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WEATHER INFLUENCES ON NEST SUCCESS OF THE ENDANGERED PUAIOHI (*MYADESTES PALMERI*)

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ABSTRACT.—The endangered Puaiohi (*Myadestes palmeri*) endemic to Kaua‘i is the island's only remaining native thrush. Given its small population of ~500 birds, it is essential to understand conditions that affect the species' recruitment and survival. Previous observations of Puaiohi suggested that weather may influence nest success and productivity, but no studies investigated this relationship empirically. Our goal was to investigate potential links between weather conditions (precipitation and temperature) in the Puaiohi's range (~20 km^2) and several measures of reproductive success, using published data from 1996–1998 and new data collected by the Kaua‘i Forest Bird Recovery Project from 2007–2009. Total rainfall in the previous wet season strongly and positively correlated with the majority of the nest success variables (three of four). Mean rainfall during the breeding season correlated positively with reproductive effort (attempts/season and length of breeding season) and with total reproductive output, but there was some evidence that too many rainy days during the peak breeding season associated with fewer young fledged per nesting attempt. Although there seem to be clear implications that weather affects reproductive output of Puaiohi, results from longer time series will be useful in refining this relationship. Given that prevailing weather conditions of the Puaiohi's range may shift with anthropogenic climate change, which in turn may alter the severity and frequency of El Niño Southern Oscillation events, our findings provide insight into future trends in reproductive output, and thus, population of this endangered species. *Received 26 September 2014. Accepted 15 June 2015.*

Key words: climate change, Hawaiian forest birds, *Myadestes palmeri*, reproductive success, small Kaua‘i Thrush, weather effects.

The Hawaiian Islands are home to some of the most rapidly disappearing, as well as rarest and evolutionarily unique bird species in the world (Banko and Banko 2009, Pratt 2009a). Of the more than 110 endemic land bird species currently known to have occurred in Hawaii prior to human colonization, only about 6% are extant and face no immediate threats of extinction (Pratt 2009b). Furthermore, of the 71 endemic species or subspecies persisting after western contact (ca. 1778), 51 are listed as endangered or worse, with 43 of these on the brink of extinction (i.e., critically endangered, extinct in the wild, or possibly extinct) or already extinct (James 1995, IUCN 2012).

The endangered Puaiohi, or small Kaua‘i Thrush, (*Myadestes palmeri*) is one of these critically endangered species. Endemic to Kaua‘i, the Puaiohi is the only remaining species in the thrush family, Turdidae, and the only remaining native frugivore on the island. At present, there is only one other thrush species extant in the Hawaiian Islands, the Island of Hawaii endemic ‘Ōma‘o (*Myadestes obscurus*). While ‘Ōma‘o's range and densities have declined, it still has a sizable and contiguous population (Scott et al. 1986, Gorresen et al. 2009) and is listed as vulnerable by the IUCN (2012). The other four thrush species or subspecies originally present in the Islands, (Kāma‘o [*Myadestes myadestinus*], ‘Āmaui [*Myadestes woahensis*], Lana‘i ‘Oloma‘o [*Myadestes lanaiensis lanaiensis*], and Moloka‘i ‘Oloma‘o [*Myadestes lanaiensis rutha*]) are all now extinct (Reynolds and Snetsinger 2001, Woodworth and Pratt 2009). The Puaiohi is also one of the last six endemic forest bird species to remain in the Alaka‘i Wilderness. Over the past three decades, five other species disappeared from the swamp following Hurricanes ‘Iwa (1982) and ‘Iniki (1992) (Conant et al. 1998). Although some of these species were rare at the turn of the 20th century (Perkins 1903), most were more common than the Puaiohi. In fact, its larger congener, the Kāma‘o, was once the most common forest bird on Kaua‘i (Perkins 1903, Scott et al. 1986), yet the Puaiohi has persisted while the Kāma‘o is now extinct.

Although this historically rare species has outlasted many others, it appears to have experienced range contraction since the 1960s (Scott et al 1986, USFWS 2006). Specifically, the Puaiohi no longer is found at the lower elevations (1,000–1,050 m)

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of its historic range and is currently restricted to a remnant of the Alaka'i Wilderness Preserve at 1,050–1,300 m, with 75% of its breeding population occurring in just 10 km^2 of forest (Richardson and Bowles 1964, USFWS 2006). As of 2012, population size was estimated at ~500 birds (Kaua'i Forest Bird Recovery Project 2013), and surveys suggest the population has remained stable since 1973 (USFWS 2006). A number of factors may affect population vulnerability, including drought, hurricanes, mammalian predation at all life stages, and habitat degradation because of feral livestock (pigs and goats) and weeds (Snetsinger et al. 2005, USFWS 2006, Woodworth and Pratt 2009). Given the species' small population size and range, it is essential for researchers to gain a better understanding of the conditions which affect recruitment and survival.

Previous work on Puaiohi has suggested that climate may be related to nest success (Snetsinger at al. 2005), but no studies have yet explicitly investigated this possible relationship. Specifically, Snetsinger et al. (2005) noted that in years with higher reproductive output, female Puaiohi successfully reared 2–4 broods of 1–2 young each. However, in other years recruitment was much lower, with less than one brood being successfully produced. This interannual variability suggests that environmental variables may drive reproductive success. Snetsinger et al. (2005) hypothesized that decreased reproductive success occurred in years of low rainfall during the wet season preceding breeding, which reduced food availability. Thus, not only was the condition of adult birds and their ability to successfully rear young affected, but also predation by rats increased as birds were forced to search more widely for food sources.

Considering predictions of anthropogenic climate change and the associated changes in weather variables, understanding how the Puaiohi's nest success is related to weather may become critical. Although changes in trade wind inversions complicate predictions of temperature and rainfall changes at higher altitudes (Cao et al. 2007, Giambelluca et al. 2008, Timm and Diaz 2009), over the past 20 years the Alaka'i has already experienced increasing mean air temperatures, declining precipitation, and changes in stream flow (Atkinson et al. 2014) that will likely continue and will impact remaining forest bird populations. In good years, the Puaiohi has high reproductive potential, which may be the key to its continued persistence in the face of its long term rarity and all the factors negatively impacting its survival and reproduction. However, if the frequency or timing of precipitation and temperature patterns change, and in turn hampers reproductive success, the Puaiohi's outlook could be quite different. The goal of this research, therefore, was to investigate potential links between prevailing weather conditions in the Puaiohi's range and breeding success, as measured by the numbers of fledglings/attempt, of nest attempts/season, of young fledged/pair/year, and the length of breeding season. Specifically, we hypothesized that increasing rain during the wet season which directly precedes the breeding season would result in more young fledged per nest, a longer breeding season which allows for more breeding attempts per season, and as a result, more young fledged/pair/season. Furthermore, increased rain during the breeding season and extreme minimum and maximum temperatures should result in fewer young fledged per attempt, shorter breeding seasons which allow for fewer nesting attempts, resulting in fewer young fledged/pair/season.

METHODS

Puaiohi inhabit native wet and mesic forests in the Alaka'i Wilderness Preserve, which is managed by Hawaii's Department of Land and Natural Resources, Division of Forestry and Wildlife. Study sites range in elevation from 1,123–1,303 m. Forest canopy is dominated by 'ōhi'a (*Metrosideros polymorpha*), koa (*Acacia koa*), ōlapa (*Cheirodendron trigynum*), lapalapa (*C. platyphyllum*), 'ōhi'a ha (*Syzygium sandwicensis*), kāwa'u (*Ilex anomala*), and kōlea (*Myrsine lessertiana*), with a diverse understory of native plants including 'ōhelo (*Vaccinium calycinum*), and kanawao (*Broussaisia arguta*) (USFWS 2006). Annual rainfall in the area follows a steep rainfall gradient ranging from ~3.5 m in the northewest to >8 m in the southeast (Giambelluca et al. 2013).

To address research objectives, we used the only two data sets of Puaiohi available. The first was collected from 1996–1998 in the upper and lower Mohihi and upper Kawaikoi streams (Mohihi study area; Snetsinger et al. 2005). Researchers surveyed potential habitat during September 1995–January 1996, and areas of suitable nesting habitat were identified at 1,250 m elevation along the upper stretches of Mohihi Stream and its tributaries as well as in the neighboring Koaie drainage. At sites where they observed pairs (1996—12 pairs, 26 nests; 1997—14 pairs, 44 nests; 1998—22 pairs, 24 nests) actively developing territories, researchers searched for nests at least once every 3 days from the onset of breeding in March through the end of breeding in August or September. Weather permitting, nests were checked every other day and nesting stage was recorded. Eggs were counted and nestlings recorded, as well as nest failures and their cause if possible. Based on these observations, researchers calculated the mean fledglings/territory, nesting attempts/territory, fledglings/attempt, and length of breeding season for each of the 3 years. Snetsinger et al. (2005) calculated length of breeding season as the period from the mean first egg laid that year through the mean final fledge or fail date.

We collected the second dataset over the 2007–2009 breeding seasons along the upper reaches of Halepa'akai and Halehaha streams (Halepa'akai study area). As with Snetsinger et al. (2005), we surveyed sites in which we observed pairs (2007—14 pairs, 30 nests; 2008—13 pairs, 20 nests; 2009—11 pairs, 16 nests) actively developing territories at least once every 3 days from March through August or September, and, as feasible, checked nests every other day. We recorded nesting stage, counted eggs and/or nestlings when possible and recorded nest failures and identified cause if possible. From these data, we calculated annual numbers of offspring/female/nesting attempt, nesting attempts/year, offspring/female/year and length of breeding season, and pooled these with the data from Snetsinger et al. (2005).

Weather information was collected from the National Climatic Data Center (Lawrimore et al. 2011, NCDC 2011) of the National Oceanic and Atmospheric Association (NOAA). The NCDC's Global Historical Climatology Network (GHCND) is a public access database of historical monthly temperature, precipitation, and snow records over global land areas. The values are a composite of climate records from numerous sources that are merged and subjected to a suite of quality assurance reviews. The GHCND-Monthly Summaries database includes 18 meteorological elements from $>$ 40,000 stations distributed across all continents.

The weather-data station used for this analysis is located at 1,097 m elevation near Koke'e State Park (ID: Kanalohuluhulu 1075, HI US GHCND: USC00513099 at [22.12972°, −159.65861°]). The Kanalohuluhulu station is the only station in the area with a recording period which covers the study period (1996–2009) and exhibits nearly continuous monthly data points at an elevation comparable to Puaiohi habitat. Of the 18 meteorological elements available, we selected five: number of days per month with $\geq$1 mm precipitation, total monthly precipitation (mm), mean maximum temperature (°C) by month, mean minimum temperature (°C) by month, and mean temperature (°C) by month.

We used several *a priori* assumptions to select these five elements. First, given the subtropical nature of the birds' habitat and its relatively moderate elevation, it was reasonable to eliminate certain elements pertaining to snow, cooling, and/or extreme minimum or maximum temperatures. Furthermore, we eliminated computed elements that measured the number of days per month that met a specific rain or temperature level, as means or presence/absence were more parsimonious. We averaged the remaining five monthly elements over three periods thought to be meaningful to reproduction of Puaiohi: peak breeding season (Apr–Jun), full breeding season (Mar–Aug), and previous wet season (Nov of the preceding year to Mar of the current year). Weather elements are correlated with each other, particularly within the temperature and precipitation measures by season (Fig. 1).

To investigate how nest success variables associated with weather variables, we evaluated simple linear regressions using Akaike's information criterion, corrected for small sample size (AIC*c*; Burnham and Anderson 2002). For each of the four dependent reproductive variables (fledglings/attempt, attempts/season, fledglings/female/season, and length of breeding season), we fit 15 regression models; each model used one of the five weather variables within one of the three time periods as the explanatory variable. Because of the very small sample size (6 years), models with more than one independent variable could not be fit reliably; reflecting this, the penalty for small sample size rendered the AIC*c* of all multivariable models too large to be competitive. We considered models with the smallest ΔAIC*c* as compared to the best fit model to be supported by the data and are reported below.

RESULTS

Nest success of Puaiohi, by all measures, appears to exhibit some degree of variability from year to year. While birds produce 2–3 young per pair most seasons (1996; 2007–2009), some years

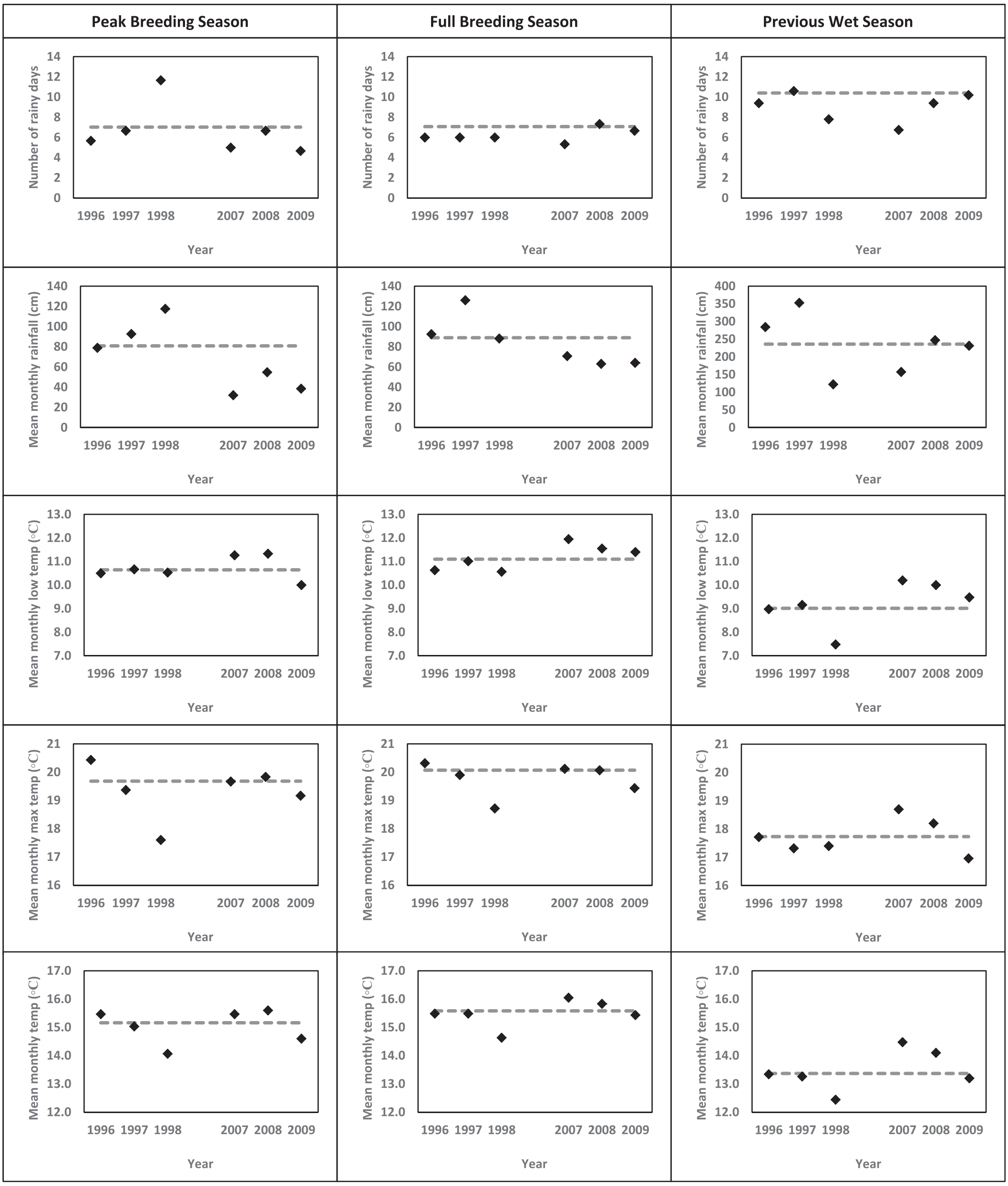

FIG. 1. Seasonal weather element values by year. Dashed lines represent average historic mean values (1965–1989).

appear to be much more (1997; 4.9 fledged/pair/year) or much less (1998; 0.4 young fledged/pair/year) successful. The length of the breeding season is similarly variable, ranging from 132 days during the very successful 1997 breeding season, to just 50 days in 2008 (Table 1).

All four nest-success variables had strong relationships with at least one weather variable (Table 2). The number of young fledged per nesting attempt strongly related ($r^2 > 0.59$ and $\Delta AICc < 2.3$) to six weather variables: number of rainy days during peak breeding season, both peak breeding and full breeding season mean maximum temperature, previous wet season mean monthly rainfall, previous wet season mean minimum temperature, and full breeding season mean

TABLE 1. Summary of nesting success, 1996–1998, upper Mohihi study area[a] and 2007–2009, Halepa'akai study areas.

Year	# of nests	# of pairs	# young fledged/attempt	# attempts	# young fledged/pair/year	Breeding season length (days)
1996	26	12	1.4	2.2	2.8	87
1997	44	14	1.7	3.3	4.9	132
1998	24	22	0.4	1.1	0.4	51
2007	30	14	1.36	2.14	2.71	86
2008	20	13	1.40	1.54	2.15	50
2009	16	11	1.38	1.45	2.00	54

[a] Snetsinger et al. (2005).

temperature. Frequent rainy days during the peak breeding season associated with fewer young fledged per nesting attempt (Fig. 2), although, interestingly, total rainfall during the breeding season was not. Specifically, each additional rainy day per month during the peak breeding season associated with a decrease of 0.148 young fledged/attempt. The other weather variables all related positively to the number of young fledged per nest attempt. Each 1 °C increase in the monthly mean high temperature and the mean temperature during the full breeding season, corresponded with an additional 0.616 and 0.719 young fledged per attempt, respectively (Figs. 3, 4). Furthermore, we saw an additional 0.337 young fledged per attempt for each 1 °C increase in the monthly mean high temperature during the peak breeding season (Fig. 3), and 0.354 additional young fledged per attempt where associated with each 1 °C increase in the monthly mean low temperature during the previous wet season (Fig. 5). Although too many rainy days during the peak breeding season associated negatively with number of young fledged, greater rainfall in the previous wet season associated with increased young fledged per attempt (Fig. 6), such that each additional 1 cm of mean monthly rain during the previous wet season associated with an increase of 0.04 young fledged per attempt.

The number of nest attempts per season strongly positively associated with rainfall both during the full breeding season and in the previous wet season (Fig. 7). An additional 1 cm of average monthly rain during the full breeding

TABLE 2. Best fit nest success models based on AIC*c* over study period ($n = 6$). For all models number of parameters (k) is 2.

Dependent variable	Explanatory variable	Relationship	r^2	AIC*c*	ΔAIC*c*	w_i
Number of young fledged per nest attempt	Average number of days with rain in peak breeding season	−	0.720	16.603	0	0.268
	Average monthly maximum temperature during full breeding season	+	0.665	17.679	1.076	0.157
	Average monthly maximum temperature during peak breeding season	+	0.661	17.75	1.147	0.151
	Average total monthly rainfall during previous wet season	+	0.639	18.142	1.539	0.124
	Average monthly minimum temperature in the previous wet season	+	0.592	18.830	2.227	0.088
	Average mean temperature in the full breeding season	+	0.591	18.889	2.286	0.086
Number of nest attempts per breeding season	Average total monthly rainfall during full breeding season	+	0.579	25.804	0	0.289
	Average total monthly rainfall during previous wet season	+	0.575	25.859	0.055	0.281
	Average monthly maximum temperature during full breeding season	+	0.326	28.626	2.822	0.070
Number of young fledged per pair per year	Average total monthly rainfall during previous wet season	+	0.706	31.141	0.000	0.552
	Average monthly maximum temperature during full breeding season	+	0.429	35.123	3.982	0.075
Length of breeding season	Average total monthly rainfall during full breeding season	+	0.691	68.490	0.000	0.597
	Average total monthly rainfall during previous wet season	+	0.443	72.033	3.543	0.102

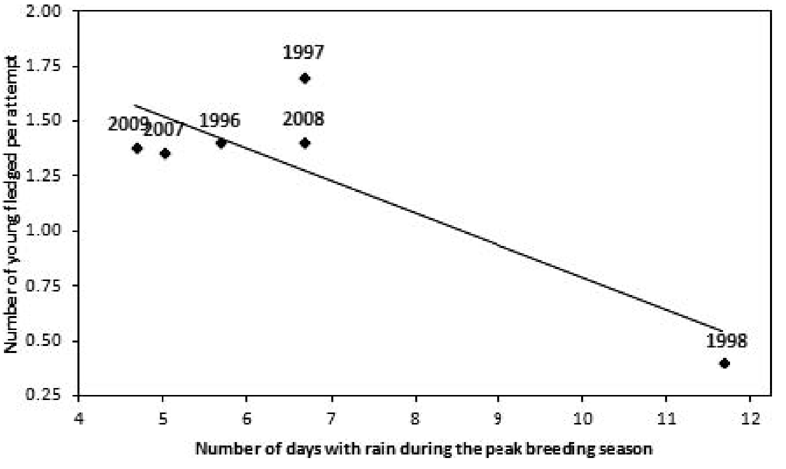

FIG. 2. Young fledged versus breeding season rainy days.

season corresponded with 0.25 additional nest attempts per season, while each additional 1 cm of average monthly rain during the previous wet season corresponded with 0.07 additional nest attempts per season. Number of young fledged per season and attempts per season were not the only measures of reproductive success for which previous wet season total rain was meaningful. Indeed, previous wet season was the only weather variable that fit the model for number of young fledged per pair per year (Fig. 8). Each additional 1 cm of average monthly rain during the previous wet season associated with an additional 0.15 young fledged per pair per breeding season.

The only measure of reproduction of Puaiohi that did not include total rainfall in previous wet season as a best fit model was length of the breeding season. Average total rainfall during the full breeding season was the only weather variable strongly correlated with the length of breeding season (Fig. 9), such that an additional 1 cm of average monthly rain during the full breeding season associated with a breeding season which lasted 11.1 days longer. The second-best variable for predicting the length of the breeding season was total rainfall in the previous wet season, though this relationship was considerably weaker than that of length of breeding season with rainfall during the breeding season ($\Delta AICc > 3.5$).

DISCUSSION

Overall, support for our hypotheses was mixed. The first hypothesis, that increased rain during the wet season prior to the breeding season is correlated

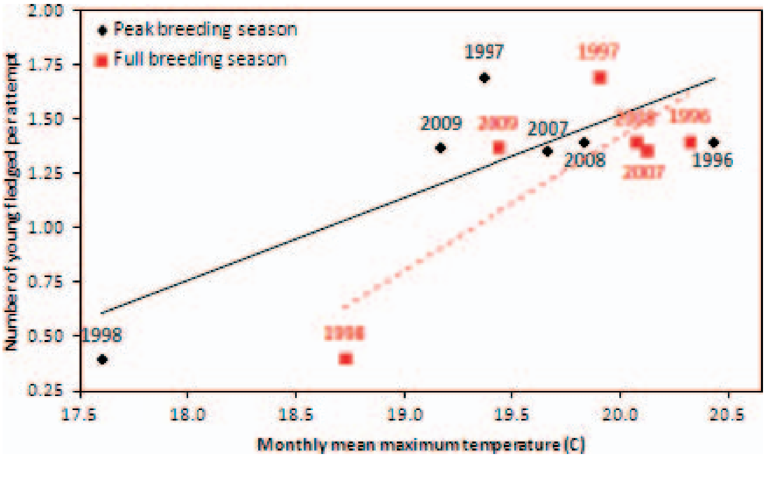

FIG. 3. Young fledged versus breeding season temperature.

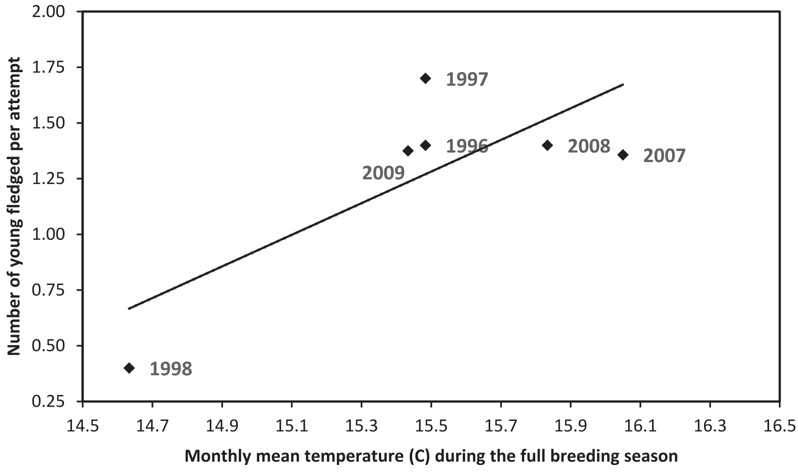

FIG. 4. Young fledged versus full breeding season mean temperature.

with greater reproductive success, was supported, with more young fledged per nest, more nesting attempts per season, and hence, more fledglings/pair/season associated with more rain in the previous wet season. Rain during the previous wet season also was the second best explanatory variable for length of breeding season, though this relationship was substantially weaker than that between length of breeding season and rainfall during the breeding season. In contrast, results did not support our second hypothesis, that increased rain and extreme temperatures during the breeding season would correlate with reduced reproductive success. Though we saw some indication that too many rainy days during the peak breeding season may be detrimental, the total amount of rain during the breeding season positively correlated with the number of attempts per season and length of the breeding season.

Although all four nesting parameters exhibited some degree of relationship to weather variables, only the number of young fledged per attempt model was well supported by multiple weather variables. Of greater note is that one weather variable, rain prior to the breeding season, is positively and moderately to very strongly related to all four measures of nest success, including overall nest success (number of young fledged/pair/year), and may serve as the primary explanatory value for nest success of Puaiohi. More rain in the previous wet season associated with increased reproductive output for all models in which it

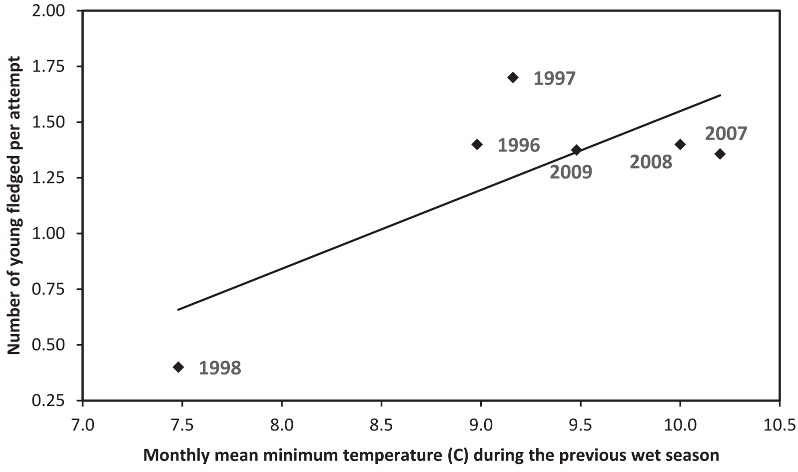

FIG. 5. Young fledged versus previous wet season mean minimum temperature.

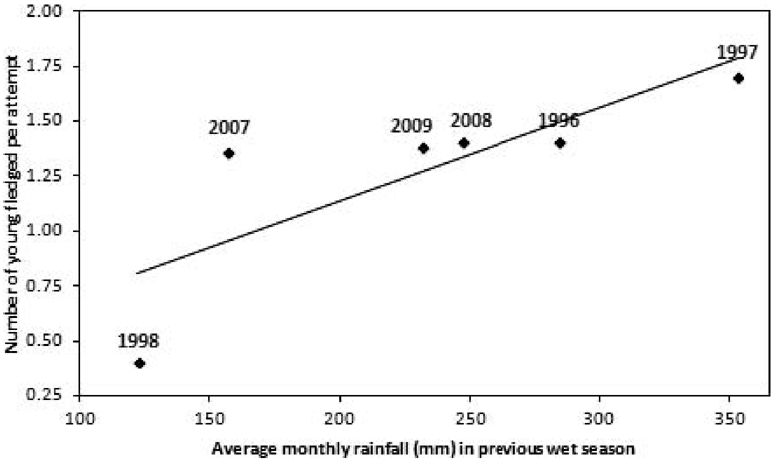

FIG. 6. Young fledged versus previous wet season rainfall.

appeared (Figs. 5, 6, and 7), with rainfall during the wet season preceding the breeding season being the single most important weather factor in predicting nest success for a season. More rain in the preceding wet season likely results in increased production of the fruits Puaiohi rely upon as a major food source, thereby increasing the birds' ability to successfully rear and fledge young. In addition, the greater food availability may lessen predation pressure, as predatory rats may be fulfilled by the relatively easy to find fruit and not invest increased effort in hunting. Alternatively, rat populations may decline following cold and wet winters, thereby posing less threat to nesting Puaiohi.

Though rain in the previous wet season was the primary factor related to measures of nest success, other factors seem to be at play as well. For instance, too many rainy days during the peak breeding season may decrease reproductive successes, perhaps because of decreased ability of parents to forage during prolonged rainy periods, as well the potentially higher energetic expenditures necessary for both parents and nestlings to stay warm. At the same time, however, sufficient rain during the full breeding season may be necessary to sustain a longer breeding season and increase number of nest attempts. Specifically, sufficient rainfall is likely needed to sustain fruit production, both supplying ample food to Puaiohi parents and young, as well as rats, thereby lessening predation pressures. Additionally, more young fledged per nesting attempt with warmer temperatures during the breeding season, a pattern

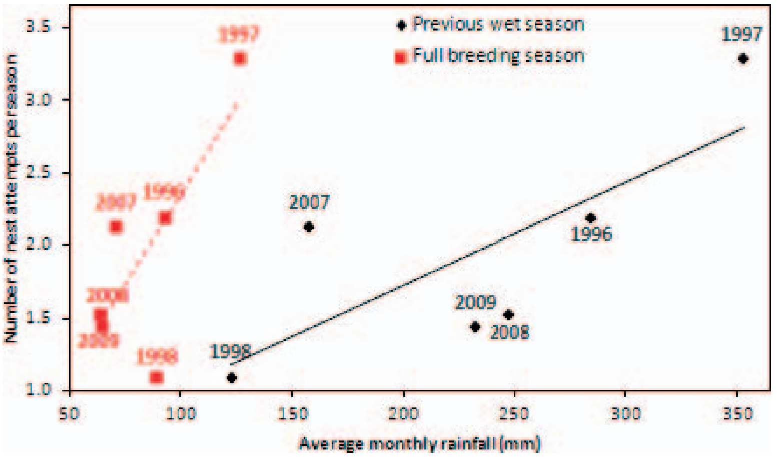

FIG. 7. Nest attempts versus seasonal rainfall.

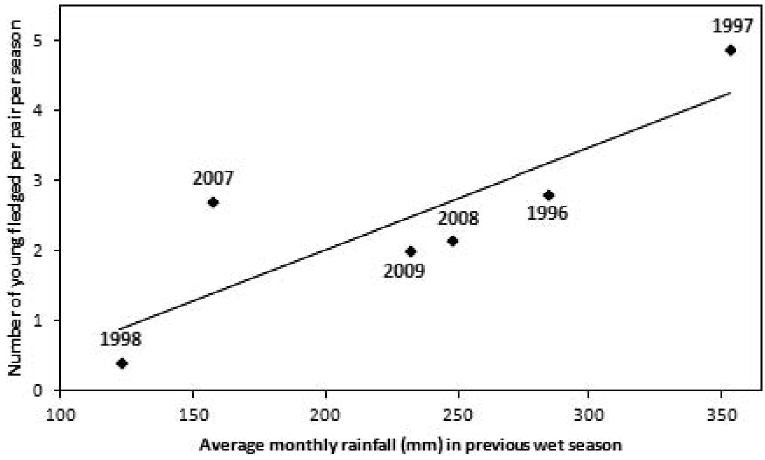

FIG. 8. Young per pair versus previous wet season rainfall.

which had not been previously suggested or hypothesized.

Although the weather-reproductive success relationships identified in this study show a significant correlation, it is important to keep in mind that most of the trends identified here are driven by two years (1997 and 1998), and there is little to no relationship between weather variables and reproductive success in the other 4 years. Given the small dataset, it is possible that relationships between weather variables and reproductive output are non-linear, such that critical thresholds exist, below which reproductive output collapses or above which reproduction is significantly increased over average levels. Regardless of whether the relationship is linear or non-linear, there is compelling evidence that the weather in 1997 and 1998 was not unusual but instead represents conditions that occur fairly commonly, and may indeed change in frequency in the near future. In 1997, Puaiohi had their most successful nesting year within the study period. The breeding season in 1997 was extended, and both fledglings per attempt and number of attempts were substantially higher than the average over all study years. The wet season prior to 1997 (Nov 1996–Mar 1997) had high mean monthly rainfall, which carried over into the breeding season when rainfall was higher than in other years, though the actual number of rainy days in the peak season was within the range of other study years (albeit at the high end). However, the opposite happened in 1998, when

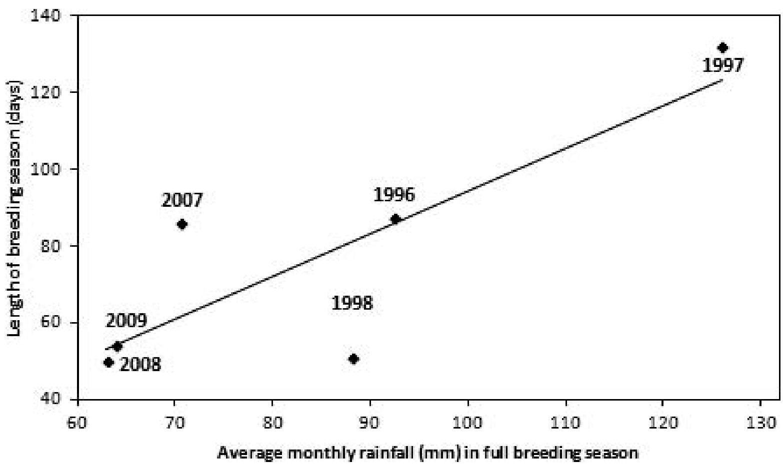

FIG. 9. Length of season versus breeding season rainfall.

Puaiohi had much lower than average nest success—fewer young fledged per attempt, pairs attempted to nest fewer times, and the overall production per pair that year was remarkably low. This breeding season and the wet season preceding it exhibited unusual weather opposite to that before and during the 1997 breeding season. In fact, the 1997–1998 wet season (Nov 1997–Mar 1998), the driest of any of the studied years, was during one of the strongest El Niño Southern Oscillation (ENSO) events in recent years, with only two others of similar magnitude in the last 60 years (Western Regional Climate Center 2013). The El Niño then transitioned into a strong La Niña, resulting in a 1998 peak breeding season (Apr–Jun) which had almost twice the number of rainy days as the next rainiest peak breeding season and was markedly colder than the other years. While rainfall in the prior wet season is similar for 1998 and 2007, the wet season prior to 2007 was warmer than that before 1998. Though both years were dry, the fact that the pre-1998 wet season was both dry and cold may have compounded the effect on subsequent productivity during the breeding season.

Hawaii tends to be drier and drought prone during strong El Niño events and wet during La Niña events, although the effect of the latter is more variable (Chu and Chen 2005, Kolivras and Comrie 2007, Chu et al. 2010). In fact, most major droughts during Hawaii's winter wet season have been preceded by a persistent El Niño event starting from March of the preceding year (Chu 1989). This relationship between drought and El Niño is of particular concern as it is believed that El Niño and La Niña events are more variable and intense over the past several decades, presumably because of the increase in environmental temperatures produced by anthropogenic climate change (Meng et al. 2012, Cobb et al. 2013, DiNezio et al. 2013). If this variability and intensity trend persists, overall yearly precipitation may decrease across Hawaii (Chu et al. 2010), which could be particularly detrimental if it affects the winter precipitation that seems to be essential to a successful breeding season of Puaiohi. However, ENSO events are inherently unpredictable, and the potential effects of anthropogenic climate change on ENSO events are as yet unclear.

A second climatic trend, which is believed to be independent of ENSO events, is an apparent negative trend in winter rainfall in Hawaii. This negative trend may be a result of increasing persistence of the trade-wind inversion (TWI; Cao et al. 2007, Giambelluca and Luke 2007), which has increased since 1979. Simulations under future anthropogenic climate change conditions suggest the TWI will continue to become more persistent and lower in height (Cao 2007). Although the connection between TWI changes and climate warming needs further study, the continuation of a more persistent inversion will produce a shift toward a drier climate in Hawaii (Giambelluca and Luke 2007), thereby reducing the amount of precipitation needed to produce adequate conditions for successful nesting of Puaiohi.

Given that the prevailing weather conditions of the Alaka'i Wilderness are predicted to alter with anthropogenic climate change (Benning et al. 2002), it is very important for conservation and management to understand how weather affects the reproductive output of Puaiohi, and all endemic species, as a means of evaluating their chances for long-term survival. A case in point is that nesting attempts of both Hawaii 'Amakihi (*Hemignathus virens*) and Palila (*Loxioides bailleui*) decreased 96% and 93%, respectively, during the 1992 El Niño drought compared to the preceding non-ENSO year (Lindsey et al. 1997). Similarly, drought conditions dominated 74% of the 2000–2010 period in subalpine Mauna Kea on Hawaii Island and correlated with a 79% decline in Palila abundance from 2003–2011 (Banko et al. 2013). While it is less clear how precipitation patterns will change habitat on Kaua'i for Puaiohi, it seems highly likely that patterns will change, becoming more variable and less stable or predictable (Loope and Giambelluca 1998, Chu et al. 2010).

While the links between Hawaiian birds and ENSO cycles may be less well studied, long term studies in the Galápagos Islands show that several species of Darwin's finches are strongly affected. During El Niño years in the Galápagos, rainfall increases and the finches tend to have both larger clutches and more breeding attempts per year, much as Puaiohi do in wet years, whereas during very dry years the finches failed to breed at all (Grant et al. 2000). Breeding success during ENSO years correlated with food supply, such that the wettest years lift the normal constraints on the breeding season, allowing the birds to breed longer and produce more young (Grant et al. 2000).

Aside from ENSO events, links between weather and nest success are found in a number of other birds. For instance, annual reproductive success of Lark Buntings (*Calamospiza melanocorys*), Song Sparrows (*Melospiza melodia*), and

Wrentits (*Chamaea fasciata*) are positively correlated with annual rainfall levels (Chase et al. 2005, Preston and Rotenberry 2006, Skagen and Yackel Adams 2012). In fact, similar to Snetsinger et al.'s (2005) hypothesis regarding increased predation of Puaiohi on the nest following a drought during the previous wet season, nest predation rates of Song Sparrows were also lower during wetter years (Chase et al. 2005). Woodlarks (*Lullula arborea*), on the other hand, seem to lay larger clutches and fledge more chicks when the weather is drier (Wright et al. 2009). Temperature is also linked to nest success in numerous species (Chase et al. 2005, Weatherhead 2005, Wright et al. 2009, Skagen and Yackel Adams 2012), although the mechanisms and relationships tend to be fairly species specific.

Relationships between weather and nest success are not limited to continental locations. For instance, several endemic Hawaiian bird studies identified weather as a cause of nest failure, including ʻAkohekohe (*Palmeria dolei*; VanGelder and Smith 2001), ʻApapane (*Himatione sanguinea*; Nielson 2000), Maui Parrotbill (*Pseudonestor xanthophrys*; Simon et al. 2000), ʻAmakihi (*Hemignathus virens*; Kern and van Riper 1984), Hawaii Creeper (*Oreomystis mana*; VanderWerf 1998), Iʻiwi (*Vestiaria coccinea*; Kuntz 2008) and Hawaii ʻElepaio (*Chasiempis sandwichensis bryani*; van Riper 1995). However, none of these studies investigated persistent patterns between weather conditions and seasonal nest success.

Overall, it seems clear that rainfall, particularly previous wet season rainfall, may be associated with nest success of Puaiohi. While the forecasted increase in dry El Niño years may make the Puaiohi's situation seem dire, the possible increase in moderately wet La Niña years may potentially offset this, provided the rainfall and lower temperatures in these years are not too severe. Given the Puaiohi's relatively long life span, individuals may be able to weather the bad years and capitalize on the good. However, this creates a highly variable breeding scheme that could destabilize an already small and threatened population. As such, it is imperative that we both better understand how variable rainfall, particularly ENSO cycles, affect these birds, as well as understand how rainfall patterns will change under future climate scenarios.

Our findings have several important implications for management. First, determining how weather and nest success relate requires detailed demographic data, indicating the need to both continue collecting such data and expanding data collection to other species. Demographic data are not only important for refining our understanding of relationships but also to developing population models and conducting population viability analyses that are urgently needed for many Hawaiian birds. Second, it is important to discern if weather also relates to nest predators, such as rats, which could inform if on-the-ground management actions need to be taken during specific times. Finally, if our findings are supported with the addition of further data, then understanding and including these relationships will become crucial to include in any structured decision or management modeling undertaken for Puaiohi.

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