Running Title: Cooperative Breeding in Hawaiian Stilts

Cooperative Breeding Behaviors in the Hawaiian Stilt (*Himantopus mexicanus knudseni*)

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Abstract— Cooperative breeding, which is commonly characterized by non-breeding individuals that assist others with reproduction, is common in avian species. However, few accounts have been reported in Charadriiformes, particularly island-nesting species. We present observations of cooperative breeding behaviors in Hawaiian Stilts during the 2012-2020 nesting seasons on the Hawaiian islands of Oʻahu and Molokaʻi. We describe three different behaviors that indicate cooperative breeding: (1) nest sharing; (2) helper at the nest; (3) cooperative chick rearing. Our observations suggest an ideal opportunity to examine the evolution of cooperative breeding behaviors in the order Charadriiformes.

Keywords: waterbird, helper-at-the-nest, nest sharing, chick rearing, colony, nesting success

Cooperative breeding is found throughout the world in both invertebrate and vertebrate animals (Faaborg & Bednarz, 1990; Reeve & Ratnieks, 1993). Cooperative breeding is commonly characterized by non-breeding individuals that assist others with reproduction, potentially even delaying or foregoing their own breeding to engage in these behaviors (Brown, 1987; Ligon, 1999; Koenig & Dickinson, 2004). Individuals may delay or forego their own dispersal and reproduction due to limitations in resources necessary for successful reproduction (Koenig & Pitelka, 1981; Walters et al., 1992), to inherit parental resources or resources in surrounding territories (Ligon & Stacey, 1991), or to increase reproductive success in related individuals (Hamilton, 1964). In many cooperatively breeding avian species, non-breeding individuals, referred to as "helpers" (Skutch, 1935), may assist the dominant breeding pair during reproduction through their assistance with nest building, incubation, predator deterrence and/or provisioning chicks (Stacey & Koenig, 1990; Koenig & Dickinson, 2016; Komdeur et al., 2017). These helpers are often closely related to the breeding individuals, and may be previous offspring of one or both breeders (half or full siblings of the brood) or siblings of one of the breeders (uncle/aunt of the brood), therefore receiving indirect fitness benefits from this behavior (Langen & Vehrencamp, 1999; McCarthy et al., 2001; Cornwallis et al., 2009). Although less commonly reported, cooperative breeding may also consist of nest sharing, by which multiple breeding individuals lay their eggs in the same nest (Brown, 1978; Cockburn, 2006). Nest sharing costs and benefits are poorly understood; however, some theories include saturation of quality habitat (Barve et al., 2019) or the need for multiple females to defend a territory from challengers (Hannon et al., 1985).

In the order Charadriiformes, or waders, gulls, and auks, biparental care is most common and cooperative breeding is facultative, whereas pairs and cooperative groups coexist and dispute

44 territories (Walters & Walters, 1980, Cockburn, 2006, Lees et al., 2013). In the family
45 Recurvirostridae (stilts and avocets), the Hawaiian Stilt (*Himantopus mexicanus knudseni*) is a
46 federally endangered, subtropical subspecies of the Black-necked Stilt that breeds in wetlands
47 across the main Hawaiian Islands. Hawaiian Stilts are pair-breeders, and it is common for both
48 the male and female to incubate eggs (Coleman, 1981). They are sexually dimorphic once they
49 reach maturity; males have metallic black plumage, while females have a lighter brown glossy
50 plumage (Coleman, 1981). Similar to other stilt species (Ackerman et al., 2014), Hawaiian Stilts
51 lay a maximum of four eggs per pair (Coleman, 1981). Although rare cases of stilt species laying
52 more than four eggs have been reported (Every, 1974; Hamilton, 1975; Coleman, 1981), they
53 have been described as intraspecific brood parasitism, or "egg dumping", by unrelated females
54 (Yom-Tov, 1980). The Hawaiian Stilt is long-lived, with the oldest, a male, observed 29 years
55 after banding as an adult on O'ahu (Reed et al., 2014). Hawaiian Stilts typically begin breeding
56 at two years of age (Reed et al., 1998). Longevity and delayed reproduction are common
57 characteristics of cooperative breeders (Brown, 1978, 1987); however, cooperative breeding
58 behavior has not been described for this species. Here we present observations of cooperative
59 breeding behavior by juvenile and non-breeding adult Hawaiian Stilts during the 2012-2020
60 nesting seasons while conducting field surveys in various wetlands across O'ahu and Moloka'i
61 (Fig. 1). We describe three different cooperative breeding behaviors: (1) nest sharing; (2) helper
62 at the nest; (3) cooperative chick rearing.
63 *Nest sharing*. During the 2018 and 2020 nesting seasons, four stilt nests were found with
64 greater than four eggs in wetlands on O'ahu. On 04 May 2018 a nest was found with seven eggs
65 in the Honouliuli wetland unit of the Pearl Harbor National Wildlife Refuge on O'ahu (Fig. 2).
66 We were unable to confirm how many adults were incubating the eggs or the fate of the nest. On

25 April 2020 a nest with five eggs was found within the Marine Corps Base Hawaii – Kāneʻohe Bay (MCBH-KB) on Oʻahu (Fig. 3a). A Bushnell trophy camera was used to monitor this nest, and using camera photos, two females, along with one male, were observed taking turns incubating the nest (Fig. 3b-c). From 18 May 2020 to 20 May 2020 this nest hatched three chicks, and on 21 May 2020 the adults stopped incubating the last two eggs and left the nesting area with the three chicks. This nest may have been shared by a mother and daughter, as this has been observed in other avian species (McRae, 1996); however, the individuals were not marked, and we do not know the relatedness of the three individuals. A nest was found within MCBH-KB on 22 May 2020 with five eggs (Fig. 4). A camera was used to monitor this nest, and only two adults, one male and one female, were confirmed incubating the eggs. One egg was depredated on 05 June 2020, two eggs hatched on 10 June 2020, and the pair stopped incubating the last two eggs on 12 June 2020. A nest with seven eggs was found on 24 June 2020 within MCBH-KB (Fig. 5). This nest was found already abandoned, as no adults were seen near the nest when first discovered and use of a nest camera confirmed no incubation or activity at the nest. For the nests with only two confirmed incubating adults, it is possible that the ‘additional’ eggs were placed by other females unrelated to the breeding pairs.

During the 2017 Molokaʻi breeding season a nest containing eight eggs incubated by an adult male and two females was discovered at the Kōheo wetland on 25 May (Fig. 6). Three eggs and two chicks were later predated; the remaining three chicks were banded and blood collected for future determination of parental lineage. Prior to this nest, two other nests with five and eight eggs were observed that year in ʻŌhiʻapilo Pond Bird Sanctuary on Molokaʻi, but no further data beyond initial identification was collected for these nests.

Helpers at the nest. On 25 May 2019 in Honouliuli wetland two males and one female were observed in camera photos taking turns incubating a nest (Fig 7). The nest consisted of three eggs, and the breeding pair was potentially being assisted by a male offspring from a previous year. During the 2012-2015 nesting seasons at the Kaunakakai Wastewater Reclamation Facility (KWWRF) on Molokaʻi, marked non-breeding individuals of Hawaiian Stilts from the same family group were observed helping related breeding pairs defend nesting territories. The observed individuals were banded as chicks, and so relatedness among individuals in this population was known. In May and June of 2012, a one-year-old female juvenile was repeatedly observed displaying defensive/territorial behavior at the nest of her parents, as well as at the nest of her grandmother. In May of 2013, that same female, her un-banded mate, and the female's four one-year-old siblings were observed defending a nest belonging to their parents from conspecifics. These five individuals also helped defend their parents' nest from conspecifics in April of 2014, along with a one-year-old female first cousin. In March of 2015 one of the non-breeding male adults that hatched in 2012 was observed defending the nest of a male sibling that hatched in 2013. Long-term studies of banded Hawaiian Stilts on Molokaʻi have provided unique insights, such as previously unknown family groups which inherit parental resources by remaining site-protective along with other family members. The average age of a stilt greater than five years on Molokaʻi is 8.3 (n = 32 banded), with the oldest a reproductively active female of 23 years - the matriarch of five generations of banded Hawaiian Stilts; it is the offspring of this matriarch that have formed a large family group.

Cooperative chick rearing. On 02 June 2019 in the Waiawa wetland unit of the Pearl Harbor National Wildlife Refuge 14 adult stilts were observed in camera photos forming a perimeter around approximately 15 chicks (Fig. 8). This may have been a defense mechanism

against predators, as the group was observed near two nests that were both confirmed by game camera photos to have been depredated by a feral cat the following day on 03 June 2019. Individuals at this site were unmarked, so relatedness could not be determined. On 07 April 2013 and 25 April 2013 at the KWWRF a family group of eight marked individuals, consisting of three generations, was observed defending chicks from unrelated conspecifics.

Cooperative breeding has rarely been documented for avian species in the order Charadriiformes (Walters & Walters, 1980; Lees et al., 2013; Cerboncini et al., 2020). The observations presented here demonstrate that three forms of cooperative breeding, nest sharing, helper at the nest, and cooperative chick rearing, occur in multiple populations of Hawaiian Stilts on two islands more than 100 km apart. Cooperative breeding is most commonly described as adult offspring delaying dispersal and reproduction to assist parents in raising young (Brown, 1987), and while this behavior was observed in this study, we also present evidence of potential nest sharing between adult female Hawaiian Stilts. Nest sharing between conspecifics may occur between closely related individuals, such as offspring breeding with their parents, but siblings may also share mates and nests (Burke et al., 1989; McRae, 1996). As breeding between closely related individuals can negatively impact reproductive success (van Noordwijk & Scharloo, 1981; Rowley et al., 1993), many species that exhibit cooperative breeding have evolved mechanisms to minimize breeding with closely related individuals, such as associative learning (Koenig & Pitelka, 1979; Piper & Slater, 1993), promiscuity (Brooker et al., 1990; Mulder et al., 1994) and possibly hormonal mechanisms (Wingfield et al., 1991); however, these remain poorly understood. It is still unclear whether nest sharing and helping to incubate or rear chicks only occurs in related individuals in the Hawaiian Stilt, as we were unable to determine relations among observed individuals in some of the cases.

Cooperative breeding has many potential benefits, including increased reproductive success (Downing et al., 2020a), predator avoidance (Sorato et al., 2012), and niche expansion (Shen et al., 2017). However, the benefits of cooperative behavior may be outweighed by increased intraspecific competition for resources (Brouwer et al., 2020) or extremely harsh environmental conditions (Bourne et al., 2020). Further, studies that quantify investment in cooperative breeding generally focus on the value of helpers (Brown, 1978; Reed & Walters, 1996; Stacey and Koenig, 1990). Most nests with helpers in this study were successful; however, our sample size was inadequate to determine whether nests with helpers had higher success than those without helpers. In contrast, nests that were suspected to be shared between females tended to be partially successful, with a portion of eggs abandoned and unhatched. McRae (1996) found that younger females within shared nests produced fewer eggs and had lower hatching success than the older females. As cooperative breeding includes additional behaviors beyond helpers (Cockburn, 2006; Teunissen et al., 2020), more research is needed that examines the potential impacts of other cooperative breeding behaviors, such nest sharing.

Hypotheses for the evolution of cooperative breeding generally attribute the benefits of these behaviors to kin selection, whereby helper individuals benefit indirectly by increasing the reproductive success of relatives genetically similar to them (Hamilton, 1964). However, this explanation is not always empirically supported (Dey et al., 2017; Wang & Lu, 2018). Other hypotheses, such as the *environmental constraints hypothesis*, suggest that cooperative behaviors arise due to environmental constraints that make it unfavorable for individuals to breed independently (Lin et al., 2019). For example, a shortage of territory openings may occur because higher quality habitats are saturated with established breeders (Russell, 1989; Arnold & Owens, 1999; Hatchwell & Komdeur, 2000), while unpredictable availability of resources could

158 make it too risky for individual pairs to reproduce in any given year (Rubenstein & Lovette,
159 2007). This hypothesis helps to explain cooperative breeding observed in non-related individuals
160 (Kokko et al., 2001; Seddon & Tobias, 2003). Furthermore, this theory may help to explain the
161 evolution of cooperative breeding on islands, which are typically colonized by pair-breeding
162 species (Cockburn, 2003). Large family groups may secure an area year-round to secure food
163 resources, initiate group predator evasion and/or intense aggression towards a predator, and to
164 potentially increase survival rates. The KWWRF is a stable environment, in that the facility is
165 surrounded by a chain-link fence, predator control is conducted year-round, and one of the two
166 1-ha ponds are maintained at a water level preferred by the Hawaiian Stilt. These conditions may
167 have led to the formation of the one large family group defending the site and cooperatively
168 breeding.
169 As island populations become denser and habitats more saturated, cooperative breeding is
170 more likely to occur (Cockburn, 2003; Covas, 2012). In our study, breeding pairs, including
171 cooperative breeders, often nested closer to other active nests (less than 50 m and in two cases, 1
172 m apart) than previously reported average nesting territories for Hawaiian Stilts (Coleman,
173 1981). Nesting in close proximity, as well as nest sharing, may be due to limited available
174 nesting habitat, as recent evidence suggests Hawaiian Stilt populations may be density-dependent
175 (van Rees et al. 2020). Alternatively, cooperative breeding in Hawaiian Stilts may also be a
176 response to reduced reproductive success caused by introduced predators, as introduced
177 predators are the major cause of nest failure in Hawaiian Stilts (Harmon et al., 2020). Indeed,
178 cooperative breeding behaviors by Hawaiian Stilts on O‘ahu were observed in areas with high
179 nest depredation, particularly by introduced Small Indian Mongooses (*Herpestes auropunctatus*),
180 rats (*Rattus spp*.), and feral cats (*Felis catus*). Prior to the 2019 nesting season, a mammal-

exclusion fence was erected around the perimeter of Honouliuli wetland. While a clutch of more than four eggs was found in Honouliuli in 2018, all breeding pairs within Honouliuli in 2019 laid four eggs (Christensen et al., 2020) and no further cooperative breeding behavior was observed that nesting season. Whether kin selection or natural selection, the drivers of cooperative breeding are likely confounded with life history traits (Gonzalez et al., 2013; Downing et al., 2020b), providing support for the mixed results commonly observed across studies. Given that multiple populations of the Hawaiian Stilt occur on most of the Hawaiian Islands, and these behaviors are known to occur in multiple populations on at least two of the islands, this offers a fascinating system to examine the evolution of cooperative breeding behaviors in the order Charadriiformes, as well as in island endemics.

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Data Accessibility

The data that support the findings of this study will be made publicly available at the University of Hawai‘i data repository, Scholarspace. A URL to this repository will be made available prior to publication.

Competing Interests

The authors declare no conflicts of interest.

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Figure Legends

Figure 1. Map of a) Oʻahu and b) Molokaʻi within the Hawaiian Islands.

Figure 2. Hawaiian Stilt nest with seven eggs found on 04 May 2018 in the Honouliuli wetland unit of the Pearl Harbor National Wildlife Refuge on Oʻahu. Photo taken by KCH.

Figure 3a. Hawaiian Stilt nest found with five eggs on 25 April 2020 in wetlands within the Marine Corps Base Hawaii – Kaneohe Bay on Oʻahu. Photo taken by JLI.

Figure 3b-c. b) Two female Hawaiian Stilts standing over the nest with five eggs found in wetlands within the Marine Corps Base Hawaii – Kaneohe Bay on Oʻahu. Photo taken from nest camera. c) One female Hawaiian Stilt incubating the nest with five eggs, while one female and one male forage near the nest site in wetlands within the Marine Corps Base Hawaii – Kaneohe Bay on Oʻahu. Photo taken from nest camera.

Figure 4. Hawaiian Stilt nest with five eggs found in wetlands within the Marine Corps Base Hawaii – Kaneohe Bay on Oʻahu on 22 May 2020. Photo taken by JLI.

Figure 5. Hawaiian Stilt nest found with seven eggs in wetlands within the Marine Corps Base Hawaii – Kaneohe Bay on 24 June 2020. Photo taken by JLI.

Figure 6. Hawaiian Stilt nest found with eight eggs in Kōheo wetland on Molokaʻi on 25 May 2017. Photo taken by ADY.

Figure 7. Two male Hawaiian Stilts foraging near a nest site, while one female incubates a nest with four eggs in the Honouliuli wetland unit of the Pearl Harbor National Wildlife Refuge on 25 May 2019. Photo taken from nest camera.

Figure 8. Approximately 14 adult Hawaiian Stilts forming a perimeter around 15 chicks in the Waiawa wetland unit of the Pearl Harbor National Wildlife Refuge on 02 June 2019. Photo taken from nest camera.