, and 15% ($n = 25$) had unknown fates (Table 1).

Of the 115 stilt nests, 44% ($n = 51$) produced at least one chick, 21% (n = 24) failed due to predation, 18% ($n = 20$) failed due to abandonment, 0% ($n = 0$) failed due to flooding, 5% ($n = 6$) failed for unknown reasons, and 12% ($n = 14$) had unknown fates (Table 1).

Predation of nests at the study sites

The proportion of successful and failed coot and stilt nests at Hāmākua Marsh and Kawainui Marsh were similar (Fisher's exact test; $P = 0.289$ for coots and $P = 0.636$ for stilts); however, proportions for gallinule nests differed significantly between sites (Fisher's exact test; $P = 0.031$ for gallinules). Among failed nests at each wetland, predation was a statistically significant contributor to nest failure at Kawainui ($\approx 2_{predation}:1_{other}$) compared to Hāmākua ($\approx 3_{predation}:7_{other}$; Fisher's exact test; $P = 0.000$).

Nest fates with cameras

Of the 395 nests, we monitored 240 nests (61%) with passive infrared motion-activated cameras. Cameras were placed on 49%, 65%, and 66% of coot ($n = 57$), gallinule ($n = 107$), and stilt ($n = 76$) nests, respectively. Of the 240 nests with cameras, 57% ($n = 136$) produced at least one chick, 20% ($n = 44$) failed due to predation, 16% ($n = 39$) failed due to abandonment, and 7% ($n = 16$) failed due to flooding. Confirmed egg predators were small Indian mongooses ($n = 26$), Hawaiian Common Gallinules ($n = 6$), and Hawaiian Coots ($n = 2$). We were unable to confirm the predator species for 10 of the depredated nests (Table 1; Fig. 3). The proportions of successful and failed waterbird nests with and without cameras were similar (Fisher's exact test; $P = 0.090$).

Hawaiian Coot

Of the 57 coot nests, 58% ($n = 33$) produced at least one chick, 12% ($n = 7$) failed due to predation, 16% ($n = 9$) failed due to abandonment, 9% ($n = 5$) failed due to flooding, and 5% ($n = 3$) had unknown fates. Confirmed egg predators were small Indian mongooses ($n = 3$) and Hawaiian Coots ($n = 1$). We were unable to confirm the predator for three of the nests (Table 1; Fig. 3). Small Indian mongooses were responsible for 75% of predated coot nests (unknown predators excluded).

Hawaiian Common Gallinule

Of the 107 gallinule nests, 57% ($n = 62$) produced at least one chick, 16% ($n = 17$) failed due to predation, 15% ($n = 16$) failed due to abandonment, 13% ($n = 14$) failed due to flooding, and 1% ($n = 1$) had unknown fates. Confirmed egg predators were small Indian mongooses ($n = 11$) and Hawaiian gallinules ($n = 3$). We were unable to confirm the predator for three of the nests (Table 1; Fig. 3). Small Indian mongooses were responsible for 79% of predated gallinule nests (unknown predators excluded).

Hawaiian Stilt

Of the 76 stilt nests, 57% ($n = 43$) produced at least one chick, 24% ($n = 18$) failed due to predation, 20% ($n = 15$) failed due to abandonment, and 0% ($n = 0$) failed due to flooding. Confirmed egg predators were small Indian mongooses ($n = 11$) and Hawaiian gallinules ($n = 3$) and a Hawaiian Coot ($n = 1$). We were unable to confirm the predator for three of the nests (Table 1; Fig. 3). Small Indian mongooses were responsible for 73% of predated stilt nests (unknown predators excluded).

Predator and waterbird nest interactions

Predation was the cause of 42% of failed nests overall. The small Indian mongooses were responsible for 76% of waterbird nest

Table 1. Summary of Hawaiian Coot (C; *Fulica alai*), Hawaiian Common Gallinule (G; *Gallinula galeata sandvicensis*), and Hawaiian Stilt (S; *Himantopus mexicanus knudseni*) nest parameters (%HS = % hatching success) and nest failures. We collected data at Hāmākua Marsh and Kawainui Marsh State Wildlife Sanctuaries as determined by passive infrared cameras and manual nest surveys in 2020–2023.

		Hāmākua			Kawainui			Total[†]
		C (*n*=76)	G (*n*=108)	S (*n*=92)	C (*n*=40)	G (*n*=56)	S (*n*=23)	*n*=395
Camera		33	70	57	24	37	19	240
Nest parameters								
	Hatched (%HS)	19 (61)[‡]	45 (64)[§]	31 (54)	13 (59)[|]	16 (43)[¶]	12 (63)[#]	136
	Clutch size	4.7	5.0	3.9	5.4	5.5	3.7	
Nest failures								
Predator	Hawaiian Common Gallinule (*Gallinula galeata sandvicensis*)		2	2		1	1[††]	6
	Hawaiian Coot (*Fulica alai*)	1		1				2
	Small Indian Mongoose (*Urva auropunctata*)	1	4	9	3	7[‡‡]	2	26
	Unknown	1[§§]		2[‖]	3[§§]	3[§§]	1[§§]	10
Other failure	Abandoned	8[¶¶]	12[##]	12[†††]	1[‡‡‡]	3[§§§]	3[|||]	39
	Flooded	1	7		2	6		16
Unknown		2[¶¶¶]			2[###]	1[¶¶¶]		5
No camera		43	38	35	16	19	4	155
Nest parameters								
	Hatched (%HS)	18 (60)	10 (50)	7 (33)	4 (31)	4 (31)	1 (25)	44
	Clutch size	4.1	3.9	2.8	5.0	4.3	3.0	
Nest failures								
Predator	Small Indian Mongoose (*Urva auropunctata*)				3	2		5
	Unknown	2[§§]	1[§§]	3[§§]	6[§§]	4[§§]	3[§§]	19
Other failure	Abandoned	5	3	5				13
	Flooded	5	1			3		9
	Unknown		5	6				11
Unknown		13	18	14	3	6		54

[†] Sum of independent hatching and nest failure events.
[‡] Partial depredation of one nest by an unknown predator.
[§] Partial depredation of four nests: one unknown predator, two Hawaiian Common Gallinule, and one Small Indian Mongoose.
[|] Partial depredation of three nests by small Indian Mongoose. All three nests hatched at least one chick, but mongooses take all chicks from each nest and all remaining eggs.
[¶] Partial depredation: 2 or 3 chicks hatched, then 3 or 4 eggs, and 2 or 3 chicks predated by a small Indian Mongoose.
[#] One nest, one egg hatched, other three eggs were inviable.
[††] One egg was destroyed by a Hawaiian Common Gallinule, and then the other three eggs were destroyed by a Hawaiian Coot.
[‡‡] One nest was depredated by a small Indian Mongoose and Hawaiian Coot serially.
[§§] Eggs were completely gone before the expected hatch date.
[‖] Nest destroyed by an unknown predator; one egg observed broken open and contained a developed fetus.
[¶¶] Five nests were abandoned for unknown reasons before expected hatch dates; three nests were incubated to full-term, likely inviable eggs.
[##] Three nests abandoned for unknown reasons before expected hatch dates; five nests were self-depredated for unknown reasons (based on banded incubating adult); two nests incubated to full-term, likely inviable eggs; one nest was abandoned after visitation from a feral cat (*Felis catus*), no eggs were taken; one nest abandoned after parent was preyed upon by an owl (based on adult Hawaiian Common Gallinule carcass found 3 m from nest). Could not determine whether the owl was a non-native Barn Owl (*Tyto alba*) or a native Hawaiian Short-eared Owl (*Pueo*; *Asio flammeus sandwichensis*) based on remains.
[†††] Five nests were abandoned for unknown reasons before expected hatch dates (one nest, a small Indian Mongoose takes all the eggs); three nests were abandoned after the full incubation period, eggs likely inviable; two nests were abandoned due to conspecific skirmish; one nest a Hawaiian Common Gallinule depredated one egg, stilt continued incubation until subsequent visit by the gallinule (later a black rat [*Rattus rattus*] was observed taking three remaining eggs serially over three consecutive nights); and one nest was abandoned after parental male depredated own nest.
[‡‡‡] Nest abandoned for an unknown reason before the expected hatch date; eggs were scavenged by a small Indian Mongoose after abandonment.
[§§§] One nest was abandoned for unknown reasons before the expected hatch date, the camera never detected the parent incubating; one nest incubated to full-term, likely inviable eggs; and one nest self-depredated before full-term.
[|||] Three nests were abandoned for unknown reasons before the expected hatch date (in one nest, a Hawaiian Common Gallinule depredated one egg, and a Hawaiian Coot predated the three remaining eggs).
[¶¶¶] Cameras were placed too late to determine the fate of nests.
[###] Vegetation obstructed the camera's view.

predation events, and Hawaiian gallinules and Hawaiian Coots were accountable for the remaining 24% of nest depredations (unknown predators excluded). Of all confirmed nest failure events for coots, gallinules, and stilts, predation contributed to 43%, 38%, and 55% of the failed nests, respectively (Fig. 4). Of the predation events among waterbird species, the small Indian mongoose predated similarly among coot (80%), gallinule (65%), and stilt (61%) nests (unknown predators excluded). Site-specific proportions of failed nests caused by predation and the small Indian mongoose were higher at Kawainui for all three endangered waterbird species (Fig. 4).

Daily survival rate (DSR) and nest success estimates

Mean DSR of coot (LRT, $\chi^2 = 1.9$, df = 1, $P = 0.167$) and stilt (LRT, $\chi^2 = 0.1$, df = 1, $P = 0.761$) nests were similar at Hāmākua and Kawainui, but DSR of gallinule nests were statistically significantly lower at Kawainui than Hāmākua (LRT, $\chi^2 = 9.5$, df = 1, $P = 0.002$; Fig. 5, Table 2).

Nest success estimates for coots, gallinules, and stilts at Hāmākua Marsh were 0.503, 0.502, and 0.466, respectively; Kawainui Marsh had similar nest success estimates for coots (0.346) and stilts (0.426), but statistically lower nest success estimates for gallinules (0.220; Table 3).

Fig. 3. Proportional causes of nest failures for Hawaiian Coot (HACO; *Fulica alai*; *n* = 57), Hawaiian Common Gallinule (HAGA; *Gallinula galeata sandvicensis*; *n* = 107), and Hawaiian Stilt (HAST; *Himantopus mexicanus knudseni*; *n* = 76) nests at Hāmākua Marsh and Kawainui Marsh State Wildlife Sanctuaries combined. All nest failure events for proportions were derived from passive infrared, motion-activated cameras.

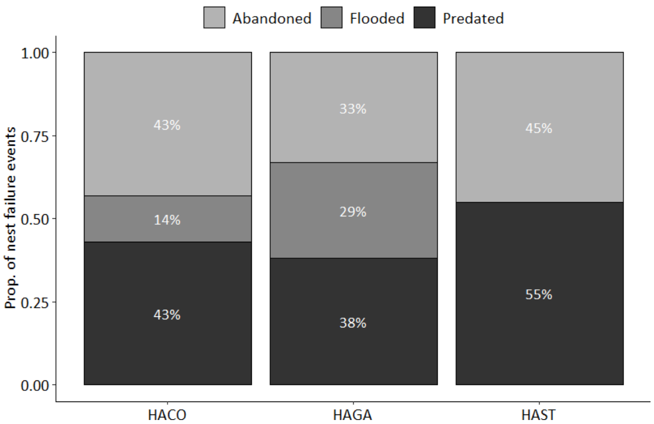
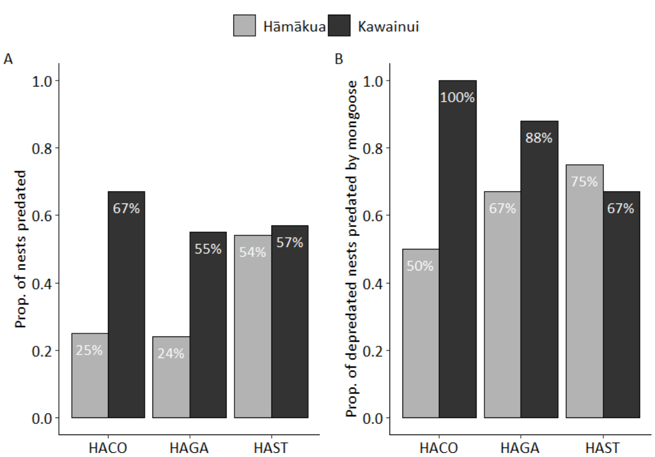


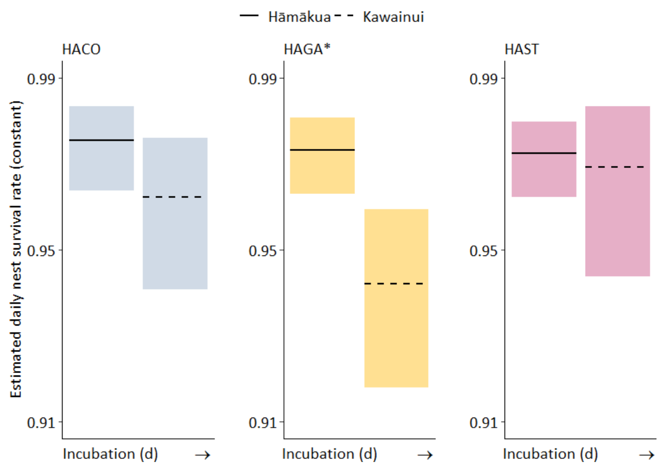
Fig. 4. (A) Proportions of predation events contributing to nest failures for each site and waterbird species; (B) proportions of small Indian mongooses (*Urva auropunctata*) contributing to depredated nests relative to each site. Both graphs compare Hāmākua Marsh and Kawainui Marsh State Wildlife Sanctuaries for Hawaiian Coot (HACO; *Fulica alai*; n = 57), Hawaiian Common Gallinule (HAGA; *Gallinula galeata sandvicensis*; n = 107), and Hawaiian Stilt (HAST; *Himantopus mexicanus knudseni*; n = 76) predation events. All nest failure events for proportions were derived from passive infrared, motion-activated cameras.



DISCUSSION

This study examined nesting phenology and daily nest survival rates and identified a predator responsible for failed nests in three endangered waterbirds on Oʻahu. Nest phenology was similar to other reported nest intervals for the same species (Byrd and Zeillemaker 1981, Coleman 1981, Pratt and Brisbin 2020, Robinson et al. 2020). At our sites, 75% of stilt nests were initiated during the dry season (peaking in May); 75% of coot and gallinule nests were initiated in the wet season (peaking in mid- and early-April, respectively). Coots and gallinules can nest year-round, but those nests were always started after stilts were finished nesting for the year, and few nests were found relative to the dominant nesting months (8% and 10% of nests, respectively).

Fig. 5. Line graphs of the mean estimated daily nest survival rates for Hawaiian Coot (HACO; *Fulica alai*), Hawaiian Common Gallinule (HAGA; *Gallinula galeata sandvicensis*), and Hawaiian Stilt (HAST; *Himantopus mexicanus knudseni*) at Hāmākua Marsh (solid black line) and Kawainui Marsh (dashed black line) State Wildlife Sanctuaries from 2020 to 2023 throughout the incubation period (d). The colored regions above and below the mean lines (solid or dashed) are the upper and lower 95% confidence intervals for daily nest survival. The * next to the species code represents statistical significance between sites for the mean constant daily nest survival.



Mean daily nest survival was higher for coots, gallinules, and stilts at Hāmākua Marsh compared to Kawainui Marsh and comports with the higher proportion of nest predation events at Kawainui. In other studies of rails, daily nest survival rates were similar to Hāmākua Marsh but higher than Kawainui Marsh, further suggesting Kawainui has a disproportionate predator issue compared to Hāmākua Marsh (Rush et al. 2010, Rogers et al. 2013, Jedlikowski et al. 2015).

Several studies have reported similar proportions of nest failure for waterbird nests (Herring et al. 2011, Ackerman et al. 2014, Croston et al. 2018, Squalli et al. 2020, Fournier et al. 2021). However, some studies have attributed a higher proportion of nest failures to predation compared to our study (Herring et al. 2011, Ackerman et al. 2014, Croston et al. 2018). In contrast, Webber (2022) found lower predation rates (6%) for Hawaiian Common Gallinule nests on Kauaʻi compared to Oʻahu, likely due to the absence of small Indian mongoose on Kauaʻi (Hays and Conant 2007, Duffy et al. 2015). Our study's findings align with the proportions of Hawaiian Stilt nest failures due to predators, as found by Harmon et al. (2021) on Oʻahu, and Black-necked Stilt nests as reported by Riecke et al. (2019) in Texas.

Table 2. Daily survival rate (DSR) estimates (mean, standard error [SE], and 95% confidence interval [CI]) for Hawaiian Coot (HACO; *Fulica alai*), Hawaiian Common Gallinule (HAGA; *Gallinula galeata sandvicensis*), and Hawaiian Stilt (HAST; *Himantopus mexicanus knudseni*) nests at Hāmākua Marsh and Kawainui Marsh State Wildlife Sanctuaries from 2020 to 2023. DSR estimates were derived from the null model.

	Hāmākua			Kawainui		
	Mean	±SE	95% CI	Mean	±SE	95% CI
HACO	0.975	0.005	(0.964, 0.983)	0.962	0.009	(0.941, 0.976)
HAGA	0.973	0.004	(0.963, 0.981)	0.942	0.010	(0.918, 0.960)
HAST	0.972	0.004	(0.962, 0.980)	0.969	0.010	(0.944, 0.983)

Table 3. Nest success estimates (mean and 95% confidence interval [CI]) for Hawaiian Coot (HACO; *Fulica alai*), Hawaiian Common Gallinule (HAGA; *Gallinula galeata sandvicensis*), and Hawaiian Stilt (HAST; *Himantopus mexicanus knudseni*) at Hāmākua Marsh and Kawainui Marsh State Wildlife Sanctuaries from 2020 to 2023. Estimates were derived from the constant daily nest survival rate model with incubation days of 27.6, 25.4, and 27.3 for HACO, HAGA, and HAST, respectively.

	Hāmākua		Kawainui	
	Mean	95% CI	Mean	95% CI
HACO	0.503	(0.362, 0.629)	0.346	(0.186, 0.513)
HAGA	0.502	(0.384, 0.610)	0.220	(0.114, 0.350)
HAST	0.466	(0.350, 0.574)	0.426	(0.206, 0.633)

The main cause of nest failures was predation, accounting for 42% of failed nests. The small Indian mongoose was responsible for 76% of nest failure events. The predation rates were found to be higher at Kawainui Marsh compared to Hāmākua Marsh, especially for coot nests (67% and 25%, respectively) and gallinule nests (55% and 24%, respectively). However, predation rates on failed stilt nests were similar at both sites (57% and 54%, respectively), suggesting that the small Indian mongoose tends to target nests more during the dry season when water levels are lower and vegetation is denser. The lower water levels may make nests more accessible to mongooses, while taller vegetation may help them remain stealthy during their movements.

The nests of coots at Kawainui were more frequently preyed upon compared to gallinule and stilt nests. This may be due to coots tending to nest alone, while stilts nest semi-colonially (Coleman 1981). Stilt families have a better chance of defending their nests because they have lookouts spread throughout their sparsely populated colony. This vigilance is followed by an alarm call in the presence of a predator, alerting the group. This gives the stilt more time to react, allowing it to defend its nest and discourage predation (Pulliam 1973, Caraco et al. 1980, Lima and Dill 1990, Van Heezik and Seddon 1990, Burger and Gochfeld 1991, Cresswell 1994, as cited in Hammer et al. 2023). Coots, on the other hand, may be more vulnerable to predation because of their more conspicuous appearance and behavior compared to gallinules. Gallinules prefer to stay hidden in covered vegetation, while coots are less secretive (Chang 1990, Engilis and Pratt 1993, DesRochers et al. 2008, Camp et al. 2014, Bannor and Kiviat 2020, Pratt and Brisbin 2020). Mongooses are adapted to hunt during the day and rely on their vision (Nellis et al. 1989). This may allow mongooses to more frequently observe the conspicuous appearance and behaviors of coots compared to the more secretive gallinules contributing to the disproportionately high predation rates in coots.

Qualitatively, the habitat at Kawainui Marsh characterizes easier access for mammalian predators relative to Hāmākua Marsh because of the lower water levels and taller vegetation during the waterbird nesting season. Lower water levels would allow for increased access for small Indian mongoose, and tall vegetation would aid in mongoose stealth when approaching nests (Nellis and Everard 1983). Frederick and Collopy (1989) suggested that water restricted the movement of mammals to wading bird colonies and that visitations by mammals only occurred after drawdowns that allowed drier access to colonies. Likewise, Schmidt et al. (2023) suggested that dewatering allowed mammalian predators access to nests they would otherwise have no access to, and Brzeziński et al. (2018, 2022) demonstrated water depth can be an important deterrent of nest predators. During the dry season, Hāmākua Marsh becomes drier and vegetation taller, allowing greater accessibility and cover for small Indian mongooses to exploit Hawaiian Stilt nests; this could explain the equal predation rates for Hawaiian Stilt nests at Hāmākua Marsh and Kawainui Marsh. Peterson et al. (2022) demonstrated that duck nests had decreased survival when closer to phragmites (*Phragmites australis*). A stand of phragmites resembles the habitat structure surrounding the study site at Kawainui Marsh and may offer similar concealment for the small Indian mongoose, lending to greater predation on nests at this site. Mechanical removal of vegetation could focus on buffer areas (outside the nesting areas) of vegetation that provide concealment for small Indian mongooses. Adding the capability of controlling water levels in the pond cells would deter vegetation re-growth, thus providing more visibility to nesting waterbirds to potential predators.

A potential explanation for the higher success of waterbird nests at Hāmākua compared to Kawainui could be the proximity of the nests to each other. Studies on waterbirds have indicated that the density of waterbird nests can influence the outcomes of the nests (Brzeziński et al. 2018). Successful nests tend to be closer to their neighboring nests, while nests that are preyed upon are more likely to be farther from neighboring nests (Ringelman et al. 2012, 2014, Bell and Conover 2023). There were significantly more nests (2.3 times) at the smaller Hāmākua Marsh (9.4 ha) compared to the larger Kawainui Marsh (12.7 ha), suggesting that nest density was higher at Hāmākua. However, differences in nest detectability at each site may have contributed to variations in nest densities. Kawainui had thicker and taller vegetation, which could make nests more difficult to detect.

Nest predations were the main contributor to nest failure, but abandonment was the second leading result. Causes for parental nest abandonment were not always clear, but for 54% of abandoned nests, a reason was concluded. Nine (43%) nests were abandoned after full incubation suggesting the eggs were inviable; seven (33%) nests were self-depredated; two (9%) nests were abandoned after intraspecies interactions; and one nest each was abandoned after a predator visited (5%), a parent was predated (5%), and an interspecies interaction (5%). Inviable eggs may be due to environmental contaminants or inbreeding depression; both can cause embryo mortality (Heber and Briskie 2010, Herring et al. 2010, Assersohn et al. 2021). Marshall et al. (2023) posited almost 14% of wild bird eggs failed to hatch and were due to early-embryo mortality, not fertilization failure (Hemmings and Evans 2020). Potential reasons for self-depredated nests could be embryonic development failure, removal of eggs because of conspecific brood parasitism (Craik et al. 2018), or the parent's eventual response to undeveloped eggs and recuperation of nutrients (Spooner et al. 1996). Predation of an incubating parent was a common cause of nest abandonment in a shorebird (Roche et al. 2010) but was not significant in our study. Predators and interspecies were not common causes of abandonment in our study because a predator and interspecific waterbird will normally depredate the nest. Thus, failure is assigned as a predation and not abandonment.

Possible mitigation for predator-induced nest failure in Hawaiian waterbirds could be installing mammal-exclusion fencing around their wetland habitat, although the application of a mammal-exclusion fence is not suitable for wetlands susceptible to flooding. In a study by Christensen et al. (2021), the wetland site with mammal-exclusion fencing had zero of nine Hawaiian Stilt nests depredated compared with six of 21 nests preyed upon in the unfenced wetland, and ≈2.5 times more eggs hatched per nest in the fenced site versus the unfenced site. Kawainui Marsh would not be a candidate for mammal-exclusion fencing because of nearly annual extreme flooding, but Hāmākua Marsh could be a potentially appropriate site.

Promisingly, a new tool for mongoose control is under development by the United States Department of Agriculture; a non-perishable, mongoose toxicant bait (Antaky et al. 2022, 2023). Current mongoose control in Hawaiʻi consists primarily of trapping (Smith et al. 2000, Barun et al. 2011). Although trapping can effectively control mongoose in the short term (Underwood et al. 2014), trapping is labor-intensive and, therefore, expensive (Roerk et al. 2022). Trapping programs must be run constantly as mongooses quickly re-colonize trapped areas and readily become trap-shy (Roy 2001, Hays and Conant 2007). An alternative to trapping could be the use of a rodenticide product. Currently, one rodenticide product labeled for use on mongoose in Hawaiʻi exists, but Sugihara et al. (2018) found the product lacking palatability and, therefore, likely ineffective at efficiently controlling mongoose. In the past, a fish-flavored mongoose-specific toxicant bait product was used efficaciously (Smith et al. 2000) but was found to deteriorate quickly in Hawaiʻi's tropical climate, and the product registration was never renewed. The development of a non-perishable, mongoose-specific toxicant bait could provide another control tool for waterbird managers to deploy to effectively reduce the mongoose population in managed wetland sites in Hawaiʻi.

Acknowledgments:

All applicable ethical guidelines for using birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair et al. 2023).

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Data Availability:

All relevant data are available on request from the corresponding author, AJW.

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