

SOCIAL LEARNING AND FORAGING PROFICIENCY OF PALILA (*LOXIOIDES BAILLEUI*) IN  
AN AVIARY SETTING

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**Abstract**

The Palila (*Loxioides bailleui*) is a critically endangered Hawaiian bird that relies on the unripe pods of Māmane (*Sophora chrysophylla*). Previous authors have shown that aviary-raised Palila drill directly into the seeds, while wild Palila peel the entire pod, and that after relocation within a wild population about one out of three aviary-raised birds begin to peel pods. In summer 2017, six aviary raised after second-year (ASY) adult birds were offered partially peeled pods to train them to fully peel pods. Tear lengths and other pod measurements were collected in 2017 and 2018. These were compared to other aviary-raised adults, second-year (SY) aviary-raised Palila, and a captive pair known to peel pods. While the training attempt was not successful, it was found that most birds can produce long tears even if the average tear length is low, and that ASY adults were far more proficient than SY adults. Depending on which measurement of foraging ability is used, females may be more proficient than males. Also, two birds that tended to create small tears survived the longest after the 2019 re-location to Pu'u Mali, a finding that has conservation implications. Some of the deaths of wild released birds were attributed to predatory birds, suggesting that predator avoidance training maybe more important for post-release survival than improving foraging proficiency.

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## Introduction

### Palila

Palila (*Loxioides bailleui*, formerly *Psittirostra bailleui*) is a Hawaiian honeycreeper finch (family Fringilidae). Though historically found in high elevation dry forests on Hawai'i Island, fossils from Barber's Point, O'ahu and Makauwahi Cave, Kaua'i show that Palila or ancestral *Loxioides* were once found throughout the islands even at sea level (Olsen and James 1982, James and Olsen 2006). The twentieth century saw the Palila's range shrink from being found on Hualālai, Maunaloa, and Maunakea in the early century (Perkins 1903) to only Maunakea at mid-century (Richards and Baldwin 1953), to around 90% of the population relegated to Pu'u Lā'au on the western slope at the century's end (Miller 1998). More recently the 2021 population estimate was 678, down from 1,312 in 2020 and 5,953 in 1998 (an 89% decline over 23 years, Genz et al. 2022). This last population is confined to a dry area (98 out of 132 months from 2000 to 2010 had drought conditions, Banko et al. 2013) which makes its persistence especially questionable. Invasive grasses fuel fire and prevent native trees from being reestablished, making it difficult to break the grass-fire cycle (Warneke et al. 2023). Burnt soil also has less nutrients and water retention, which hampers germination (Cordell et al. 2019).

It is difficult to overstate the close relationship between the Palila and the Māmane tree (*Sophora chrysophylla*). Populations are denser in pure Māmane forest than in mixed forest, and even in mixed forest the birds spend more time in Māmane, perhaps because the closed canopy of mature *S. chrysophylla* shelters them from birds of prey. They nearly always choose to nest in mature Māmane (Miller 1998). In a foraging study in mixed woodland more Māmane flowers than pods are eaten, though more time was spent eating pods in both forests (Miller 1998). The seeds and leaves of native understory plants are also taken and could serve as famine food during droughts (Hess et al. 2014). The Palila is a specialist forager with its diet consisting nearly entirely of Māmane seeds (Banko et al. 2013) which may put them at greater

risk of population decline than generalist foragers (Banko et al. 2013). Banko et al. (2013) stress that the dwindling *L. bailleui* population can persist or even recover if the Māmane forest can be sufficiently expanded. Restoration has been underway since the 1980s via fencing (to exclude sheep and goats) and outplanting of Māmane seedlings (Conrad 1988). Though *S. chrysophylla* is slow growing, tree-ring dating suggests that “degraded *S. chrysophylla* forests can potentially be restored within only a few decades” (Francisco et al. 2015).

Population growth can be limited by a male-skewed sex ratio, as only females produce young. A catch and release study by Lindsey et. al. (1995) reported that in adult Palila females are outnumbered by males (36.3% females and 67.7% males), possibly from predation while incubating eggs. This is probably a limiting factor for population growth and may explain the presence of “helper males” at four out of eight nests observed by Miller (1998); for instance, a male helped feeding nestlings after the female was killed by a feral cat. Cats, mongoose, and rats are non-native predators of Palila and are targeted by predator control (Bisher 2020). Snetsinger et. al (1994) has proposed that the native owl (Pueo, *Asio flammeus sandwichensis*) on Maunakea mainly prey on birds because rats are less common there compared to lower elevations. Obviously, this species interaction complicates Palila conservation.

Miller (1998) also observed fledgling Palila learning to forage. Early on juveniles eat Naio (*Myoporum sandwicense*) berries and Māmane (*S. chrysophylla*) flowers. They may perch beside an adult tearing apart a green pod, observing and occasionally taking a seed from its pod (personal observation). As their bill darkens and grows stronger, they begin to eat unripe Māmane seed pods, picking out shorter pods than adults, with an average 2.22 expanded seeds per pod for after second-year (ASY) birds compared to 1.27 for hatch year (HY) birds, (Miller 1998). As juveniles progress, they spend less time watching and soliciting other birds for food, and more time foraging on their own. Māmane flowers may be plucked from the tree and carried to a perch and dissected for their nectar and pollen while the petals are discarded,

perhaps a kind of practice for the more difficult pods. Hess et al (2014) also describes Palila carrying Naio fruits to perches where the pulp is then eaten, and the seed thrown away. Males tend to provide more care to fledglings, giving females a chance to reneest. A juvenile may also follow and watch more experienced juveniles, suggesting that an adult tutor may not be strictly necessary and that naïve birds can sharpen their skills together (Miller 1998).

Through Keauhou Bird Conservation Center's (KBCC) captive breeding program it was found that aviary-raised Palila are naturally drawn to unripe *S. chrysophylla* pods. While following their parents, helpers, and peers to beg for food, wild juveniles observe experienced birds rip or peel the pod's outer wall to expose the soft seeds and copy this technique (Miller 1998). Aviary raised Palila have taught themselves to chew directly into each seed. One could compare these two foraging techniques to peeling a banana and eating corn on the cob, respectively. Frayne (2007) refers to these foraging modes as "ripping" and "attacking". At the time of his work, KBCC Palila "almost exclusively" used the attacking technique. Once relocated to aviaries at Pu'u Mali (on the North slope of Maunakea, where birds were held temporarily prior to release into the wild) 29% of KBCC birds combined the two modes. This was either due to trial and error in a new environment where *S. chrysophylla* pods were a stable food, or from directly observing wild Palila at Pu'u Mali. Frayne (2007) notes that aviary raised birds never fully abandoned the attacking mode, though combining the two techniques reduced the time spend per seed eaten.

### **Social Learning**

Palila exhibit behaviors that suggest social learning. Firstly, fledgling Palila follow their parents and peers throughout their juvenile phase. Juveniles are more likely to be seen sharing a tree with another Palila than adults, 36% of observations for juveniles compared to 25% for adults (Miller 1998). Secondly, Palila are occasionally seen as helpers around the nests of other Palila breeding pairs. About 92% of these helpers are ASY males. (Miller 1998). An explanation

for the existence of these helpers is a male-skewed population in a monogamous bird. In addition to giving an opportunity to replace the male should he die, “a helper could gain experience in providing care” to his own future nests (Miller 1998). This together with Miller’s (1998) observations of fledglings following other Palila and becoming more skilled foragers, along with Frayne’s (2007) findings that aviary raised Palila took on some wild-type pod opening techniques after being transferred to a wild Palila population, suggest that Palila are social learners. The possibility that after second year (ASY) males could gain experience in nest care by acting as helpers would suggest that adults can learn as well. Another instance of social learning are Blue Tits (*Cyanistes caeruleus*) learning to open milk bottles to sip the cream (Fisher and Hinde 1949). Aplin et al. (2013) tested the social learning ability with waxworms in a container with a foil cap. Innovative Blue Tits learned to either pierce or peel of the foil (which mirrors the Māmane harvesting methods identified by Frayne (2007)). About 50% of naive birds provided with an innovator learned to open the lids, while none of the control birds (lacking such a demonstrator) did, which suggests that social learning is important for transferring this skill between birds. Aplin et al. (2013) also note that juvenile females be more likely to learn than adult females, though this wasn’t the case for juvenile males regarding adult males. This suggests that there is a critical learning period for Blue Tits. Social learning has also been induced experimentally. Aviary Blue Tits and Great Tits (*Parus major*) can learn to avoid packets of bitter food (marked with a conspicuous square) over packets of palatable food (cryptic cross) through a video demonstration (Hamalainen et al. 2020). Likewise, Zebra Finches (*Taeniopygia guttata*) copy video demonstrators that choose a specific-colored feeder or nest material (Guillette and Healy, 2017 and 2019).

Foraging skill can also improve through simple trial and error. For instance, Fox (2015) observed 19 banded adult and juvenile Bullfinches (*Pyrrula pyrrula*, a small songbird that forages mainly on leaves, flowers, and seeds, much like the Palila) husk sunflowers seeds in

rural Jutland over 75 days. Through the 330 observations taken between August and November, Fox found that all birds improved their de-husking technique over the season. For juvenile finches this improvement was more drastic for those that started as the least skillful huskers (from 4.8 to 8.3 seeds/minute, vs 6.5 to 9.1 for adults). Here, there was no difference in male and female foraging proficiency. Fox (2015) suggests that these first summer Bullfinches are more likely to drop seeds than adults, leading to the lower initial proficiency. It appears that these improvements came from trial and error rather than birds learning from each other. Fox (2015) points out that Kestrels frequent the area, possibly making slow eaters likely targets.

The purpose of my work with KBCC's Pallia birds was to further characterize their foraging abilities. I did this by following up on Frayne's (2007) study on aviary-raised birds to see if providing some with partially opened green *S. chrysophylla* pods could shift their foraging mode. This would be an example of artificial social learning. The hypotheses for this study were:

**Hypothesis 1:** Wild taught Palila will have a greater percentage of pod torn and fraction of seeds eaten than aviary taught Palila, as well as shorter feeding times.

**Rationale:** Frayne (2007) found that wild Palila at Pu'u Lā'au have shorter feeding times and produce longer tears than Palila at KBCC.

**Hypothesis 2:** Aviary-raised Palila will differ in percent pod torn, fraction seeds eaten, and feeding time, by sex (male or female) and by age (higher identification numbers are younger birds).

**Rationale:** Miller (1998) found that fledgling Palila at Pu'u Mali are slower eaters than adults.

**Hypothesis 3:** Individual aviary-raised birds will increase the percent pod torn and fraction of seeds eaten, and have shorter feeding times, after interactions observing wild birds than before observing wild birds.

**Rationale:** Frayne (2007) found that KBCC Palila released at Pu'u Lā'au reduced their feeding times, presumably after observing wild Palila.

**Hypothesis 4:** Individual aviary-raised birds taught experimentally by people to tear pods will have increased percent pod torn and fraction seeds eaten, and reduced feeding times, than birds that are simply self-taught.

**Rational:** Aplin et al. (2013) successfully taught Blue Tits (*Cyanistes caeruleus*) to open containers of waxworms, showing that birds can be given new foraging techniques experimentally by people.

## Methods

### Study Location

Apart from Palila, species raised at KBCC include 'Alalā (*Corvus hawaiiensis*) (Flanagan et. al. 2023), and 'Akikiki (*Oreomystis bairdi*) (Flanagan et. al. 2024). In their study of aviary raised 'Akikiki, Flanagan et. al. (2024) describes the KBCC aviaries as having a size from approximately 2.4 m by 2.4 m by 2.3 m to 6.0 m by 3.0 m by 3.0 m., made of predator-resistant wire mesh and mosquito netting, with live, native flora growing in different levels (such as an undergrowth and canopy), with provide perches and cover. (Flanagan et. al. 2024). Near Kilauea's summit, KBCC is at a relatively high elevation, chilly in winter and hot in summer (personal observation).

### From June-August 2017

**Relevant Birds:** The three treatment pairs were identified, and included Pa 96 (male)/Pa 125 (female), Pa 85 (male)/Pa 132 (female), and Pa 122 (male)/Pa 136 (female). The two control pairs were Pa 98 (male)/Pa 124, and Pa 110 (male)/Pa 141 (female). The oldest bird is Pa 85 (hatched May 2008), the youngest was Pa 141 (hatched August 2015). Pa 122, Pa 124, and Pa

125 are siblings, all hatched August 2014 and sired by Pa 83. A few of Pa 83 and Pa 114's spent pods were photographed to be sure they were peeling the pods. A list of all birds that were a part of the study is included (**Table 1**).

As part of testing both Hypothesis 1 (here comparing the foraging of Palila males vs females) and Hypothesis 4 (testing the efficacy of artificial social learning in Palila) between June 19 and August 16, 2017, I offered sliced green Māmane pods to the three treatment Palila pairs. Frozen pods were defrosted, their length measured, and seeds counted. A slice was made lengthwise with scissors prior to provisioning, always starting at the end opposite the stem and cutting towards stem. The slice's length was measured. Initially (June 19-July 3, 2017) only seeds were counted, and no measurements were taken. From July 4 onward pod and slice lengths were measured and were photographed with a ruler. About 40-50% of the pod length was sliced, starting at the end furthest from the stem (**Figure 1**). Food pans were removed immediately before each Māmane provision session so the birds could focus on the pods and returned at the end. In the wild, nearly the entire Palila diet consists of Māmane seeds (Banko et al. 2013), so providing only Māmane during each session was suitable for sustenance. The sessions were usually around an hour per aviary, and observations were taken between 8 am and 2 pm. There was no order for which pairs were observed first or last. Feeding times were measured on a stopwatch. Issues that complicated these sessions were:

- 1) Observing two birds with one timer: if one bird began a pod while the other was already being timed, that pod was either not counted, or a "lap" was set on the stopwatch.
- 2) Dense foliage obscuring the bird or catching the pod: cut branches provided by KBCC staff give the birds security and enrichment (Palila need leaves and wood to work their bill on) however this occasionally hampered observations. In addition, pods caught in high branches could not be collected.

- 3) Sharing or stealing between birds: as noted earlier wild juveniles may perch beside an experienced bird eating and take a seed, gaining both technique and food. In the aviaries entire pods were often shared between birds. Frequently a bird would perch next to its feeding aviary mate and attempt to take away its pod. The feeding bird would either allow this or take the pod to another perch. In this context, it cuts feeding time short and makes the pod itself unusable for analysis.
- 4) Scavenging of eaten pods: often a bird would take an eaten pod off the ground or from a branch and add new tears to it. As with pod sharing, this benefits the birds (eaten pods often had seeds remaining and were likely easier to harvest) but scavenged pods were unsuitable for measuring as there was no way to tell which bird made a particular tear.

While the focus was on the three pairs named earlier, two additional pairs were occasionally observed eating whole, unsliced pods. These were Pa 110 (M) and Pa 141 (F) (aviary 13), and Pa 110 (M) and Pa 141 (F) (aviary 9). They were observed on June 26<sup>th</sup>, 28<sup>th</sup>, and 29<sup>th</sup>, and July 11<sup>th</sup> and 12<sup>th</sup>, and were considered the “control birds” to the six “treatment birds”. One pair absent from 2017 sessions was Pa 83 (M) and Pa 114 (F). They were brooding in summer 2017 and could not be disturbed, as one goal of KBCC is to create new birds to supplement threatened wild populations. However, on June 14<sup>th</sup> I was able to observe them feed and collect their spend pods, showing that in 2017 they were both using the ripping mode.

On August 17<sup>th</sup> and 18<sup>th</sup> 2017 the six treatment birds were given whole unsliced pods. Their lengths and seed counts were also recorded before the session. Some pods from throughout the summer were saved in labeled plastic bags and frozen for later. Between June 20 and August 18 2017, around 480 usable feeding times were recorded, about 300 of which have measured pods attached to them (meaning that seconds per seed eaten can be gauged from them).

**From March-April 2018**

**Relevant Birds:** The treatment pair that was followed up on in 2018 was Pa 85 (male)/Pa 136 (female) and control bird Pa 110 was also followed up. “Wild” pair Pa 83 (male, captured from the wild and brought to KBCC in 2007 as an ASY bird)/Pa 114 (female, paired with Pa 83 in 2016) were first directly observed. In 2017, a few spent pods were also collected from them, showing that they were peeling pods then. However, they were brooding that year, and a more detailed study took place a year later.

To continue to test Hypothesis 1 (foraging of the “wild pair” compared to the both KBCC Palila), in March 2018 I returned to KBCC to offer the aviary Palila whole pods to gauge their proficiency after nearly one year. Between March 21 and April 16, I collected 404 pods from five birds. These included treatment birds Pa 85 (male) and Pa 136 (female), and control bird Pa 110 (male), also wild male Pa 83 and his mate since 2016, Pa 114. Forty-four feeding times were also taken from these birds (except Pa 110), unfortunately these times are divorced from their respective pods and 2018 does not include seconds per seed eaten. As in 2017, these pods were frozen for later measurement.

### **From February-May 2019**

**Relevant Birds:** Four second-year (SY) adult birds were observed this year (Pa 144, Pa 145, Pa 146, and Pa 147, hatched in 2018). Birds videotaped were in 2019 were Pa 83 (male, wild)/Pa 136 (female, 2017 treatment), Pa 85 (male, 2017 treatment)/Pa 114 (female, wild), Pa 98 (male, 2017 control)/Pa 125 (female, 2017 treatment), Pa 96 (male, 2017 treatment)/Pa 124 (female, 2017 control), Pa 122 (male, 2017 treatment)/Pa 141 (female, 2017 control). Pa 110 (male, 2017 control) was videotaped eating pods, but is aviary mate Pa 132 (female, 2017 treatment) was not seen eating pods. A previously unobserved bird (Pa 112, aviary raised male) was videotaped but his aviary mate (Pa 133, aviary raised female) was not.

To continue testing Hypothesis 1 (differences between the wild-taught pair and the aviary-taught birds), Hypothesis 2 (differences between males and females, and SY birds and ASY birds), and Hypothesis 4 (the progress of the treatment birds), and to begin testing Hypothesis 3 (if birds change after interacting with the wild-taught pair), I returned to KBCC in February 2019. Between February 21 and April 15, I collected 112 feeding times from 12 birds, including all 2017 treatment and control birds (excluding Pa 132, who would not eat Māmane pods during my observations), wild male Pa 83 and his 2016-2019 mate Pa 114 (at this time they had been repaired to male Pa 85 and female Pa 136), and a previously unobserved male Pa 112. Between April 23 and May 2, 2019, I visited the soft release aviaries at Pu'u Mali. Here, I measured 41 times from six birds at three release aviaries; in Aviary 1 were Pa 96 (2017 treatment male) and Pa 124 (2017 control female), in Aviary 2 were Pa 122 (2017 treatment male) and Pa 141 (2017 control female), and finally in Aviary 3 were Pa 98 (2017 control male) and Pa 125 (2017 treatment female). Though I left Pu'u Mali on May 2, 2019, Bischer (2020) describes the outcome of this release attempt, though using different Palila identification numbers than used here.

The only pod measurements of 2019 were from Pa 110 (who was paired with Pa 132, the bird which would not eat pods during my observations) and four young birds hatched in 2018 (Pa 144, Pa 145, Pa 146, and Pa 147). The inclusion of these four was serendipitous; an unplanned opportunity to compare aviary-raised SY adults to older aviary raised ASY adults (2017 control female Pa 141 was hatched on August 20, 2015, 2017 treatment male Pa 85 on May 14 2008; these two are the youngest and oldest ASY adult aviary-raised birds). In 2019 I also recorded 28 videos of Palila feeding, 26 of which focus on 1 bird, while two videos include 2 birds. Most of these videos were recorded on March 20, 22, 25, 26, and April 15. These give 29 videotaped feeding times.

### **Post Observation Measurements and Statistical Analysis**

Measurements were taken from preserved frozen spent pods, and in the case of 2017 from photos of spent pods placed near a ruler. Pod and tear lengths were measured in centimeters, and total expanded and eaten expanded seeds were counted. Dividing the sum of each pod's tears by pod length gives a percent pod torn (PPT). For the 2017 treatment bird's pods, the length of the cut is subtracted from total pod length to give usable pod length, and tears made on the cut portion were not measured. Dividing expanded seeds eaten by total expanded seeds gives fraction seeds eaten (FSE). As with pod length, for the 2017 treatment birds expanded seeds within the cut were not counted. When feeding time (seconds) and seeds eaten could be linked to one pod, seconds/seeds eaten (or seconds per seed, SPS) can be found. Descriptive statistics for tear length, PPT, FSE, overall feeding time, and SPS were calculated and two-sample t tests assuming unequal variances were used to compare differences between different groups of birds (Pa 83 and Pa 114 vs all other adults, males vs females, 2017 treatment birds vs 2017 control birds, SY adults vs older ASY adults) and between individual birds. A two-sample t test was used to compare overall feeding times between males with females, and to compare Pa 83 and Pa 114 with the other adults (RStudio Team 2020).

As mentioned earlier, the pods from the four second year (SY) birds were in one group (SY). A t test requires that each group includes at least two values. In order to compare the second year (SY) adults to the after second year (ASY) adults through a t test, SY measurements were separated into February 2019 and March 2019. For good measure, when SY birds were used in tests comparing males to females or wild-taught to aviary taught, two t tests were used for each comparison (one using total SY measurements and one using the two monthly measurements) (**Table 2**).

## Results

### Hypothesis 1: Wild Pair (Pa 83 and Pa 114) vs Other Birds

The “wild” pair is composed of wild born male Pa 83, (brought to KBCC in 2007 as an ASY adult, meaning he learned to peel pods from his wild peers as described by Miller 1998) and aviary born female Pa 114 (paired with Pa 83 in 2016, and by June 14, 2017, she was peeling pods). The wild-taught female (Pa 114) made some of the longest tear lengths measured (**Figure 2**), her percent pod torn measurements tended to be higher than other birds (**Figure 3**), and nearly all her collected pods were fully harvested based on the fraction of seeds eaten (**Figure 4**).

The wild taught pair had a mean PPT of 61.87% and a mean FSE of 0.87 while the means of the other birds were ~44% and 0.72 for PPT and FSE respectively (**Table 2**). When the means of the wild-taught pair’s (wild-born male Pa 83 and aviary-born female Pa 114) PPT and FSE were tested against the means of all other birds, there was no significant difference. This was true whether all measurements of the four youngest birds were tested together ( $t=-1.4$ ,  $df=1$ ,  $p=0.39$  for PPT,  $t=-1.8$ ,  $df=1$ ,  $p=0.31$  for FSE) or if their measurements were separated into February and March 2019 ( $t=-1.5$ ,  $df=1$ ,  $p=0.38$  for PPT,  $t=-1.9$ ,  $df=1$ ,  $p=0.31$  for FSE) (**Table 2**). Likewise, there was no significant difference between the feeding times of the wild taught and aviary taught birds ( $t=-0.6$ ,  $df=3$ ,  $p=0.62$ ) (**Table 2**).

### **Hypotheses 2, Part 1: Males vs Females**

When the mean PPTs and FSEs of the males and females compared, the SY birds are presumed male. When the SY adults are as one mean, the difference is not significant ( $t=0.5$ ,  $df=9$ ,  $p=0.6$  for PPT,  $t=-0.2$ ,  $df=8$ ,  $p=0.84$  for FSE) (**Table 2**), nor is there a significant difference when the SY adults are as two means ( $t=0.8$ ,  $df=9$ ,  $p=0.46$  for PPT,  $t=-0.1$ ,  $df=8$ ,  $p=0.94$  for FSE) (**Table 2**). The overall female means are 48.69% and 0.73 for PPT and FSE respectively (**Table 2**). For males the means for PPT are 45.19% and 43.56% (for the four young birds as one or two means respectively) and the mean FSE is 0.74 (**Table 2**).

### **Hypothesis 2, Part 2: Second-Year (SY) Adults vs After Second-Year (ASY) Adults**

By dividing the SY adults PPT and FSE into February and March 2019, we have two means to compare to the older ASY birds. Though not actually significantly different from the ASY birds, they are approaching significance ( $t=3.4$ ,  $df=2$ ,  $p=0.08$  for PPT,  $t=2.4$ ,  $df=4$ ,  $p=0.07$  for FSE) (**Table 2**). With two means, the mean PPT is 27.51% and mean FSE is 0.66 (close to the original means of 27.77% and 0.65) (**Table 2**).

### **Hypothesis 3: Before vs After Interacting with Wild Pair (Pa 83 and Pa114)**

In February 2019 the 2017 taught male, Pa 85, was placed with the wild-born male's partner of three years, aviary-born female Pa 114, while 2017 taught female Pa 136 was placed with the wild-born male, Pa 83. Pa 85 and Pa 136's 2019 pod measurements are exclusively as feeding times and fraction seeds eaten, with the FSE derived from a few videos. Pa 85's mean FSE did raise by nearly 0.2 between 2018 and 2019 (0.75 to 0.94 for 2018 and 2019 respectively), while Pa 136's rose slightly (means 0.83 in 2018 to 0.87 in 2019) (**Table 3**). However there was no significant difference in mean feeding times and FSE for Pa 85 and Pa 136 between 2018 and 2019 (**Table 4**). The insignificant difference in mean feeding times is in spite of Pa 136's mean feeding time in 2019 being nearly 150 seconds shorter than her 2018 feeding time (362.8 seconds in 2018 vs 213.9 seconds in 2019) (**Table 5**) (**Figure 5**). As the 2019 FSE are based on videos rather than measured pods, the comparison is not as strong as those for feeding time or for Hypotheses 1 and 2 (which is based on measured pods).

In the few videos of male Pa 85 (2 videos) and female Pa 136 (3 videos), Pa 85 appears to have used the ripping mode (peeling pods) on two out of two pods, while Pa 136 seems to have used the attacking mode (drilling seeds individually) on three out of three pods. Their new aviary mates, the wild-taught pair male Pa 83 and female Pa 114, appeared to use the ripping mode on 7 out of 8 and 4 out of 4 pods respectively. Based on the better sample size of

recorded feeding times, it seems that 2017 taught female Pa 136 individually improved her seconds per seeds eaten from 2018 to 2019 (362.8 s in 2018 to 213.9 s in 2019) (**Table 5**). Also based on total observations, taught male Pa 85 individually appeared to improve fraction seeds eaten in 2018 (Pa 85 went from 0.75 in 2018 to 0.94 to 2019) (**Table 3**).

#### **Hypothesis 4: Taught Birds Progress over 2017, and 2017 vs 2018**

The monthly mean tear lengths from 2017 (as well as the mean tear lengths from the last day of the 2017 observations) went up and down through the summer of 2017 (**Table 6**). When mean daily tear lengths are used to track tear lengths over the summer of 2017, there is no significant increase in tear length for any of the five taught birds (treatment female Pa 132 made only a few tears that summer), if anything taught male Pa 85's mean daily tear length significantly decreased (R-squared=0.466) (**Figure 6**) (**Table 7**).

Percent pod torn also tends to swing up and down from month to month (**Table 8**) and plotting average PPT overtime shows that 4/5 birds decreased their percentage, two significantly (R-squared=0.157 and 0.297 for males Pa 85 and Pa 96 respectively) (**Table 7**). Though female Pa 136's PPT did increase (**Figure 7**), this was very slight ( $p=0.62$ , R-squared=0.01) (**Table 7**). Unlike tear lengths and PPTs, three taught birds did significantly increase mean daily fraction seeds eaten, males Pa 122 and Pa 85 ( $p=0.001$  and R-squared=0.414,  $p=0.016$  and 0.195 respectively) and female Pa 136 ( $p=0.012$ , R-squared=0.226) (**Figure 8**) (**Table 8**).

Seconds per seed eaten is different than tear length, percent pod torn, and fraction seeds eaten as a decrease in seconds per seed eaten suggests improved foraging efficiency. Though a few birds monthly SPS swings up and down (Table of 2017 SPS), the overall trend for three birds (males Pa 122 and Pa 85, and female Pa 125) is downwards (**Figure 9**), and for Pa 85 this is significant ( $p=0.009$ , R-squared=0.296) (**Table 7**). Overall, most of the taught birds

had similar ranges of SPS as the four control birds (**Figure 10**), except for taught female Pa 132 who gave only two very different SPS in 2017. This is why she was excluded from the regression tests.

Comparing the monthly mean pod measurements from 2017 and 2018 of taught male and female Pa 85 and Pa 136 (**Table 9**) yielded no significant difference between the two years on any of the four types of pod measurements, with percent pod torn being the closest to significant ( $t=1.9$ ,  $df=8$ ,  $p=0.16$ ) (**Table 10**). Likewise, there is no significant difference between the untaught bird's (male Pa 110) 2017 and 2018 measurements.

### **Discussion:**

The purpose of this study was to understand how aviary Palila learn to remove unripe Māmane seeds, through social learning (either through observing other birds, or with some artificial assistance), or autodidactically (through trial and error without outside help). Examples of social learning in Palila come from Miller (1998) who followed fledgling wild Palila as they learned from adults and older peers, and Frayne (2007) who measured improved foraging proficiency of reintroduced aviary Palila when they observed wild birds. Artificial social learning has succeeded in other birds. For instance, Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*) have learned to distinguish palatable and bitter food through videos of other birds (Hamalainen et al. 2020), Savannah Sparrows (*Passerculus sandwichensis*) have adopted new songs from loudspeakers (Mennill et al. 2018), and Zebra Finches (*Taeniopygia guttata*) have preferred the color of nest material picked by a video demonstrator (Guillette and Healy 2019). In contrast, trial and error learning seems to be the main explanation for Fox's (2015) Bullfinches improving their sunflower seeds eaten per minute. Fox (2015) notes that juvenile bullfinches have a higher rate of improvement than adults, though they started off less proficient than adults at the start of the study, and never quite reached the adults' final state of foraging proficiency (Fox 2015).

The first hypothesis was that the two wild-taught birds would have different pod measurements (and so foraging proficiency) than the other Palila at KBCC. These wild-taught birds are male Pa 83, who was raised in the wild and brought to KBCC as a ASY adult in 2007, and Pa 114, an aviary-raised female paired with Pa 83 in 2016. From a handful of their spent pods collected in June 2017, I judged that both were making long tears. However, though the two wild taught birds did create a few particularly long tears and appeared more likely to finish their pods, comparing their yearly mean measurements revealed no significant difference for tear length, percent pod torn, fraction seeds eaten, or feeding time. This is despite the relatively inept second-year (SY) birds being included. While this is inconsistent with Frayne's (2007) work comparing wild Palila at Pu'u Lā'au to KBCC raised Palila, Frayne (2007) was able to include more than two wild birds. Though the wild birds here provided dozens of pods for study, it was not appropriate to inflate the observations from only two individuals, hence yearly means were compared. The first hypothesis was not supported.

The second hypothesis was that comparing some other traits among KBCC Palila would reveal a difference between them. The two traits chosen were sex and age, divided into males vs females and SY birds vs ASY birds. The SY birds' pods were collected from the aviary floor in early 2019 by KBCC staff and grouped together as a class of bird (this was also done with the paired ASY birds; however, this was a mistake and those other 2019 pods had to be excluded from the study as they could not be linked to one individual ASY bird). A significant difference was found when comparing the SY adults with ASY adults. The tear lengths from the SY Palila were significantly shorter. Though percent pod torn, and tear length did not meet the threshold for significance, they are closer to significant than any of the differences between the wild-taught and aviary-taught Palila. This is consistent with Miller's (1998) observations that younger birds are less proficient than their older counterparts.

However, there was no significant difference between males and females on any pod measurements. While Miller (1998) did find that juvenile males are somewhat faster eaters than their female peers, for instance handling pods at a faster rate (1.09 pods per 100 seconds vs 0.95 pods per 100 seconds), and interacting with more pods per 100 seconds, this difference was probably not significant. Like Frayne (2007), Miller (1998) had more than two wild birds observed. The lack of significant between the male's and female's pod measurements would run counter to Aplin et al. (2013), who did find that female Blue Tits are more likely than males to acquire the skill to open milk bottles through social learning, with juvenile females being twice as likely as adult females to do so. Miller (1998) notes that in the wild the male Palila tends to teach the fledglings foraging skills to give the female an opportunity to re-nest. It could be plausible that some aviary-raised female Palila have spent time that would otherwise be used to nest to improve their foraging skills, putting their skills on par with aviary-raised males. The second hypothesis was only supported when comparing SY birds to ASY birds, at least for tear length. Comparing males and females did not support the second hypothesis.

The third hypothesis was that aviary birds given an opportunity to observe the wild pair forage will become more proficient. Re-pairing with a wild bird should give an opportunity not just to observe, but also access to spent or partially eaten pods (as in an aviary Palila often pick old pods from the ground or even take them from another bird mid foraging). In early 2019, the wild pair were separated and re-paired with aviary birds which favor the attack mode (2017 taught male and female Pa 85 and Pa 136). Unfortunately, in 2019 I asked KBCC staff to collect all spent pods from the aviaries to increase sample size. I forgot that this would make it impossible to tell which of the two birds in an aviary a pod belonged to. This is why the only 2019 pods come from the SY birds (4 birds in the same age group) and 2017 untaught control male Pa 110 (who was housed with 2017 taught female Pa 132, a bird which did not eat any pods when I tried to observe her), but there are also a few videos from 2019 of Palila foraging. From

this small sample size, 2017 taught female Pa 136 seems to have used the attacking mode on three out of three pods, and 2017 taught male Pa 85 on zero out of two (meaning the ripping mode on both). Feeding times were successfully gathered in 2019, and fraction seeds eaten was tentatively calculated from the few feeding videos. However, comparing the mean feeding times and fraction seeds eaten of these two taught birds (male Pa 85 and female Pa 136) showed no significant difference, so the third hypothesis was not supported. The two birds used to test hypothesis four were fully fledged adults. Pa 85 was hatched in 2008 and Pa 136 in 2015. They would have been 11 and 4 years old respectively in 2019 when they were reassigned to the wild-taught pair. Pa 114 was hatched in 2013 and would have been three years old when paired with Pa 83. Aplin et. al (2013) notes that juvenile female Blue Tits learned the bottle faster than adult females, though this relationship was not found in males. It is possible that Pa 85 and Pa 136 would have been too old to readily learn new foraging techniques in 2019, and that Pa 114 was just old enough in 2016. ASY males (at youngest three years old) have been observed helping at nests that are not their own, likely gaining experience in caring for their own future nests (Miller 1998). This would suggest that ASY Palila (minimum three years old) are capable of picking up new skills, much as adult bullfinches are capable of learning to shell sunflower seeds faster, though less rapidly than juveniles (Fox 2015).

The fourth and last hypothesis was that my version of social learning, offering pods to simulate a pod partially harvested with the ripping mode, would influence proficiency. Though experimental social learning has shown promise in other birds, such as Zebra Finches (Guillette and Healy 2019) and Blue Tits (Hamalainen et. al. 2020), these studies used video demonstrations instead of partially opened food items. Within 2017, only two measures of foraging proficiency saw improvement. These are fraction seeds eaten (for Pa 136 and Pa 85 only) increasing, suggesting that pods were being more completely eaten, and seconds per seed eaten (for Pa 85 only) decreasing, implying that pods are being harvested more

completely. However, both Pa 85's mean tear length and percent pod torn significantly decreased over 2017. From these four changes, we could infer that he was making shorter tears, while also more completely harvesting the pod more quickly. Pa 85 and Pa 136's increase in FSE does not seem to carry over to 2018, as there was no significant difference between 2017 and 2018 FSE, or for tear length, percent pod torn, and feeding time. The untaught control bird (male Pa 110) was also similar between years on these same measurements. Based on this Hypothesis 4 was not supported.

The Palila appears to be a social learner in the wild. Miller (1998) writes that "there was evidence of learning" as juvenile Palila followed adults foraging, and that "juvenile Palila were found to be somewhat more social than adult birds". Juveniles were sharing a tree with another bird in 36% of observations, compared to 25% of observations for adults (Miller 1998). Some adult Palila were seen as "helpers" around the nests of other Palila. These helpers were generally ASY males, likely unable to start their own nest due to a male-skewed population. Miller (1998) suggests that helpers could gain experience in the care of their own future nests, which would mean that adult Palila are capable of learning, rather than juveniles alone being able to learn.

The main objective was to shift their foraging mode from drilling holes above the seeds ("attacking") to ripping the pod ("ripping"), which would manifest as longer tear lengths and higher PPT. From 2019, we do have a few videos of the taught treatment and untaught control birds. From this small sample size, we have wild-born male Pa 83 and 2017 taught female Pa 125 using exclusively the ripping mode (sample size two and three respectively), 2017 taught male Pa 96 using the ripping mode on one pod and the attacking mode on two, and 2017 taught male and female Pa 122 and Pa 136 using exclusively the attacking mode (sample size one and three respectively). However, this is a very small sample size and the pods were not collected afterwards, so they have less weight than the 2018 spent pods. Based on comparing 2018 and

2017, as well as the trends within 2017, the attempt to change foraging mode was unsuccessful. Aplin et al. (2013) did successfully train 8 Blue Tits to open the lids of containers holding a waxworm (to use these 8 as demonstrators to study social learning). However, their training used multiple steps. First, the trainees were given a solved puzzle. They were then given increasingly difficult versions of the enclosed waxworm puzzle until the birds could complete the task each time. For Aplin et al. (2013) this took between 3-6 hours per bird. This “step progression method” which started with a solved puzzle was more successful than my offering of a half-solved puzzle (a half-sliced pod). KBCC Palila were only denied non-Māmane food during the training, while the Blue Tits in Aplin et al. (2013) were denied food up to one hour before training, which may have increased hunger and interest in the puzzle. Palila are critically endangered, and one goal of KBCC is to produce endangered birds to supplement struggling wild populations. When working with critically endangered animals, it is often not desirable to conduct “experiments”. As a result, and out of an abundance of caution, food pans were not removed during the 2018 and 2019 observations in order to allow full provisions of all food items. Similarly, this is also why all food items were not removed nor food denied prior to training.

There are several ways this work could have been improved. The sample sizes for some of the 2017 birds is quite low (all 4 control birds, and two treatment females, Pa 125 and Pa 132, which provided 22 and 3 tears respectively), which undermines statistical significance. This was due to the limited number of birds in captivity. Low sample sizes for 2017 untaught control birds (males Pa 110 and Pa 98, females Pa 124 and Pa 141) mean that the absence of outliers for Pa 110, Pa 124, and Pa 141 in 2017 is less noteworthy than the lack of outliers for untaught control male Pa 110 in 2018, the wild-taught male's female pupil Pa 114 in 2018, and taught female Pa 125 in 2017, as these birds had better sample sizes that year (wild-born male Pa 83 has three outliers, however the third quartile reaches 6 cm). Photos should have been taken of

the spent pods in each year, instead of just in 2017. Pods should have been collected right after the birds finished them, which could then have allowed seconds per seed eaten to be measured in each year, instead of just in 2017 (as seconds per seed eaten comes from dividing feeding time with seeds eaten). Videos of the birds foraging should have been taken each year instead of just in 2019. Being able to match videos with measured tear lengths, percent pod torn, fraction seeds eaten, and feeding times would have made these data much stronger. The 2018 follow ups should also have included taught treatment males Pa 122 and Pa 96, and taught treatment females Pa 125 and Pa 132, as well as untaught control male Pa 98 and control females Pa 141 and Pa 124, instead of just taught treatment males and females Pa 85 and Pa 136 and untaught control male Pa 110.

The reason for the attempt to improve aviary-raised Palila foraging proficiency was to increase survival after relocation and returning the birds to the wild. The idea was that the “ripping” mode is more time efficient than the “attacking” mode (based on Frayne’s 2007 study of these two modes) and therefore should improve survival. However, fraction seeds eaten is a better measure of how well Palila use their available resources. Māmane pod abundance fluctuates according to rainfall, with droughts contributing to the declining Palila population. Feeding time shows how time is used, and seconds per seed eaten show how both time and resources are used. Seeds eaten per unit time was also measured by Fox (2015), though in that case seed flower seeds eaten by bull finches was measured.

A test of this idea was the April-May 2019 release of KBCC aviary birds at Pu’u Mali. In my short time (April 23 to May 2, 2019) at Pu’u Mali, I saw six birds brought to the site. From my notes in Aviary 1 were Pa 96 (male, treatment, short median tear length) and Pa 124 (female, control, long median tear length), in Aviary 2 were Pa 122 (male, treatment, short median tear length) and Pa 141 (female, control, longest median tear length), and in Aviary 3 were Pa 98 (male, control, short median tear length) and Pa 125 (female, treatment, 3rd longest median

tear length). However, Bischer (2020) notes that 17 birds were brought to Pu'u Mali, and 9 were returned due to stress (leaving 8 that were released), and Bischer uses a new numbering system based on cohort number (G), aviary number (A), and sex (M or F). It was confirmed that "G1A1M" and "G1A1F" refer to Pa 96 and Pa 124 respectively (B. Masuda, pers. comm.) reflecting that the six birds I saw at Pu'u Mali were part of the first cohort (G1, the first brought to the site in 2019), and they were in aviary 1 (which housed male 2017 taught male Pa 96 and 2017 untaught female Pa 124). These two (G1A1M and G1A1F) are important as they were the longest surviving birds, lasting two months. Bischer writes that "we believe the cause of death for half of them was predation, mostly from native raptors" (non-native mammalian predators were meticulously trapped in the months preceding the release). Additional and follow-up assessments determined that at least two Palila released in 2019 appeared to have been predated by a raptor (B. Masuda, pers. comm.). Bischer (2020) also tells us that though supplemental feed was provided near the aviaries, the birds dispersed far from these aviaries, suggesting that lack of wild Māmane pods was not an issue at Pu'u Mali. This food abundance and predation likely mean that it does not matter which foraging mode a released bird happens to have, as 1) with adequate pods they will be able to make use of the attacking mode anyway, and 2) determining the value of and if necessary teaching predator avoidance may offer a better chance of survival than shifting foraging mode. However, predator avoidance training does not guarantee success. Vera Cortez et al. (2015) found that while 2 months of exposure to a taxidermized predator (in their case a Puma, *Puma concolor*) resulted in only 1 of 12 released Greater Rheas (*Rhea americana*) being killed by Pumas, all 12 were killed by other animals within 8 months. Greggor et. al. (2021) also used both a taxidermized Hawaiian Hawk ('Io, *Buteo solitarius*) and its recorded calls to encourage Hawaiian Crow ('Alalā, *Corvus hawaiiensis*) to avoid the raptor. While released 'Alala were seen showing defensive behaviors (including both fleeing from and confronting, or mobbing, Hawks), no less than 29% (8 out of 27) were lost to 'Io, including birds release some years earlier. Though better than the total lack of

survivors within a year seen by Bischer (2020) and Vera Cortez et al. (2015), these losses are still not sustainable. On O‘ahu, endangered Hawaiian Stilt (Ae‘o, *Himantopus mexicanus knudensi*) have been preyed upon by Pueo (Garcia-Heras et al. 2024). While native predators (such as Hawaiian raptors) can be detrimental to critically endangered native birds such as ‘Alalā and Palila, ‘Io and Pueo have immense cultural significance in Hawai‘i, meaning that “removal of native predators is unlikely to be appropriate” (Garcia-Heras et al 2024). A suggestion Greggor et al. (2021) offer is conditioning predators to avoid certain prey (usually attempted for large predators that endanger people and livestock, Snijders et al. 2019), as well as selecting release areas with fewer predators.

If experimental social learning in Palila were to be attempted again, it would be better to use video-taped demonstrators, as Hamalainen et. al. (2020) and Guillette and Healy (2019) did with other songbirds, rather than my unsuccessful attempt with sliced Māmane pods. My 2019 videos of Pa 125, Pa 83, and Pa 114 ripping pods (3, 7, and 4 videos respectively) might be put to good use here. While the Palila bird’s ability to harvest unripe Māmane seeds may be worth further study as an example of a novel foraging technique (comparable to the Blue Tit-milk bottle example, Aplin et al. 2013), we need to remember that unlike the Blue Tit, the Palila is critically endangered due to predation, loss of habitat, and the threat of wildfire. Addressing these issues must take priority.

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## Appendix

### Tables 1-10:

Table 1. List of relevant bird identification numbers, with corresponding sex and description of how they are relevant to the study.

Bird ID	Sex	Description
Pa 110	Male	2017 untaught (control) bird, also observed in 2018
Pa 112	Male	First observed in 2019 feeding times (see <b>Table 7</b> )
Pa 114	Female	Paired with wild male (Pa 83) from 2016-2019
Pa 122	Male	2017 taught (treatment) bird, sired by Pa 83
Pa 124	Female	2017 untaught (control) bird, sired by Pa 83
Pa 125	Female	2017 taught (treatment) bird, sired by Pa 83
Pa 132	Female	2017 taught (treatment) bird, produced very few spent pods and so excluded from analysis
Pa 136	Female	2017 taught (treatment) bird, also observed in 2018
Pa 141	Female	2017 untaught (control) bird
Pa 144 through Pa 147	Unsure, Maybe Male	Hatched 2018, observed in 2019 as SY adults
Pa 83	Male	Wild bird brought to KBCC as a ASY adult in 2007
Pa 85	Male	2017 taught (treatment) bird, also observed in 2018
Pa 96	Male	2017 taught (treatment) bird
Pa 98	Male	2017 untaught (control) bird

Table 2. Table of t tests comparing mean tear length, percent pod torn (PPT), fraction seeds eaten (FSE), and feeding time between males and females, wild-taught (Pa 83 and Pa 114) vs aviary-taught, and second-year (SY) adults (Pa 144 through Pa 147) vs after second-year (ASY) adults (H1 and H2 Tests).

<b>2-Sample t Tests Comparing Means</b>				
<b>First 6 Tests (Second Years=1 mean)</b>				
<b>Males vs Females</b>	<b>df</b>	<b>t Stat</b>	<b>p Value</b>	<b>Notes</b>
Tear Length	9	1.07	0.313	Not Significant
Percent Pod Torn	9	0.5	0.6	Not Significant
Fraction Seeds Eaten	8	-0.2	0.84	Not Significant
Feeding Time (No Second Year Feeding Times)	24	1.16	0.26	Not Significant
<b>Aviary Taught vs Wild Taught</b>	<b>df</b>	<b>t Stat</b>	<b>p Value</b>	<b>Notes</b>
Tear Length	1	-1.5	0.38	Not Significant
Percent Pod Torn	1	-1.4	0.39	Not Significant
Fraction Seeds Eaten	1	-1.8	0.31	Not Significant
Feeding Time (No Second Year Feeding Times)	3	-0.6	0.62	Not Significant
<b>Second 6 Tests (Second Years=2 means)</b>				
<b>Males vs Females</b>	<b>df</b>	<b>t Stat</b>	<b>p Value</b>	<b>Notes</b>
Tear Length	8	1.17	0.28	Not Significant
Percent Pod Torn	9	0.8	0.46	Not Significant
Fraction Seeds Eaten	8	-0.1	0.94	Not Significant
<b>Aviary Taught vs Wild Taught</b>	<b>df</b>	<b>t Stat</b>	<b>p Value</b>	<b>Notes</b>
Tear Length	1	-1.5	0.38	Not Significant
Percent Pod Torn	1	-1.5	0.38	Not Significant
Fraction Seeds Eaten	1	-1.9	0.31	Not Significant
<b>Post Second Year vs Second Year</b>	<b>df</b>	<b>t Stat</b>	<b>p Value</b>	<b>Notes</b>
Tear Length	5	2.8	0.04	Significant (2 <sup>nd</sup> Years Shorter)
Percent Pod Torn	2	3.4	0.08	Not Significant
Fraction Seeds Eaten	4	2.4	0.07	Not Significant
<b>Means For Percent Pod Torn and FSE</b>	<b>Mean PPT</b>	<b>PPT Sample Size</b>	<b>Mean FSE</b>	<b>FSE Sample Size</b>
Males (Second Year Birds as 1 mean)	45.19%	10	0.74	10
Males (Second Year Birds as 2 means)	43.56%	11	0.74	11
Females	48.69%	7	0.73	7
Aviary Taught (Second Year Birds as 1 mean)	44.60%	15	0.72	15
Aviary Taught (Second Year Birds as 2 means)	43.51%	16	0.72	16
Wild Taught	61.87%	2	0.87	2
Post Second Year Birds	47.80%	16	0.74	16
Second Year Birds (1 mean)	27.77	1	0.65	1
Second Year Birds (2 means)	27.51	2	0.66	2

Table 3. Summary table for fraction seeds eaten (FSE) from all years (2017, 2018, and 2019 when available). \*=Pa 85 and Pa 136's 2019 FSE were inferred from videos.

Bird ID(Year)	Mean	Median	Max	2nd Max	Min	2nd Min	Range	Sample Size
<b>SYA (2019, 4 Birds)</b>	0.65	0.6	1	1	0.1	0.14	0.9	160
<b>Pa 110 (2017)</b>	0.78	1	1	1	0.13	0.3	0.86	7
<b>Pa 110 (2018)</b>	0.75	0.8	1	1	0.25	0.33	0.75	67
<b>Pa 110 (2019)</b>	0.65	0.6	1	1	0.16	0.25	0.83	46
<b>Pa 114 (2018)</b>	0.94	1	1	1	0.5	0.5	0.5	66
<b>Pa 122 (2017)</b>	0.79	1	1	1	0.17	0.2	0.83	63
<b>Pa 124 (2017)</b>	0.63	0.6	1	0.8	0.33	0.4	0.67	4
<b>Pa 125 (2017)</b>	0.83	1	1	1	0.25	0.25	0.75	21
<b>Pa 132 (2017)</b>	0.54	0.5	1	0.5	0.13	0.5	0.88	3
<b>Pa 136 (2017)</b>	0.76	0.78	1	1	0.2	0.25	0.8	62
<b>Pa 136 (2018)</b>	0.83	1	1	1	0.13	0.2	0.88	131
<b>Pa 136 (2019)*</b>	0.87	1	1	1	0.6	1	0.4	3
<b>Pa 141 (2017)</b>	0.58	0.4	1	1	0.17	0.33	0.83	5
<b>Pa 83 (2018)</b>	0.79	1	1	1	0.13	0.14	0.88	83
<b>Pa 85 (2017)</b>	0.76	0.8	1	1	0.2	0.25	0.8	104
<b>Pa 85 (2018)</b>	0.75	0.83	1	1	0.13	0.17	0.88	57
<b>Pa 85 (2019)*</b>	0.94	0.94	1	0.88	0.88	1	0.13	2
<b>Pa 96 (2017)</b>	0.85	1	1	1	0.25	0.25	0.75	137
<b>Pa 98 (2017)</b>	0.65	0.5	1	1	0.4	0.4	0.6	7
<b>Wild (Pa 83 +Pa 114)</b>	0.86	1	1	1	0.13	0.14	0.88	148
<b>Older Aviary Adults</b>	0.78	1	1	1	0.13	0.13	0.88	697
<b>Females</b>	0.83	1	1	1	0.13	0.13	0.88	288
<b>Females (No Pa 114)</b>	0.80	1	1	1	0.13	0.13	0.88	226
<b>Males</b>	0.78	1	1	1	0.13	0.13	0.88	558
<b>Males (No Pa 83)</b>	0.78	1	1	1	0.13	0.13	0.88	488
<b>All Older Adults</b>	0.79	1	1	1	0.13	0.13	0.88	863

Table 4. Table of t Tests for Hypothesis 3, Comparing Pa 85 and Pa 136's Feeding Times and Fraction Seeds Eaten in 2018 and 2019 (using means vs means).

<b>Table of t Test Results for Hypothesis 3 (Pa 85 and Pa 136 Before and After Interacting with Wild Birds)</b>					
<b>Variable Tested</b>	<b>Birds Tested</b>	<b>df</b>	<b>t</b>	<b>2-tailed p</b>	<b>Notes</b>
Fraction Seeds Eaten (Means)	Pa 85+Pa 136 (2018 vs 2019)	2	-2.2	0.16	Not Significant
Feeding Time (Means)	Pa 85+Pa 136 (2018 vs 2019)	2	-2.2	0.52	Not Significant
<b>Variable</b>	<b>Birds (Year)</b>	<b>Mean</b>	<b>Sample Size</b>		
Fraction Seeds Eaten	Pa 85+Pa 136 (2018)	0.79	2		
Fraction Seeds Eaten	Pa 85+Pa 136 (2019)	0.91	2		
Feeding Time	Pa 85+Pa 136 (2018)	281.3	2		
Feeding Time	Pa 85+Pa 136 (2019)	205.3	2		

Table 5. Summary table of overall yearly feeding times, by bird ID and year.

Overall Feeding Times (Seconds)								
Bird ID and Year	Mean	Median	Max	2nd Max	Min	2nd Min	Range	Sample Size
Pa 110 (2017)	372.5	332.5	838	544	41	147	797	6
Pa 110 (2019)	102.6	81	179	124	64	65	115	5
Pa 112 (2019)	124.1	139	190	175	48	60	142	9
Pa 114 (2018)	362	324.5	715	439	155	225	560	8
Pa 114 (2019)	164.1	159	350	389	320	39	67	15
Pa 122 (2017)	305.1	295	971	760	35	59	936	69
Pa 122 (2019)	177.8	180	206	197	140	166	66	5
Pa 124 (2017)	268.7	217	552	342	140	144	412	7
Pa 124 (2019)	194.7	148	313	275	121	125	192	7
Pa 125 (2017)	357.4	257	1084	760	102	120	982	21
Pa 125 (2019)	255.8	178	877	540	38	57	839	18
Pa 132 (2017)	197.3	141	538	190	53	121	485	6
Pa 136 (2017)	295.9	290	770	730	41	46	729	77
Pa 136 (2018)	362.8	377	843	532	114	125	729	15
Pa 136 (2019)	213.9	176.5	519	510	73	102	446	14
Pa 141 (2017)	208.3	148	553	302	45	67	508	7
Pa 141 (2019)	180.9	167.5	605	285	57	68	548	16
Pa 83 (2018)	358.5	256	873	740	115	201	873	12
Pa 83 (2019)	168.2	150.5	432	422	67	73	365	26
Pa 85 (2017)	236.6	205	788	714	40	40	748	143
Pa 85 (2018)	199.8	197	336	290	52	117	284	9
Pa 85 (2019)	196.7	194.5	288	271	110	122	178	6
Pa 96 (2017)	261.3	233	898	640	25	43	873	158
Pa 96 (2019)	131.2	118	238	224	42	42	196	17
Pa 98 (2017)	224.8	192	413	365	40	133	373	13
Pa 98 (2019)	210.7	179.5	490	394	71	74	419	18
Wild (Pa 83+Pa 114)	230	191	873	746	39	67	834	61
Older Aviary Adults	255.4	215.5	1084	971	25	35	1059	646
All Females	272.4	220	1084	877	38	39	1046	211
Females without Pa 114	277.2	225	1084	877	38	41	1046	188
All Males	244.9	210	946	898	25	35	946	496
Males without Pa 83	246.4	211	971	898	25	35	946	458

Table 6. Descriptive statistics summary table for five 2017 taught birds, tear lengths, comparing tear lengths among birds by month, with August 18, 2017 (the day treatment birds were given whole pods to test their progress). Dates are in month, day, and year.

Tear Lengths (cm) by Month (2017)									
Pod Types	Bird ID	Mean	Median	Max	2nd Max	Min	2nd Min	Range	Sample Size
Sliced Pods	Pa 122 (July 2017)	1.4	1	3.7	3.5	0.7	0.8	3	24
Sliced Pods	Pa 122 (8/1-16 2017)	1.4	0.9	5.7	5.1	0.4	0.5	5.3	56
Whole Pods	Pa 122 (8/18, 2017)	1.3	1.1	5.8	1.6	0.6	0.7	5.2	18
Sliced Pods	Pa 125 (July 2017)	5.3	5.3	6.7	3.9	3.9	3.9	2.8	2
Sliced Pods	Pa 125 (8/1-16, 2017)	3.1	3	5.4	5.3	0.9	1.1	4.5	18
Whole Pods	Pa 125 (8/18, 2017)	5.4	5.4	7.7	3	3	7.7	4.7	2
Sliced Pods	Pa 136 (June 2017)	2.2	2.4	4.4	4	0.5	0.6	3.9	22
Sliced Pods	Pa 136 (July 2017)	1.0	1	2.7	2.3	0.4	0.5	2.3	45
Sliced Pods	Pa 136 (8/1-16, 2017)	1.4	1	3.9	3.4	0.5	0.7	3.4	33
Whole Pods	Pa 136 (8/18, 2017)	3.6	3.1	7.9	7.3	1.1	1.3	6.8	7
Sliced Pods	Pa 85 (June 2017)	2.2	1.8	4.8	4.4	0.5	0.6	4.3	24
Sliced Pods	Pa 85 (July 2017)	1.3	0.9	5.9	5.4	0.4	0.4	5.5	72
Sliced Pods	Pa 85 (8/1-16, 2017)	1.1	0.9	3.2	3.1	0.4	0.4	2.8	91
Whole Pods	Pa 85 (8/18, 2017)	0.8	0.8	1.1	0.9	0.6	0.7	0.5	12
Sliced Pods	Pa 96 (July 2017)	1.1	1.0	5.5	2.5	0.4	0.5	5.1	110
Sliced Pods	Pa 96 (8/1-16, 2017)	1.3	0.9	3.8	4	0.4	0.5	3.8	119
Whole Pods	Pa 96 (8/18, 2017)	1.3	1.2	3	2.5	0.6	0.7	2.4	20
Whole Pods	Pa 110 (2017, Control)	3.9	2.9	8.2	7.5	1.2	1.7	7	11
Whole Pods	Pa 124 (2017, Control)	2.6	2.3	4.3	4.2	1.3	1.3	3	8
Whole Pods	Pa 141 (2017, Control)	5.1	4.5	9.7	8.8	1.3	1.6	8.4	6
Whole Pods	Pa 98 (2017, Control)	1.6	1.2	4.4	3.4	0.8	0.9	3.6	22
Whole Pods	All Control Birds	2.7	1.8	9.7	8.8	0.8	0.9	8.9	47
Whole Pods	All August 18 Tears	1.6	1.1	7.9	7.7	0.6	0.6	7.3	59

Table 7. Results for regression tests for five taught birds in 2017, including significance-F, trendline slope, and R-squared. Measurements tested were mean daily tear length, mean daily percent pod torn, mean daily fraction seeds eaten, and mean daily seconds per seed eaten.

<b>Regression for Mean Daily Tear Length (2017)</b>				
<b>Bird ID (2017)</b>	<b>Significance-F</b>	<b>Slope</b>	<b>R-squared</b>	<b>Notes</b>
Pa 122 (2017)	0.55	-0.03	0.0256	Non-Significant Decrease
Pa 125 (2017)	0.23	-0.14	0.155	Non-Significant Decrease
Pa 136 (2017)	0.76	-0.0075	0.0038	Non-Significant Decrease
Pa 85 (2017)	<0.001	-0.0514	0.466	Significant Decrease (Reduced Proficiency)
Pa 96 (2017)	0.79	0.004	0.0034	Non-Significant Increase
<b>Regression for Mean Daily Percent Pod Torn (2017)</b>				
<b>Bird ID (2017)</b>	<b>Significance-F</b>	<b>Slope</b>	<b>R-squared</b>	<b>Notes</b>
Pa 122 (2017)	0.37	-0.486	0.0383	Non-Significant Decrease
Pa 125 (2017)	0.13	-1.9134	0.2111	Non-Significant Decrease
Pa 136 (2017)	0.62	0.2463	0.0099	Non-Significant Increase
Pa 85 (2017)	0.037	-0.5156	0.1573	Significant Decrease (Reduced Proficiency)
Pa 96 (2017)	0.001	-0.7492	0.2973	Significant Decrease (Reduced Proficiency)
<b>Regression for Mean Daily Fraction Seeds Eaten (2017)</b>				
<b>Bird ID (2017)</b>	<b>Significance-F</b>	<b>Slope</b>	<b>R-squared</b>	<b>Notes</b>
Pa 122 (2017)	0.001	0.0186	0.4139	Significant Increase (Increased Proficiency)
Pa 125 (2017)	0.85	-0.0044	0.0039	Non-Significant Decrease
Pa 136 (2017)	0.012	0.0134	0.226	Significant Increase (Increased Proficiency)
Pa 85 (2017)	0.016	0.0079	0.1952	Significant Increase (Increased Proficiency)
Pa 96 (2017)	0.22	0.0025	0.0488	Non-Significant Increase
<b>Regression for Mean Daily Seconds/Seeds Eaten (2017)</b>				
<b>Bird ID (2017)</b>	<b>Significance-F</b>	<b>Slope</b>	<b>R-squared</b>	<b>Notes</b>
Pa 122 (2017)	0.93	-7.6557	0.3099	Non-Significant Decrease
Pa 125 (2017)	0.71	-2.0401	0.016	Non-Significant Decrease
Pa 136 (2017)	0.91	-0.2863	0.0007	Non-Significant Decrease
Pa 85 (2017)	0.009	-2.8002	0.2955	Significant Decrease (Increased Proficiency)
Pa 96 (2017)	0.93	0.0766	0.0004	Non-Significant Increase

Table 8. Percent pod torn (PPT, %) for 2017 by month. Dates are in month, day, and year.

Pod Types	Bird ID	Mean	Median	Max	2nd Max	Min	2nd Min	Range	Sample Size
Sliced Pods	Pa 122 (June 2017)	62.7	73.9	92.3	86.7	14.9	27.5	77.4	13
Sliced Pods	Pa 122 (July 2017)	41.9	42.6	70	63.9	11.1	23.4	58.9	14
Sliced Pods	Pa 122 (8/1-16 2017)	48.4	46.4	82.6	80	18.2	23.9	64.4	28
Whole Pods	Pa 122 (August 18 2017)	38.3	39.5	67.2	49.2	7.2	28.2	60.0	5
Sliced Pods	Pa 125 (June 2017)	65.9	65.9	65.9	65.9	65.9	65.9	0	1
Sliced Pods	Pa 125 (July 2017)	78.8	78.8	95.7	61.9	61.9	95.7	33.8	2
Sliced Pods	Pa 125 (8/1-16 2017)	56.5	60.8	86.5	79.1	17.1	27.9	69.4	16
Whole Pods	Pa 125 (8/18 2017)	62.3	62.3	100	24.6	24.6	100	75.4	2
Sliced Pods	Pa 136 (June 2017)	56.3	50	95.5	95.2	21.2	24.6	74.3	17
Sliced Pods	Pa 136 (July 2017)	33.3	33.3	60.3	59.7	5.8	4.5	54.5	21
Sliced Pods	Pa 136 (8/1-16 2017)	49.7	49.7	84.8	76.7	12.3	17.7	72.5	16
Whole Pods	Pa 136 (August 18 2017)	58.6	64.0	83.2	75.8	23.9	52.6	59.6	4
Sliced Pods	Pa 85 (June 2017)	52.8	52.0	91.1	82.5	10.4	15.6	80.7	18
Sliced Pods	Pa 85 (July 2017)	39.9	35.7	100	84.3	11.6	13.9	88.4	32
Sliced Pods	Pa 85 (8/1-16 2017)	37.6	36.8	69.0	68.9	11.8	11.9	57.2	43
Whole Pods	Pa 85 (8/18 2017)	25.4	26.6	29.9	29.9	18.7	23.2	11.3	4
Sliced Pods	Pa 96 (June 2017)	69.6	72.0	95.7	93.9	15.6	34.8	80.1	36
Sliced Pods	Pa 96 (July 2017)	45.7	45.3	82.8	82.1	13.6	14.9	69.1	44
Sliced Pods	Pa 96 (8/1-16 2017)	46.9	46.5	88.1	79.6	8.9	13.3	79.3	48
Whole Pods	Pa 96 (8/18 2017)	42.4	39.3	62.7	55.8	25.3	30.8	37.3	6
Whole Pods	Pa 110 (2017, Control)	59.6	67.7	87.8	82.4	13.3	26.4	74.5	7
Whole Pods	Pa 124 (2017, Control)	44.8	36.7	79.1	45.9	29.9	27.5	52.1	4
Whole Pods	Pa 141 (2017, Control)	53.8	49.1	98.0	83.0	10	29.0	88.0	5
Whole Pods	Pa 98 (2017, Control)	37.3	35.4	56.4	49.6	17.3	19.7	39.1	7
Whole Pods	All Control Birds	43.5	40.6	87.8	79.1	10	17.3	77.8	16
Whole Pods	All 8/18 (Except Pa 132)	39.2	33.7	83.2	67.2	7.2	18.7	76.0	18

Table 9. Table of Monthly Means for Using in Testing Hypothesis 4 (Non-Regression).

<b>Percent Pod Torn</b>					
<b>Bird (Month Year)</b>	<b>Year</b>	<b>Mean PPT</b>	<b>Median PPT</b>	<b>PPT Sample Size</b>	<b>Taught or Untaught</b>
Pa 136 (June 2017)	2017	56.26	50	17	T
Pa 136 (July 2017)	2017	33.34	33.33	21	T
Pa 136 (August 2017)	2017	51.45	52.98	20	T
Pa 136 (March 2018)	2018	34.47	29.25	36	T
Pa 136 (April 2018)	2018	36.02	33.04	95	T
Pa 85 (June 2017)	2017	52.77	51.96	18	T
Pa 85 (July 2017)	2017	39.93	35.71	32	T
Pa 85 (August 2017)	2017	36.55	36.21	47	T
Pa 85 (March 2018)	2018	45.07	45.68	25	T
Pa 85 (April 2018)	2018	36.12	31.89	32	T
<b>Bird (Month Year)</b>	<b>Year</b>	<b>Mean PPT</b>	<b>Median PPT</b>	<b>PPT Sample Size</b>	<b>Taught or Untaught</b>
Pa 110 (June 2017)	2017	50.17	52.46	4	U
Pa 110 (July 2017)	2017	72.17	67.67	3	U
Pa 110 (March 2018)	2018	48.73	41.18	19	U
Pa 110 (April 2018)	2018	45.3	37.27	48	U
<b>Fraction Seeds Eaten</b>					
<b>Bird (Month Year)</b>	<b>Year</b>	<b>Mean FSE</b>	<b>Median FSE</b>	<b>FSE Sample Size</b>	<b>Taught or Untaught</b>
Pa 136 (June 2017)	2017	0.72	0.75	17	T
Pa 136 (July 2017)	2017	0.68	0.67	21	T
Pa 136 (August 2017)	2017	0.87	1	24	T
Pa 136 (March 2018)	2018	0.81	0.83	36	T
Pa 136 (April 2018)	2018	0.84	1	95	T
Pa 85 (June 2017)	2017	0.65	0.67	18	T
Pa 85 (July 2017)	2017	0.78	0.8	32	T
Pa 85 (August 2017)	2017	0.79	1	54	T
Pa 85 (March 2018)	2018	0.698	0.8	25	T
Pa 85 (April 2018)	2018	0.79	1	32	T
<b>Bird (Month Year)</b>	<b>Year</b>	<b>Mean FSE</b>	<b>Median FSE</b>	<b>FSE SS</b>	<b>Taught or Untaught</b>
Pa 110 (June 2017)	2017	0.61	0.65	4	U
Pa 110 (July 2017)	2017	1	1	3	U
Pa 110 (March 2018)	2018	0.71	0.67	19	U
Pa 110 (April 2018)	2018	0.77	0.938	48	U
<b>Tear Length</b>					
<b>Bird (Month Year)</b>	<b>Year</b>	<b>Mean Tear Length</b>	<b>Median Tear Length</b>	<b>Tear Length Sample Size</b>	<b>Taught or Untaught</b>
Pa 136 (June 2017)	2017	2.19	2.4	22	T

Pa 136 (July 2017)	2017	1.04	1	45	T
Pa 136 (August 2017)	2017	1.81	1.1	40	T
Pa 136 (March 2018)	2018	1.08	1	102	T
Pa 136 (April 2018)	2018	1.22	1	217	T
Pa 85 (June 2017)	2017	2.16	1.75	24	T
Pa 85 (July 2017)	2017	1.25	0.9	72	T
Pa 85 (August 2017)	2017	1.03	0.9	103	T
Pa 85 (March 2018)	2018	2.55	1.7	42	T
Pa 85 (April 2018)	2018	1.26	1	74	T
<b>Bird (Month Year)</b>	<b>Year</b>	<b>Mean Tear Length</b>	<b>Median Tear Length</b>	<b>Tear Length Sample Size</b>	<b>Taught or Untaught</b>
Pa 110 (June 2017)	2017	4.7	5.05	4	U
Pa 110 (July 2017)	2017	3.43	2.9	7	U
Pa 110 (March 2018)	2018	2.84	2.9	26	U
Pa 110 (April 2018)	2018	2.41	1.65	76	U

Table 10. Table of t-tests used for Hypothesis 4.

<b>t Tests for Hypothesis 4 (Monthly 2017 vs 2018 Measurements)</b>			
<b>Taught Birds (Pa 85 and Pa 136)</b>	<b>df</b>	<b>t</b>	<b>p (2 tailed)</b>
Tear length	5	0.1	0.9
Percent Pod Torn (PPT)	8	1.9	0.16
Fraction Seeds Eaten (FSE)	8	-0.8	0.45
<b>Untaught Bird (Pa 110)</b>			
Tear length	1	2.2	0.28
Percent Pod Torn (PPT)	1	1.3	0.42
Fraction Seeds Eaten (FSE)	1	0.3	0.8
<b>Means and Sample Sizes</b>			
<b>Bird(s)-Year</b>	<b>Mean</b>	<b>Sample Size</b>	
Pa 85 and Pa 136 (2017)	1.6	6	
Pa 85 and Pa 136 (2018)	1.5	4	
Pa 110 (2017)	4.1	2	
Pa 110 (2018)	2.6	2	
<b>Percent Pod Torn (PPT)</b>	<b>Mean</b>	<b>Sample Size</b>	
Pa 85 and Pa 136 (2017)	37.90	6	
Pa 85 and Pa 136 (2018)	37.90	4	
Pa 110 (2017)	61.25	2	
Pa 110 (2018)	47.00	2	
<b>Fraction Seeds Eaten (FSE)</b>	<b>Mean</b>	<b>Sample Size</b>	
Pa 85 and Pa 136 (2017)	0.75	6	
Pa 85 and Pa 136 (2018)	0.79	4	
Pa 110 (2017)	0.81	2	
Pa 110 (2018)	0.74	2	

Figures 1-10:

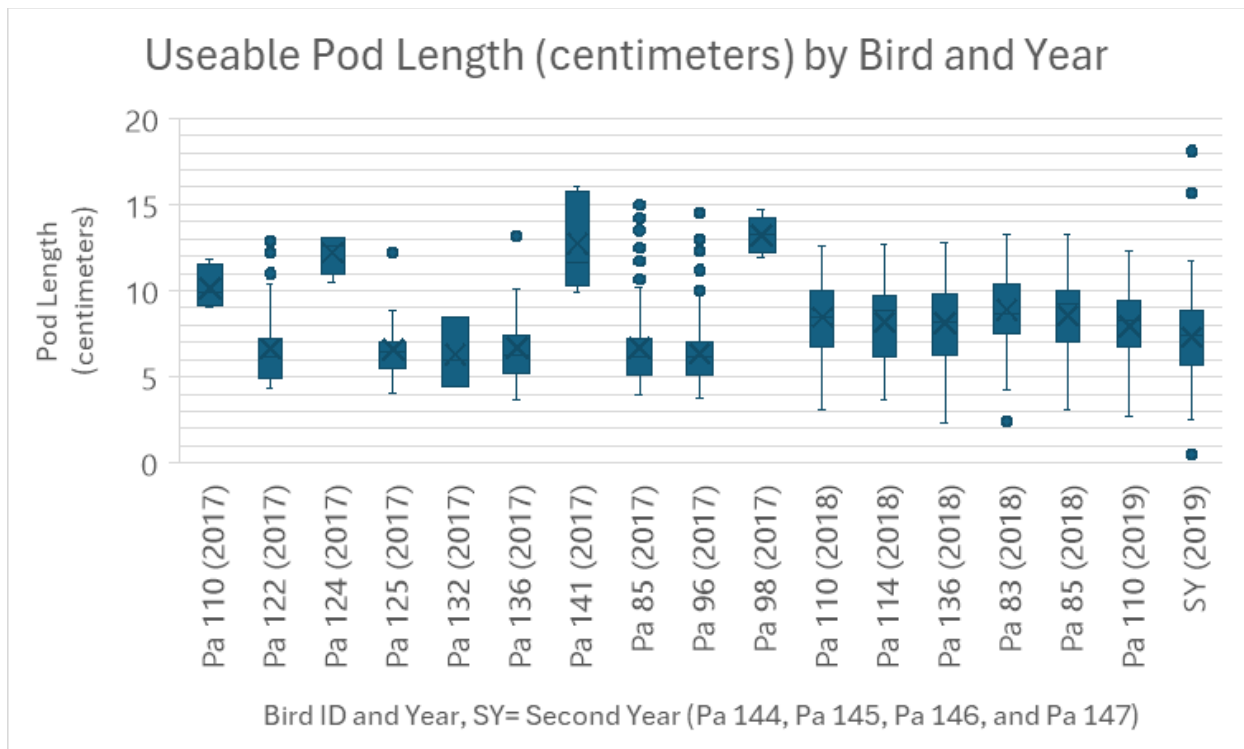


Figure 1. Usable pod length (centimeters) by bird ID and year, starting with 2017. While pod lengths from 2018 and 2019 have a similar range regardless of bird, 2017 pods are longer for control birds and shorter for treatment birds.

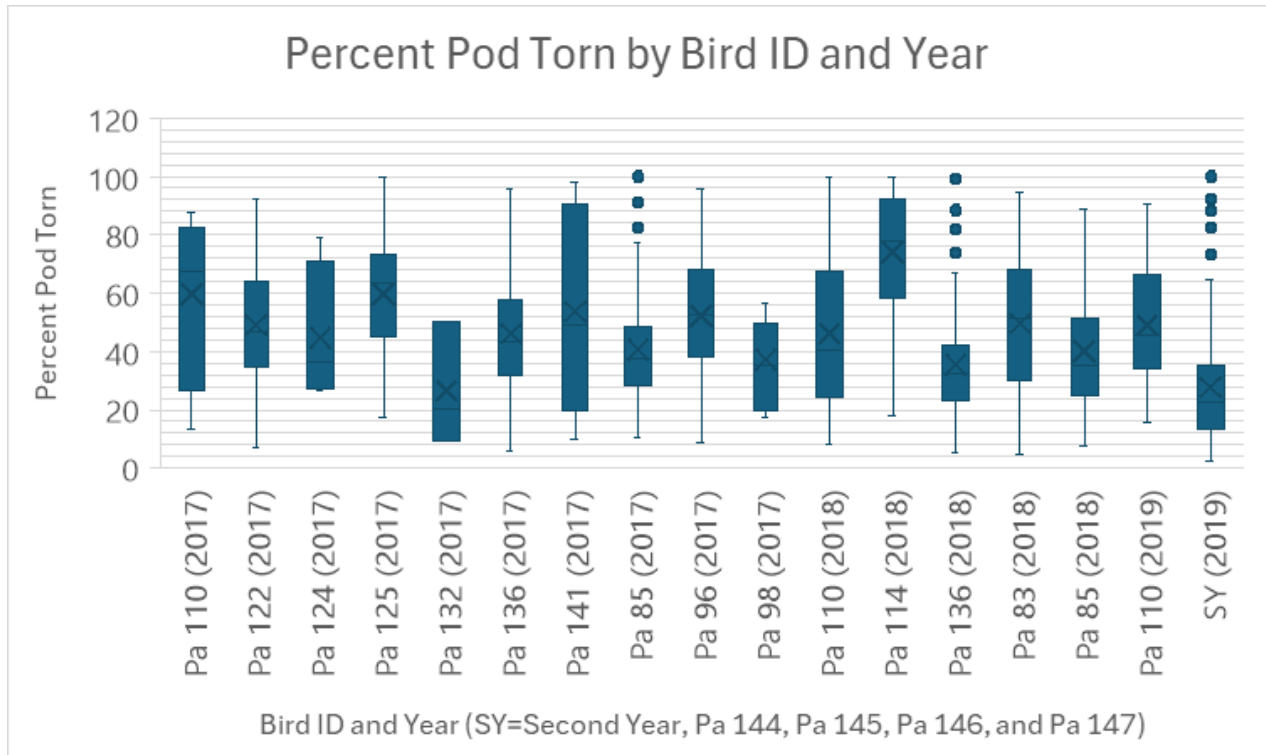


Figure 2. Box and whisker plot of tear length (centimeters) from all birds across multiple years, starting with 2017. The second-year adults (Pa 144, Pa 145, Pa 146, and Pa 147) were hatched in 2018, and were in their second year of life in February and March 2019 when these pods were eaten. Untaught control male Pa 110's 2019 pods were included with his 2019 aviary mate (2017 taught female Pa 132) who was not observed eating Māmane in spring 2019, and so pods from aviary 8 (forest bird barn 1) are most likely from control male Pa 110. All birds here can create tears at least 6 cm long, though these are outlier tears for all but five birds (control male Pa 110, wild-born male Pa 83, his mate of three years, female Pa 114, 2017 taught female Pa 125, and 2017 untaught control female Pa 141).

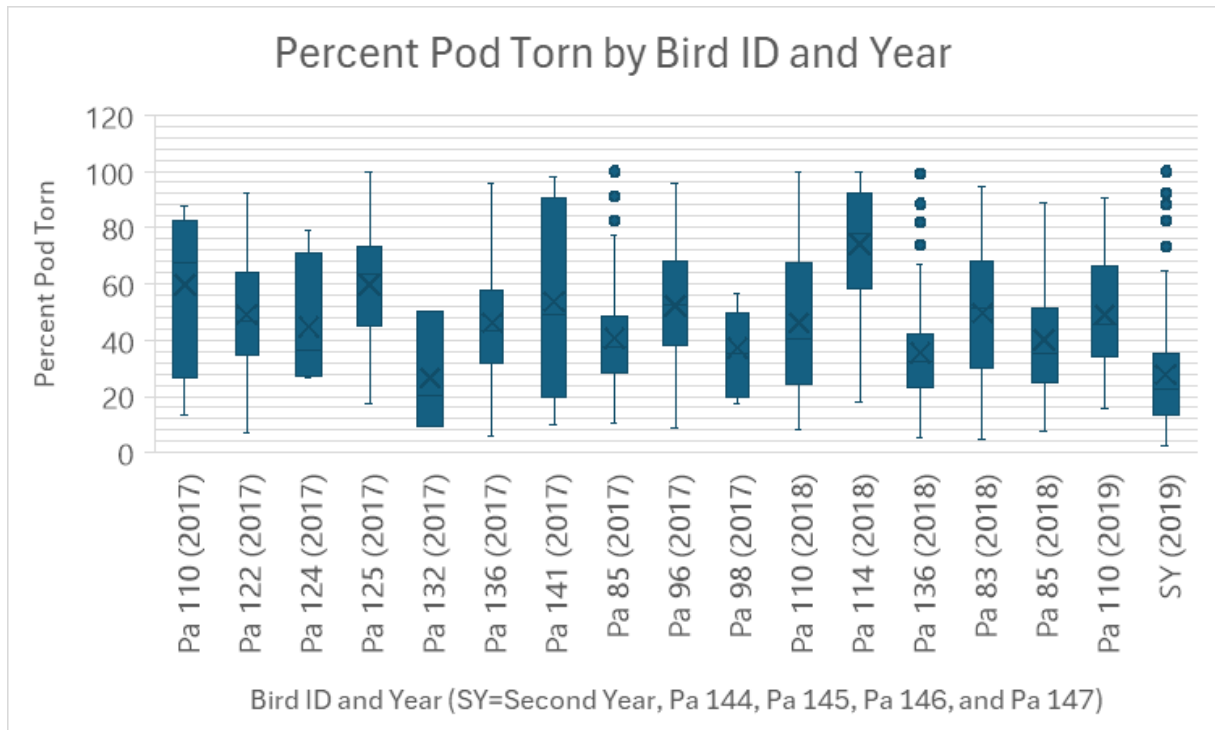


Figure 3. Percent pod torn sorted by bird identification number and the year those pods were eaten. Here the adults seem more like each other than they were when comparing tear lengths, as many small tears can cover a large percentage of the pod.

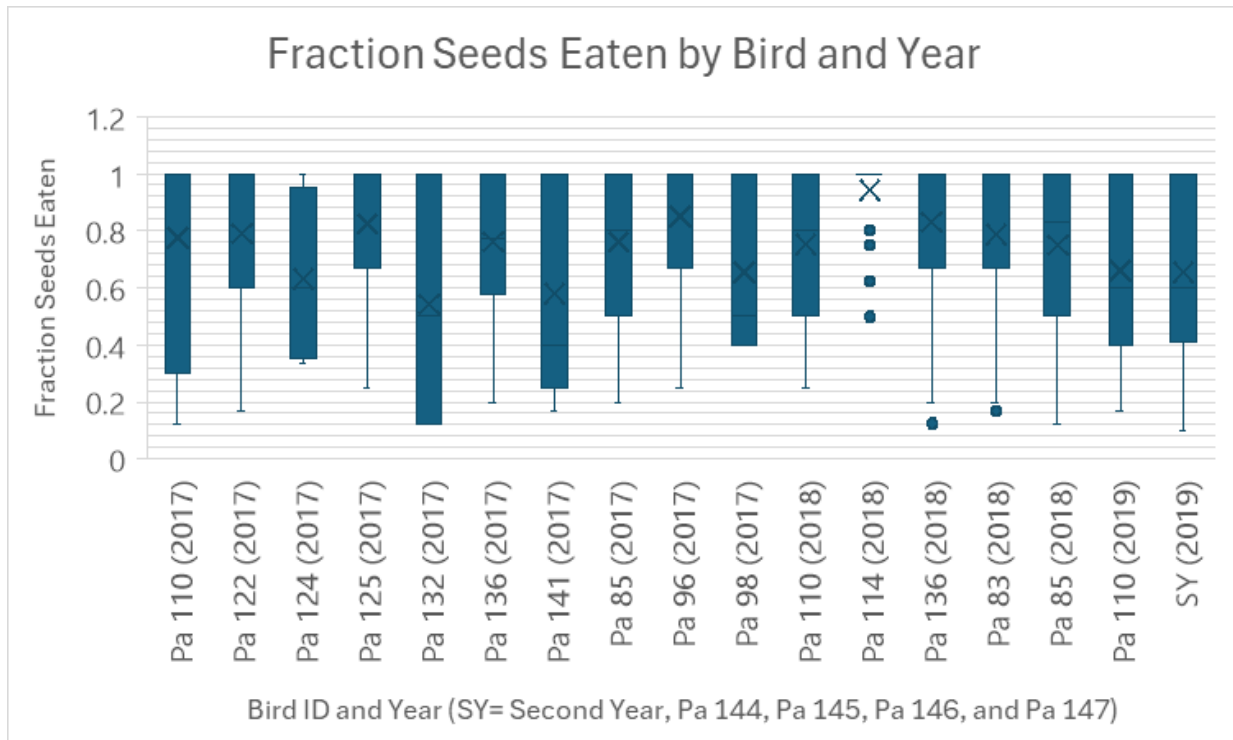


Figure 4. Fraction seeds eaten by bird ID and year, starting with 2017. Here Pa 114 stands out as the most likely to finish a pod.

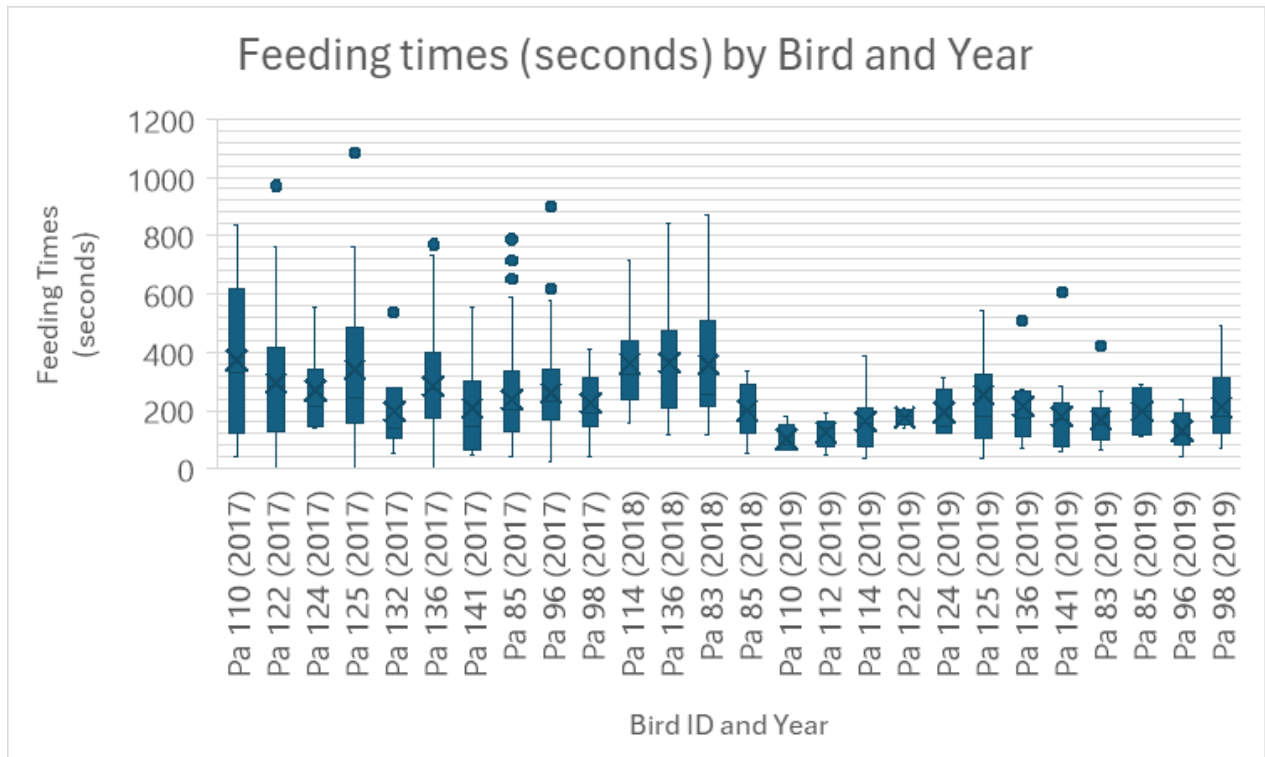


Figure 5. Overall feeding times by bird and year, starting with 2017.

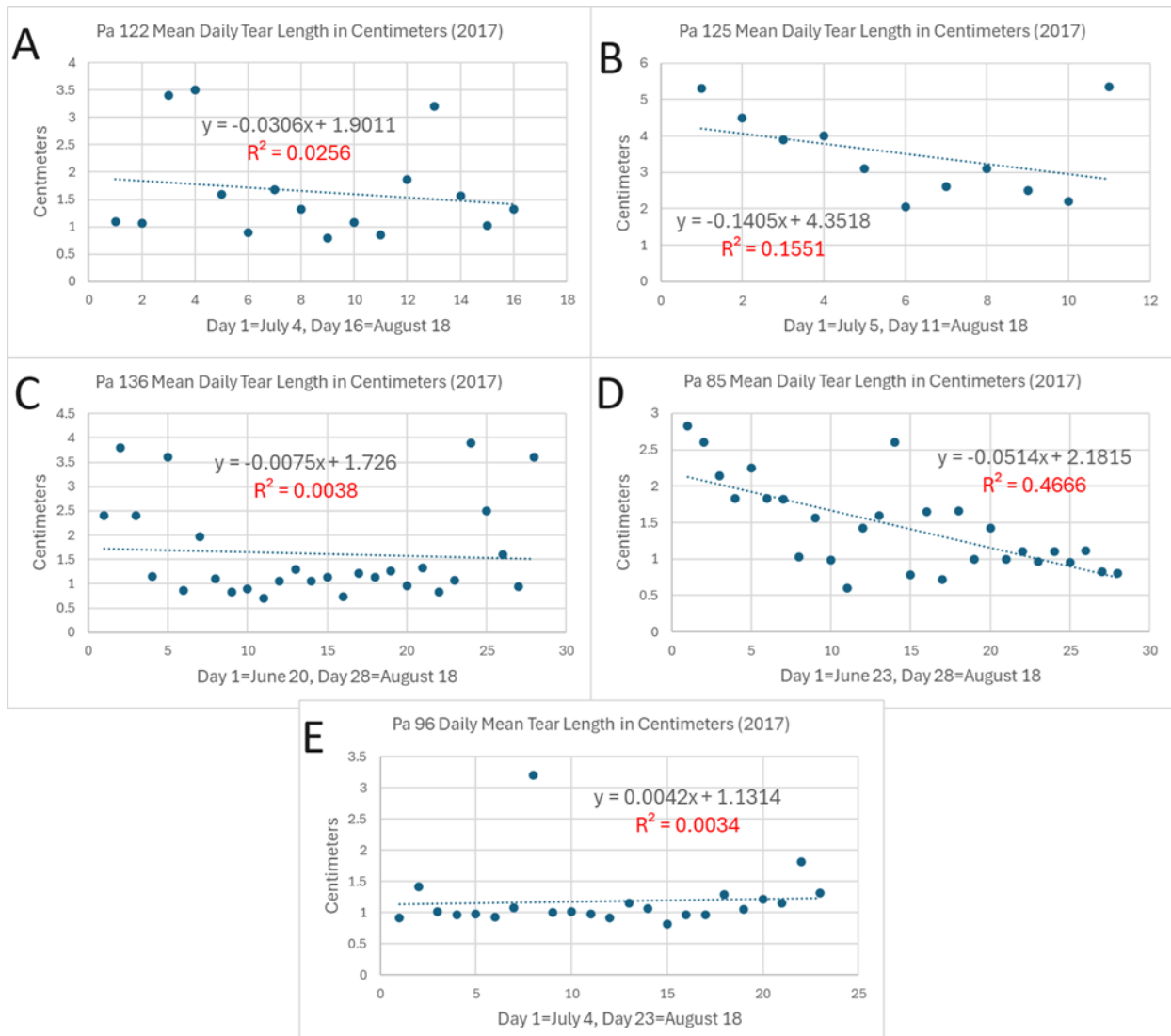


Figure 6. Regression plots with trend line equation and R-squared for 2017 tear length (centimeters) for five taught birds, male Pa 122 (6A), female Pa 125 (6B), female Pa 136 (6C), male Pa 85 (6D), and male (6E). None of these birds significantly increased tear length during 2017.

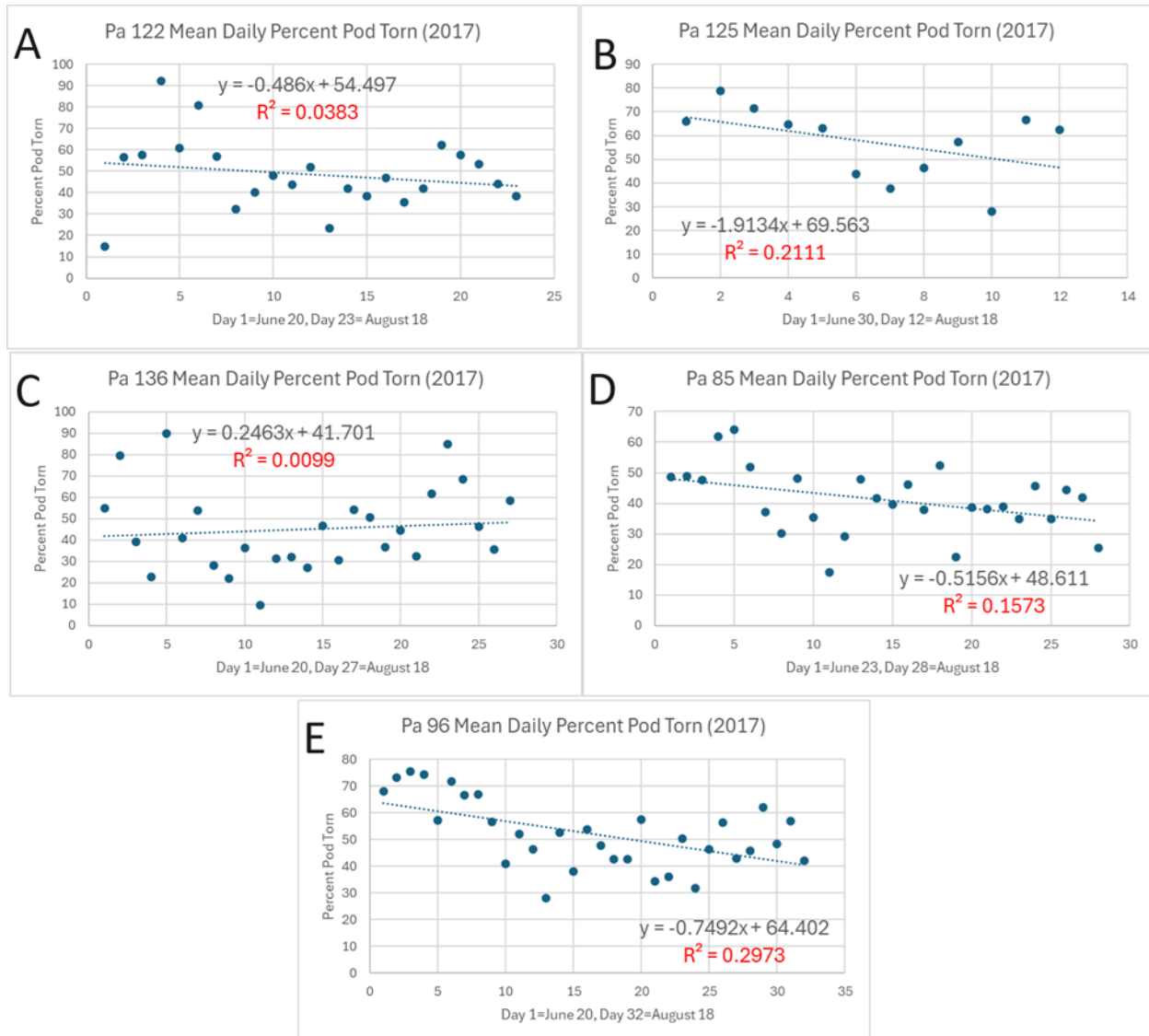


Figure 7. Regression graphs with trend line equations and R-squared for 2017 percent pod torn for five taught birds, male Pa 122 (7A), female Pa 125 (7B), female Pa 136 (7C), male Pa 85 (7D), and male (7E). None of these birds significantly increased PPT during 2017.

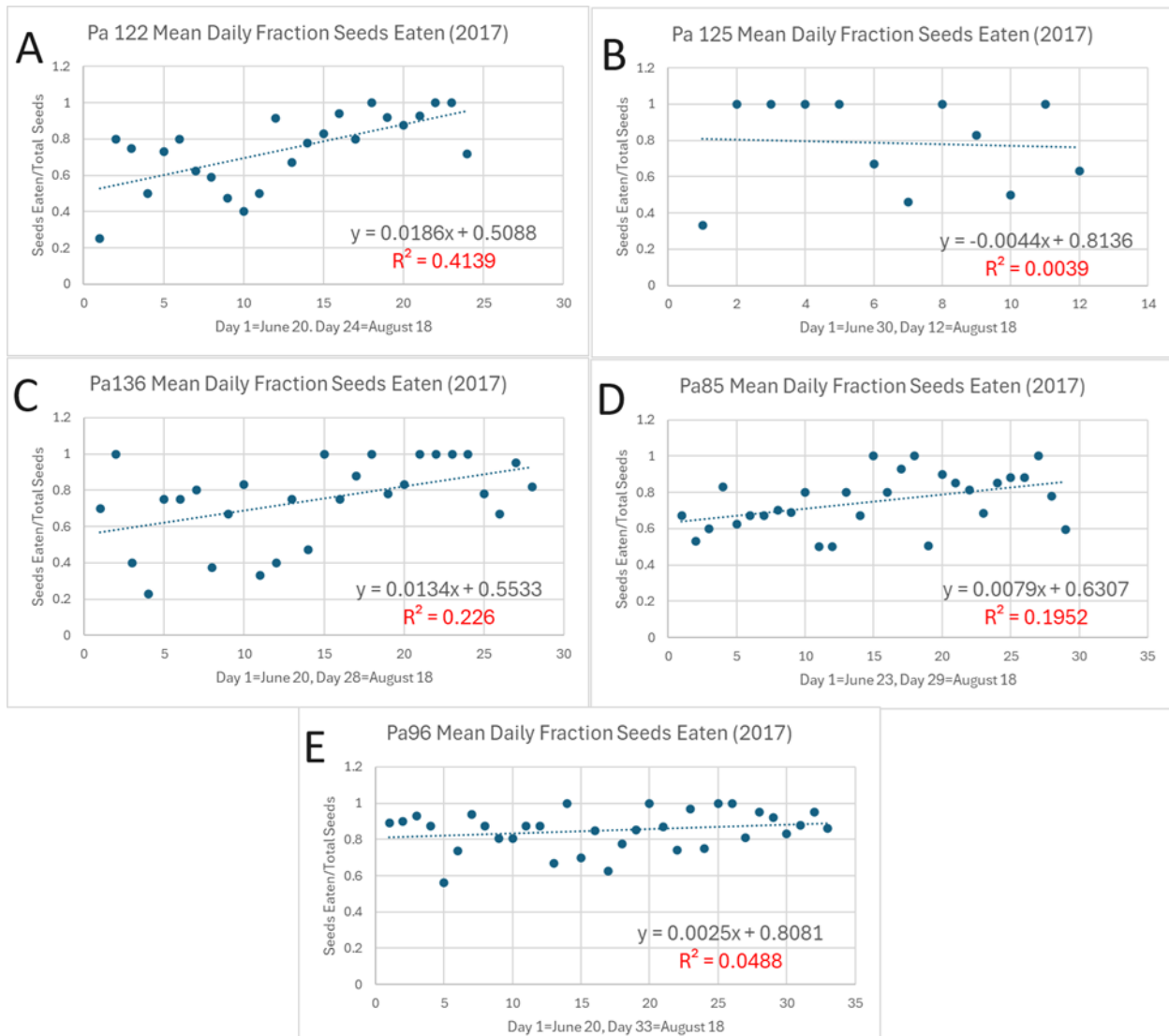


Figure 8. Regression graphs with trend line equations and R-squared for 2017 fraction seeds eaten for five taught birds, male Pa 122 (8A), female Pa 125 (8B), female Pa 136 (8C), male Pa 85 (8D), and male (8E). Pa 122, Pa 136, and Pa 85 significantly increased their fraction seeds eaten during 2017.

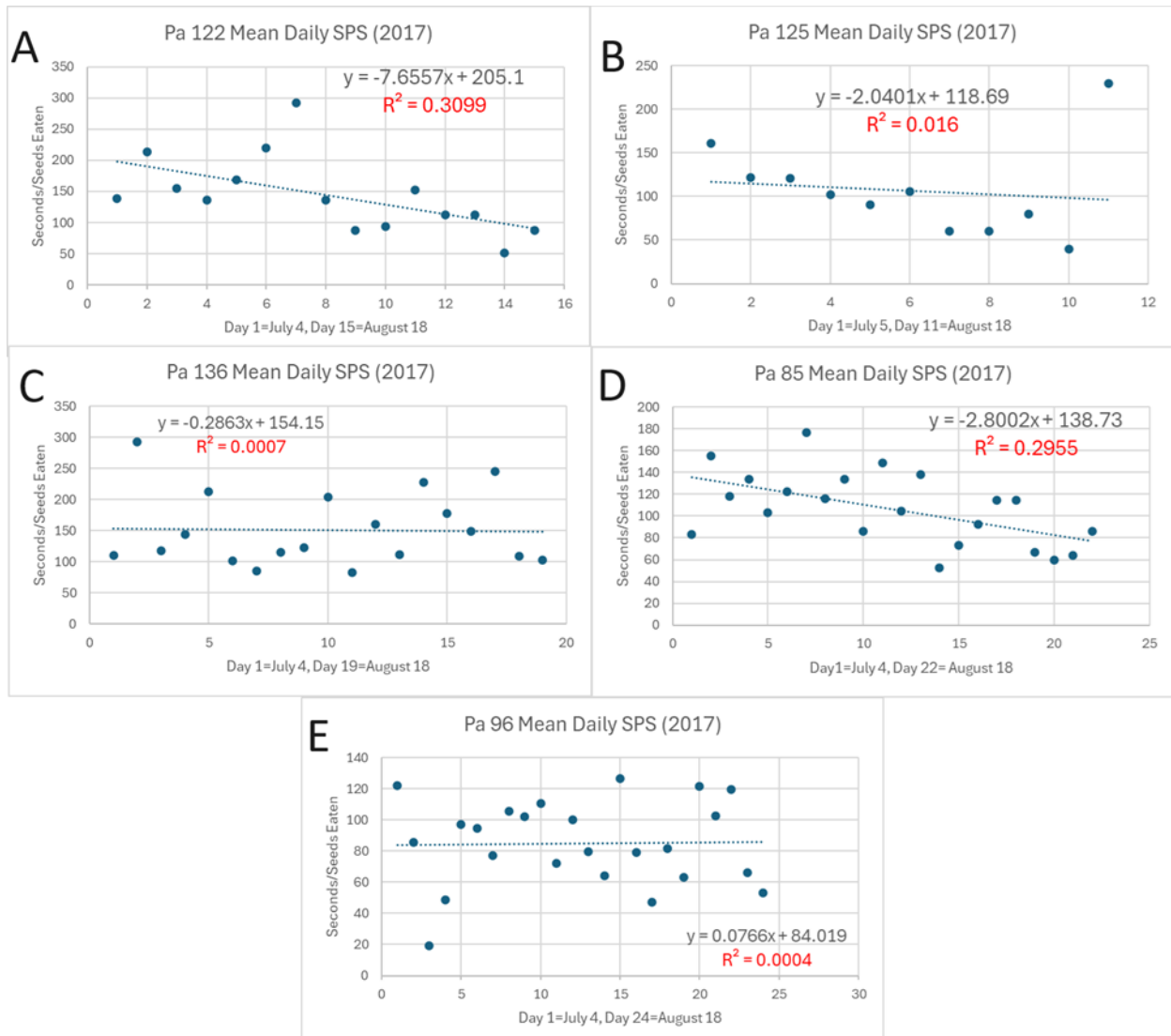


Figure 9. Regression graphs with trend line equations and R-squared for 2017 seconds per seed eaten for five taught birds, male Pa 122 (9A), female Pa 125 (9B), female Pa 136 (9C), male Pa 85 (9D), and male (9E). Pa 85 significantly decreased his seconds per seed eaten in 2017.

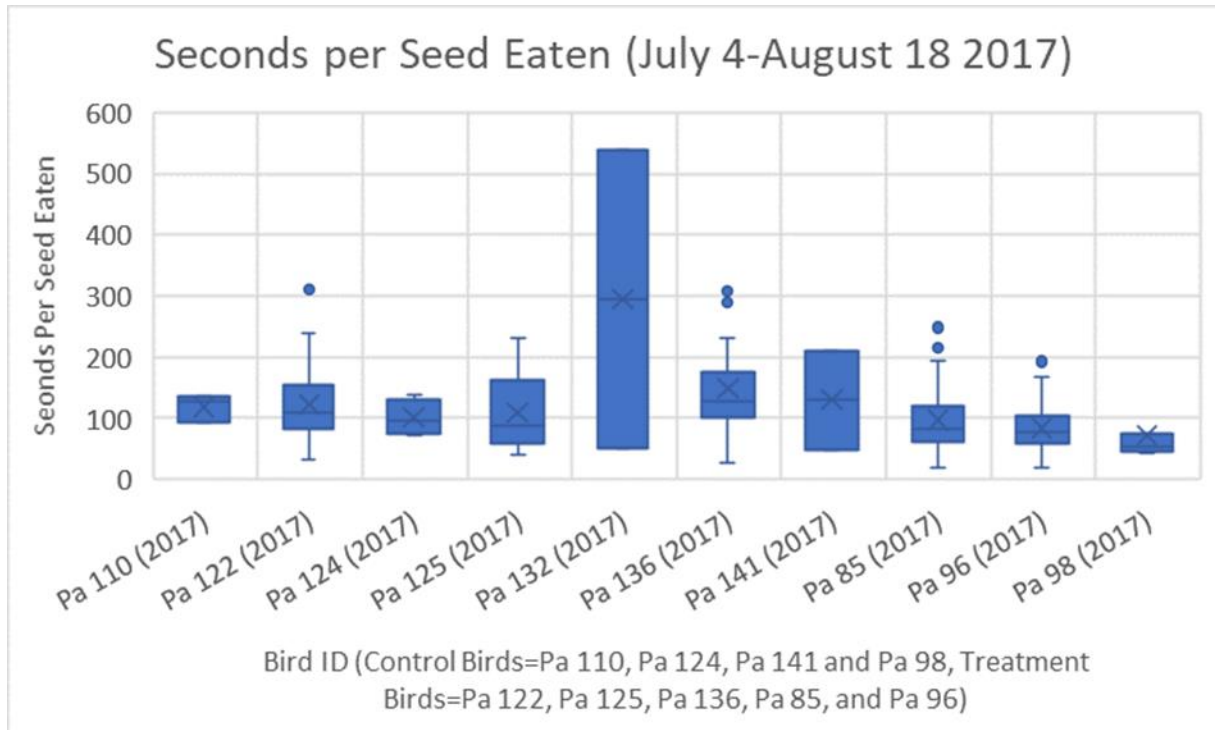


Figure 10. Seconds divided by seeds eaten for July 4-August 18, 2017.