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Breeding season shift by the Oahu Elepaio (*Chasiempis ibidis*) in response to changing rainfall patterns

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ABSTRACT—Anthropogenic climate change is affecting many bird species in a variety of ways, causing changes in their distribution, abundance, and food supply, and triggering responses such as shifting migration and nesting seasons. Most studies have focused on migratory birds that breed in temperate areas and little is known about effects of climate change on tropical birds. We used a 24 year dataset that included 1,632 nesting events of the Oahu Elepaio (*Chasiempis ibidis*), an endangered forest bird endemic to Hawaii, to investigate whether breeding phenology and performance were related to rainfall and whether a recent shift in the breeding season is related to changes in rainfall. Fecundity of the Oahu Elepaio was closely related to rainfall, with more offspring produced during years with higher rainfall. During the first 19 years of this study, from 1996 to 2014, all nests were initiated from November to June. From 2015 to 2019, up to 33% of annual reproduction occurred from August to October. Higher rainfall caused parallel increases in reproduction during the normal nesting season and the atypical season, with some birds nesting in both seasons. The change in breeding phenology of the Oahu Elepaio is unusual because it was not a gradual transition, but a sudden change of 6 months. The shift in breeding phenology coincided with unusually high summer and fall rainfall from tropical storms associated with a novel climate pattern in the northern Pacific Ocean from late 2014–2016 termed the warm blob. This pattern of warmer water and more frequent storms is expected to become more prevalent in the Central Pacific, so summer–fall breeding in the Oahu Elepaio is likely to continue and perhaps become more common. The Oahu Elepaio is flexible, adaptable, and may not be seriously affected by changing climatic conditions. *Received 28 June 2020. Accepted 16 March 2021.*

Key words: breeding phenology, climate change, Hawaiian birds, nesting success, rainfall.

Cambios en la temporada reproductiva del elepaio de Oahu (*Chasiempis ibidis*) en respuesta a variaciones en patrones de precipitación

RESUMEN (Spanish)—El cambio climático antropogénico está afectando a muchas especies de aves de diversas maneras, provocando cambios en su distribución, abundancia, suministro de alimentos y provocando respuestas como desplazamientos en las temporadas de migración y anidación. La mayoría de los estudios se han centrado en las aves migratorias que se reproducen en zonas templadas y se sabe poco sobre los efectos del cambio climático en las aves tropicales. Utilizamos un conjunto de datos de 24 años que incluía 1,632 eventos de anidación del elepaio de Oahu (*Chasiempis ibidis*), un ave de bosque en peligro de extinción endémica de Hawái, para investigar si la fenología y el rendimiento de la reproducción estaban relacionados con la lluvia y si un cambio reciente en la temporada de reproducción esta relacionado con cambios en la precipitación. La fecundidad del elepaio estuvo estrechamente relacionada con la lluvia, con mayor descendencia producida en los años con mayor precipitación. Durante los primeros 19 años de este estudio, de 1996–2014, todos los nidos se iniciaron de noviembre–junio. Desde 2015–2019, hasta el 33% de la reproducción anual ocurrió de agosto–octubre. Una mayor precipitación causó aumentos paralelos en la reproducción durante la temporada normal de anidación y la temporada atípica, con algunas aves anidando en ambas estaciones. El cambio en la fenología reproductiva del elepaio es inusual porque no fue una transición gradual, sino un cambio repentino de 6 meses. El cambio en la fenología reproductiva coincidió con las lluvias inusualmente altas en verano y otoño por las tormentas tropicales asociadas con un nuevo patrón climático en el norte del Océano Pacífico desde finales de 2014–2016 denominado la burbuja cálida. Se espera que este patrón de aguas más cálidas y tormentas más frecuentes se vuelva más frecuente en el Pacífico Central, por lo que es probable que la reproducción continúe de verano-otoño en el elepaio y quizá se haga más común. El elepaio de Oahu es flexible, adaptable y puede no verse seriamente afectado por las condiciones climáticas cambiantes.

Palabras clave: aves hawaianas, cambio climático, éxito de anidación, fenología de la reproducción, lluvias.

Anthropogenic actions over the past several decades to centuries are causing rapid changes to the earth's environment, particularly the climate, and these in turn are affecting plants and animals (Parmesan 2007, Socolar et al. 2007, Bellard et al. 2012, Dunn and Møller 2019). The response by a species to changing climate may include phenotypic or behavioral plasticity, evolution through selection and adaptation, and shifts in movement patterns and spatial distribution (Visser 2008, Charmantier and Gienapp 2014, Freeman and Freeman 2014, Oostra et al. 2018). Failure to respond to environmental change can result in decreased breeding performance, survival, or geographic range, resulting in population declines and eventual extirpation or even extinction (Dickey et al. 2008, Miller-Rushing et al. 2010, Skagen and Yackel Adams 2012, Yandow et al. 2015). The vulnerability of a species to climate change can be affected by many aspects of its life history and its environment (Dawson et al. 2011).

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Island-endemic species often are especially sensitive to environmental change because their limited range can prevent geographic relocation and they can have lower genetic variation that limits selection and adaptation (Lind and Johansson 2007, Foden et al. 2013).

In birds, several life history attributes have been documented to be shifting in response to climate change, including the timing and pattern of migration, foraging ecology, egg laying date, and other aspects of breeding phenology (Sanz 2003, Dickey et al. 2008, Skagen and Yackel Adams 2012, Charmantier and Gienapp 2014, Imlay et al. 2019). Temperature is the environmental factor most often related to recent changes in avian life histories, but precipitation, wind, and ocean currents are also known to be affecting certain birds (Weimerskirch et al. 2012, Imlay et al. 2018, Dunn 2019). The effects of climate change have been predicted to be more serious in tropical bird species than in temperate bird species (Şekercioğlu et al. 2012) and modeling has shown that changing rainfall regimes could negatively affect demography of tropical birds (Brawn et al. 2017). Only a few studies have collected empirical evidence of the effect of variation in weather on demography of tropical birds (Hau 2001, Aranzamendi et al. 2019).

The breeding season of most temperate and polar breeding bird species is regulated primarily by day length (photoperiod) and temperature; other factors that can influence breeding phenology include precipitation, wind, population density, and food abundance (Dawson 2008, Voigt et al. 2011, Dunn 2019). Breeding phenology of tropical bird species can be regulated by small seasonal differences in day length, and in bird species inhabiting deserts or regions with highly seasonal or unpredictable weather, breeding may be tied primarily to rainfall and consequent effects on food availability (Hau 2001, Dawson 2008, Perfito et al. 2008, Aranzamendi et al. 2019).

In this study, we investigated whether the breeding phenology and performance of the Oahu Elepaio (*Chasiempis ibidis*), an endangered forest bird endemic to the Hawaiian island of Oahu, was related to weather patterns, specifically rainfall. Moreover, in 2015 we began to observe elepaio nesting during the summer and fall, several months outside the normal breeding season, and we wanted to determine whether this recent shift in nesting phenology was caused by changing rainfall patterns.

Methods

Study species

The Oahu Elepaio is a monarch flycatcher (Monarchidae) endemic to the Hawaiian island of Oahu (VanderWerf 2018). Other elepaio species occur on the islands of Kauai and Hawaii, and are fairly common (Scott et al. 1986, Paxton et al. 2016), but the Oahu Elepaio has declined severely in the last few decades and is now rare. In 2011, the total population was estimated to be 1,261 birds (95% CI = 1,181–1,343) and the range was fragmented and estimated to be 5,187 ha (Fig. 1; VanderWerf et al. 2013). The Oahu Elepaio was listed as Endangered under the U.S. Endangered Species Act in 2000 (USFWS 2000, 2006) and is considered Endangered by the International Union for the Conservation of Nature (Birdlife International 2016). The primary threats to the Oahu Elepaio are nest predation by nonnative black rats (*Rattus rattus*) and mosquito-borne diseases, particularly avian pox virus (*Poxvirus avium*; VanderWerf et al. 2006, VanderWerf 2009). Rodent control has been shown to cause increases in elepaio reproduction and survival of nesting females and has become the cornerstone of the conservation strategy for the species (VanderWerf 2009, VanderWerf et al. 2011).

Elepaios are nonmigratory, sedentary, and pairs defend all-purpose territories year-round (VanderWerf 2018). They are insectivorous and eat insects, spiders, and other arthropods that they catch from many different substrates in a variety of forest types (VanderWerf 1994, 2018). The nesting season of the Oahu Elepaio traditionally has been January to June, with a peak in egg laying from February to April (VanderWerf 2018). The timing of breeding is thought to be related to rainfall (VanderWerf 2018), and in most areas of Hawaii rainfall typically is highest in the winter months of November–March (Giambelluca et al. 2013). Both elepaio sexes help build the nest, incubate the eggs, and feed the nestlings. Only the female incubates at night, leading to higher predation on females by nocturnal rats and a skewed sex ratio in some areas (VanderWerf 2009, VanderWerf et al. 2013). The clutch size is usually 2 eggs, occasionally 1 or 3.

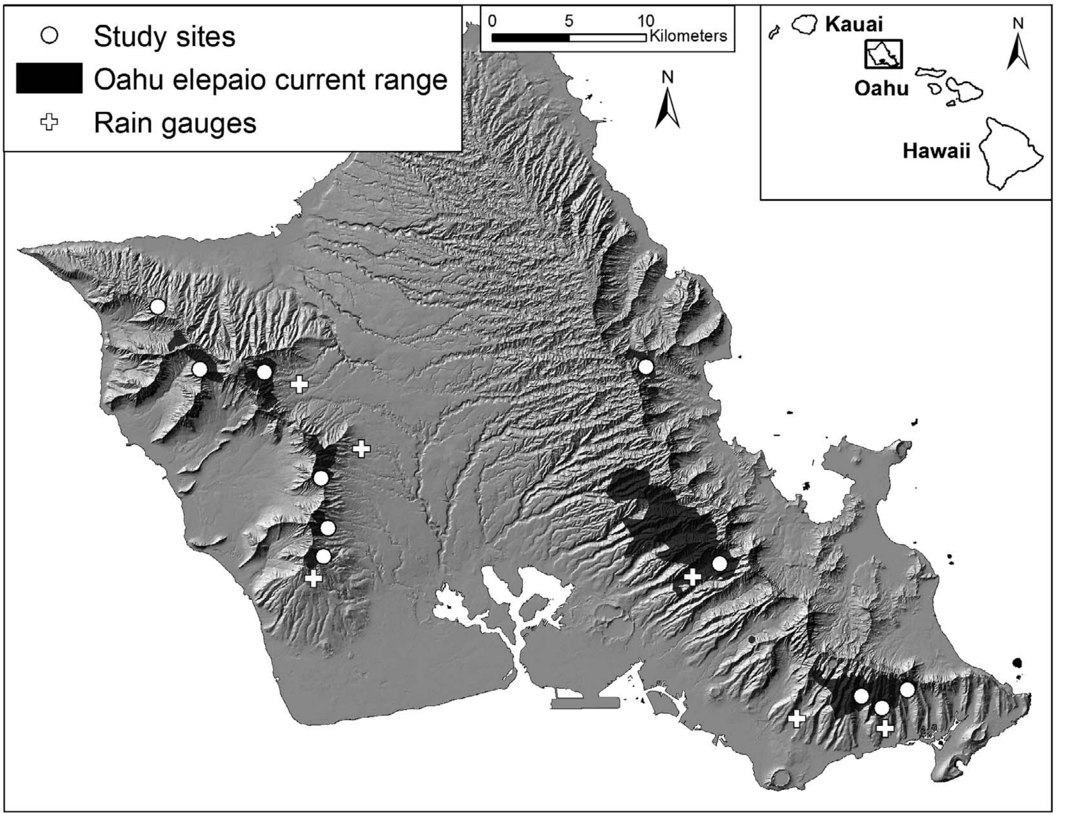

Figure 1. Current range of the Oahu Elepaio, study sites, and location of rain gauges used in this study.

Rainfall

To measure rainfall, we used data from 6 National Weather Service rain gauges that were geographically closest to our elepaio study sites and that had time series long enough to encompass the period over which we monitored elepaio at each site. These gauges recorded daily rainfall amounts automatically. We obtained monthly totals for each gauge from the Honolulu Office of the National Weather Service. The rain gauges were located at Moanalua Stream, Palolo Fire Station, Niu Valley, Kunia, Schofield Barracks, and Palehua (Fig. 1). We calculated a single rainfall measure from December to June and July to November each year by averaging the values from the 6 gauges. We broke the data into these 2 time periods because they represent the typical winter wet and summer dry seasons in Hawaii (Giambelluca et al. 2013). The months from July to November also correspond to the hurricane season in the North Pacific.

Elepaio monitoring

We monitored the Oahu Elepaio in 11 sites that encompassed all remaining large populations of the species (Fig. 1). The study duration and number of elepaio pairs we monitored varied among the sites, but overall the study encompassed 24 years, from 1996 to 2019 (Table 1). At each site, we searched for and monitored elepaio nests on weekly or bi-weekly visits during the normal breeding season of December–June. In addition, we mist-netted and banded elepaio in all months throughout the study to allow identification of individual birds and facilitate demographic monitoring, and we used the presence of a brood patch (females) or cloacal protuberance (males) in mist-netted birds as an indication of breeding. The breeding condition of elepaio we captured in mist nets indicated that we did not overlook nests in the atypical season prior to 2015. From 1995 to 2014, 39 of 298 (13%) elepaio captured from December to June had a brood patch or cloacal protuberance,

Table 1. Study duration and sample size of nests found at 11 Oahu Elepaio study sites from 1996 to 2019.

Site name	# Years monitored	Years monitored	# nests found
Ekahanui	19	2000–2019	320
Kuliouou Valley	4	1996–1999	14
Makaha Valley	5	2005–2009	37
Makua Military Reservation	5	2005–2009	3
Moanalua Valley	13	2006–2017, 2019	259
Palehua	13	2007–2019	155
Palikea	3	2016–2018	11
Pia Valley	10	1996–2001, 2004–2005, 2017–2018	81
Schofield Barracks West Range	16	2000, 2005–2019	298
Waikane Valley	3	2007–2008, 2014	4
Wailupe Valley	22	1998–2019	450
Total	24	1996–2019	1,632

but zero of 199 elepaio captured from August to November had a brood patch or cloacal protuberance. From 2015 to 2019, the proportion of elepaio captured with physiological evidence of breeding was 11% from December to June and 4% from August to November. The proportions of elepaio in breeding condition generally were low because nesting is not synchronous, some birds did not breed in some years, and males have a cloacal protuberance for a relatively short time.

We calculated the date on which each nest was initiated using the date it was found, the stage at which it was found (building, incubation, or nestling), a 10 d mean nest building period, an 18 d incubation period, and a 16 d nestling period (VanderWerf 2018). The incubation period is not known to vary, but the nestling period can range from 15 to 17 d (EAV, unpubl. data). If the nest was found during building, we used the apparent completeness of the nest to estimate when it was initiated. For example, if the nest appeared to be 70% complete, we assumed it was initiated 7 d before it was found. Similarly, we used apparent age of nestlings to estimate the date they hatched and backdated to determine the laying date and nest initiation date. If no information was recorded about the appearance of the nest or the size of the nestlings, we assumed the nest was discovered midway during that stage of the nesting cycle. In cases where we observed a fledgling but did not find the nest, we estimated the age of the fledgling based on its appearance and behavior and backdated to determine the fledging, laying, and nest initiation dates. We used this method only for fledglings that were less than 5 weeks of age, after which they are fully grown and are no longer fed by the parents, making it difficult to determine their age.

Statistical analyses

We categorized each breeding event as having been initiated in the normal (Dec–Jun) or atypical (Jul–Nov) season. We calculated a numerical measure of initiation date for each nest as the days since 1 December. We examined whether nesting phenology differed between the time periods 1996–2014 and 2015–2019 using a general linear model, with site as an additional factor to account for variation among sites. To further investigate whether nesting phenology of the Oahu Elepaio has changed within the normal breeding season, we conducted a regression of mean nest initiation date on year and on mean rainfall from December to June.

We categorized the outcome of each nest as abandoned, failed, successful, or unknown (n = 1,632). We counted nests as successful if they fledged at least 1 chick and we calculated nest success as the successful proportion of total nests. We counted nests as abandoned if building was not completed or if building was completed but we did not observe eggs or incubation behavior. Nests with an unknown outcome (n = 133) were excluded from analyses of nest success but were included in analyses of nesting phenology. We tested whether nest success differed between the normal and atypical breeding seasons with χ^2 analysis of the number of abandoned, failed, and successful nests.

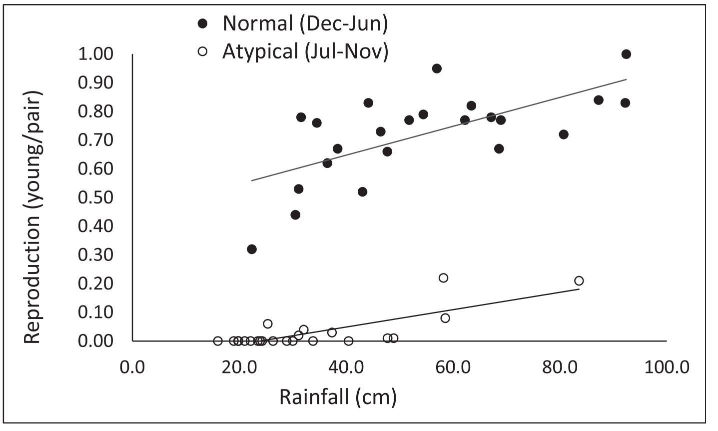

Figure 2. Relationship between fecundity of Oahu Elepaio and rainfall from 1997 to 2019 during the normal breeding season of December–June and the atypical breeding season of July–November. Each point is the average fecundity of all elepaio pairs at all sites monitored that year. See Table 1 for study sites monitored each year.

We measured elepaio reproduction as the number of young produced per pair each year, and we divided reproduction into the normal season (Dec–Jun) and the atypical season (Jul–Nov). We used linear regression to examine the relationship between elepaio reproduction and rainfall, using the average number of young raised per pair each year as the dependent variable and rainfall as the independent variable, and with separate regressions for the normal nesting season and the atypical season.

Because reproduction of the Oahu Elepaio is seriously affected by nest predation from nonnative rats (VanderWerf 2009, VanderWerf et al. 2011), in analyses that involved nest success or fecundity we included only elepaio territories in which rats were controlled. Rats were controlled using a variety of methods including snap traps, automated pneumatic traps, poison bait stations, and, at Schofield Barracks in 2018, aerial broadcast of rodenticide. For more details on rat control methods, see VanderWerf (2009) and VanderWerf et al. (2011). We did all analyses with the statistical package Minitab (Minitab 2010).

Results

Reproduction of the Oahu Elepaio was closely related to rainfall, with more young raised during years with higher rainfall (Fig. 2), and similar patterns during the normal breeding season of December–June ($F_{1,21} = 16.76$, $P = 0.001$, $R^2 = 44.4\%$) and the atypical season of July–November ($F_{1,21} = 33.31$, $P < 0.0001$, $R^2 = 61.3\%$). The relationship between reproduction and rainfall was not as strong when data were pooled over the entire year ($F_{1,21} = 8.11$, $P = 0.01$, $R^2 = 27.9\%$), demonstrating the importance of dividing the data into 2 seasons.

Mean annual fecundity was 0.75 $\pm$ 0.02 fledglings per pair (range 0.32–1.00). Reproduction during the atypical season accounted for a mean of 16% of total reproduction in the years when it occurred, with a maximum of 33% in 2016 (Fig. 3). We found no difference in nest success between the normal and atypical breeding seasons (47.6% vs. 47.8%, respectively; $\chi^2 = 1.14$, df = 2, $P = 0.57$).

The mean nest initiation date, measured as days since 1 December, was 24 d later in 2015–2019 (124.5 $\pm$ 2.9) than in 1996–2014 (101.4 $\pm$ 1.1; $F_{1,2026} = 70.63$, $P < 0.001$). Prior to 2015, virtually all reproduction occurred during the normal breeding season of December–June (Fig. 3). Since 2015, reproduction has occurred every year during the atypical season of August–October. We observed a few nests that were initiated in late November in 2004, 2006, 2007, and 2014 (Fig. 3), but these may have been the earliest nests of the normal season. There was no reproduction in July–October until 2015 (Fig. 4). Reproduction occurred in the atypical season only when rainfall exceeded 25 cm, with the 2 highest proportions of reproduction when rainfall exceed-

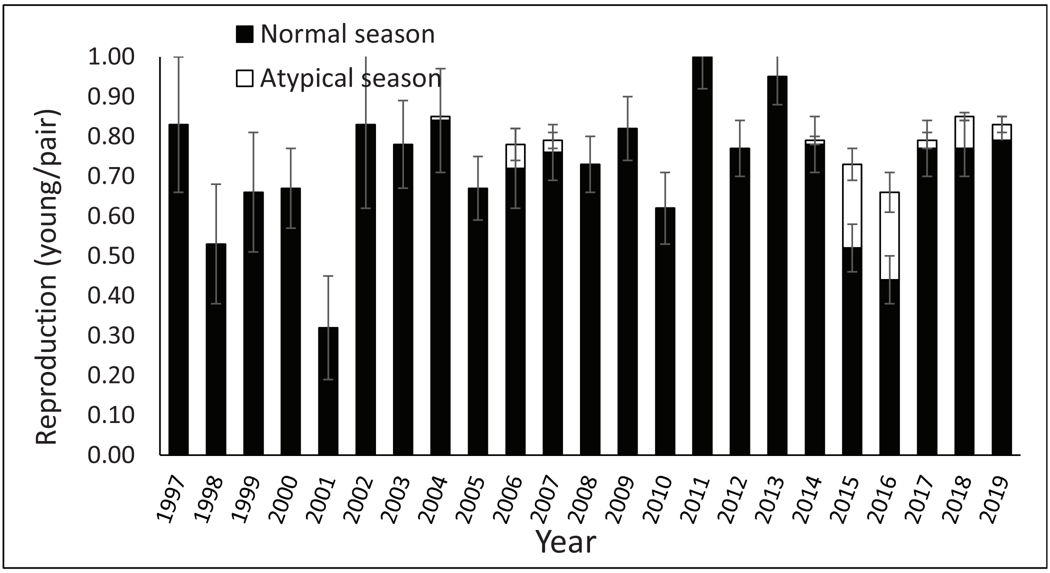

Figure 3. Fecundity of Oahu Elepaio by year from 1997 to 2019. Normal fecundity is the number of young raised per pair December–June; atypical fecundity is the number of young raised per pair July–November. Error bars are SE.

ed 58 cm. Nest initiation date during the normal season alone was not related to year ($F_{1,20} = 1.09$, $P = 0.31$) or rainfall ($F_{1,20} = 0.08$, $P = 0.79$), indicating the phenological difference between the time periods before and after 2015 was caused by nesting during the atypical season and not by a shift within the normal season.

Discussion

Results of this study showed that breeding phenology and breeding performance of the Oahu Elepaio were closely tied to rainfall. Moreover, the breeding phenology of the Oahu Elepaio has shifted recently in response to changes in seasonal rainfall patterns. During the first 19 years of this study from 1996 to 2014, all nests were initiated from late November to June. Every year since 2015, some Oahu Elepaio have nested during an atypical period from August to October. The highest rates of reproduction during the atypical period occurred during the first 2 years of this episode in 2015 and 2016 when summer rainfall was highest, but this phenomenon has persisted and elepaio nesting phenology has not returned to normal.

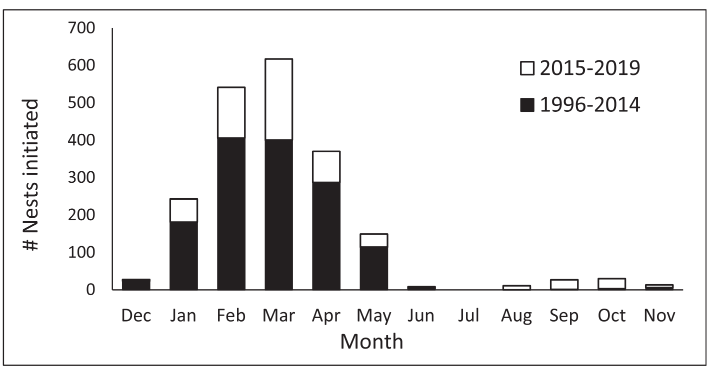

Figure 4. Number of Oahu Elepaio nests initiated each month in 2 time periods, 1996–2014 and 2015–2019.

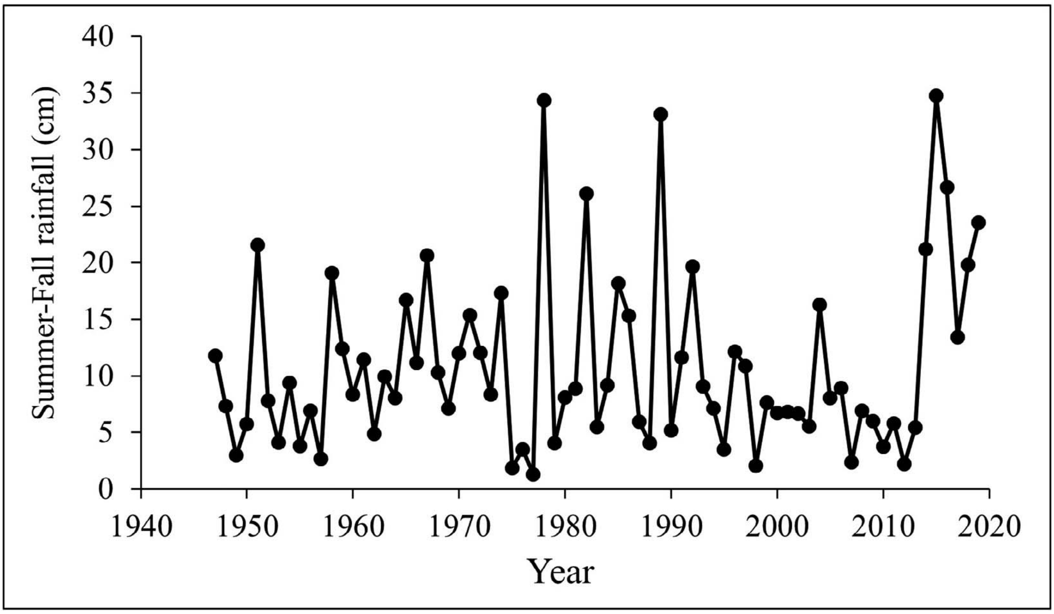

Figure 5. Rainfall at the Honolulu airport from June to October since record keeping began in 1947. Three of the 6 years with highest summer–fall rainfall have occurred since 2015.

The commencement of breeding in the atypical season in 2015 coincided with exceptional amounts of summer and fall rainfall associated with a novel weather pattern in the North Pacific Ocean from late 2014 to 2016 known as the "the warm blob" (Cavole et al. 2016). Rainfall at the Honolulu airport from June to October 2015 was the highest recorded during those months since record keeping began in 1947 (Fig. 5). There were 2 previous years with summer rainfall nearly as high (1978 and 1989), but those were more isolated events compared to the pattern since 2015, which includes 3 of the 6 years with highest summer rainfall. El Niño Southern Oscillation (ENSO) events also cause higher than normal summer rainfall in Hawaii (Giambelluca et al. 2013), but previous ENSO events are not known to have triggered atypical breeding phenology in the Oahu Elepaio.

The warm blob phenomenon was different and more extreme than typical ENSO events because it involved movements of large masses of warm water away from the equator, where it typically occurs during ENSO periods, into a broad area of the northern Pacific (Brainard et al. 2018, Herring et al. 2018, IPCC 2019). The warm blob facilitated formation of an unusually large number of named tropical storms in the central Pacific in the summers of 2015 and 2016 (Knapp et al. 2018), each of which released torrential rains across the Hawaiian Islands, resulting in some of the wettest summers ever recorded in Hawaii. This pattern of warmer water, heat waves, and more frequent storms has persisted to some extent since 2015 and is expected to become more prevalent in the Pacific as ocean temperatures rise (Capotondi et al. 2012, Cavole et al. 2016, Frölicher and Laufkötter 2018, IPCC 2019). It can therefore be expected that summer–fall breeding in the Oahu Elepaio will continue and perhaps become more prevalent.

The mechanism regulating breeding phenology of many animals is food availability, often as a result of seasonal variation in temperature or precipitation (Hau 2001, Socolar et al. 2007, Chmura et al. 2019). Changes in breeding phenology resulting from climate change have been observed in many bird species and other animals, primarily in response to increases in temperature, but usually the changes have been incremental, with gradual shifts of a few days or weeks over a period of decades (Dunn and Winkler 1999, Parmesan 2007, Socolar et al. 2007, Imlay et al. 2019). The breeding phenology shift we observed in the Oahu Elepaio was unusual because it involved a change of 6 months, from a time of increasing photoperiod in the winter/spring to a time of decreasing photoperiod in the summer/fall, demonstrating that food abundance was the proximate trigger and not photoperiod (Perfito et al. 2008, Dunn 2019). Higher rainfall presumably led to greater vegetative growth and consequent higher abundance of the invertebrates preyed on by elepaio.

The shift in breeding was likely due to individual variation in breeding behavior, i.e., plasticity, rather than adaptation by selection (Charmantier and Gienapp 2014). The shift occurred within the lifespan of many individual birds, and some individuals bred in the normal and atypical seasons. Elepaio foraging behavior also is plastic, with individual birds using different behaviors and substrates to capture food in different habitats (VanderWerf 1994). This plasticity has enabled them to withstand anthropogenic threats better than most other endemic Hawaiian birds.

There are other examples in which breeding by tropical birds has been triggered by rainfall and consequent food abundance. In Small Ground-Finches (*Geospiza fuliginosa*) living in an unpredictable environment in the Galápagos, breeding occurred at any time of year in response to heavy rainfall (Hau 2001). Similarly, Aranzamendi et al. (2019) documented flexible breeding phenology and rapid breeding response to rainfall and consequent increase in food resources in the Purple-crowned Fairywren (*Malurus coronatus*) in Western Australia. The breeding phenology of the Oahu Elepaio is beginning to resemble that of forest birds in the Mariana Islands, where typhoons are frequent, and nesting can occur at any time of year in response to high rainfall events (Radley et al. 2011). In an 18 month study of the Tinian Monarch (*Monarcha takatsukasae*), a close relative of elepaios, there were 3 peaks in nesting in September, January, and May, each of which occurred after a period of heavy rain (USFWS 1996).

Climate change is expected to have strong negative effects on many bird species (Bellard et al. 2012, Şekercioğlu et al. 2012, Dunn and Møller 2019). For endemic Hawaiian forest birds, rising temperatures will allow cold-intolerant mosquitoes that carry avian malaria (*Plasmodium relictum*) and avian pox virus to invade high-elevation forests that previously provided refuges from disease (Benning et al. 2002, Atkinson and LaPointe 2009, Garamszegi 2011, Fortini et al. 2017). Increasing disease transmission is already decimating the remaining forest bird populations at the highest elevations on the island of Kauai (Paxton et al. 2016). Other effects of climate change on Hawaiian birds are more difficult to predict, but changes in rainfall amounts and patterns could alter habitat distribution, allow increasing invasion by nonnative plants, and affect food availability by disrupting fruiting or flowering phenology of native plants.

The Oahu Elepaio, however, may not be strongly affected by climate change. The 3 elepaio species have greater immunity to introduced diseases than do most Hawaiian honeycreepers, and their current range is not limited by the distribution of mosquitoes or disease (VanderWerf et al. 2006, VanderWerf 2012a, 2012b). The Oahu Elepaio is a flexible, adaptable species that preys on a variety of native and nonnative invertebrates and can use forests composed of nonnative plant species (VanderWerf 2018). Moreover, the plasticity of the Oahu Elepaio breeding season and similar nesting success at different times of year indicate that changes in seasonal rainfall patterns are unlikely to reduce its reproduction.

Acknowledgments

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