



universität
wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Darwin's finches habitually anoint their feathers with leaves of the endemic tree *Psidium galapageium* during the non-breeding season“

verfasst von / submitted by

Timo Schwemhofer, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of
Master of Science (MSc)

Wien, 2021 / Vienna, 2021

Studienkennzahl lt. Studienblatt /
degree programme code as it appears on
the student record sheet:

UA 066 878

Studienrichtung lt. Studienblatt /
degree programme as it appears on
the student record sheet:

Masterstudium Verhaltens-, Neuro- und
Kognitionsbiologie

Betreut von / Supervisor:

Mag. Dr. Sabine Tebbich, Privatdoz.

Abstract

Birds host a wide range of ectoparasites and have developed behavioural strategies to combat them, such as preening, dust bathing and water bathing. In addition, a wide range of avian taxa anoint their feathers with insects or plants that have pharmaceutical properties, though most observations on anointing are anecdotal. Darwin's finches preen with leaves of an endemic tree (*Psidium galapageium*) and a previous laboratory study has shown that this plant has compounds that repel both mosquitoes and the invasive parasitic fly *Philornis downsi*, whose larvae suck blood from nestlings and incubating females and cause high nestling mortality. In the current study, we tested the hypothesis that preening with *P. galapageium* leaves serves to repel these parasites with an indirect approach. Mosquitoes and *P. downsi* affect their hosts mainly during the bird breeding season and *P. downsi* only affects breeding females, but not adult males. To test our hypothesis, we gathered quantitative data on leaf-preening behaviour in Darwin's finches during their breeding and non-breeding season and also investigated the influence of time of day and humidity, as humid conditions facilitate the release of volatile organic compounds. Contrary to our predictions, anointing occurred significantly more often during the non-breeding season when mosquito and *P. downsi* numbers are lower. Four Darwin's finch species anointed their feathers habitually and during the non-breeding season 56 % of all preening events were with leaves. We found no effect of sex but preening with leaves occurred predominately in the morning when leaves were wet. Our study is the first to provide quantitative data on anointing behaviour in birds and the high percentage of preening with leaves in the non-breeding season suggests that the behaviour has an adaptive value. However, further studies are needed to test whether it reduces the negative impact of parasites other than mosquitoes and *P. downsi*.

Abstract

Vögel sind Wirte für eine große Anzahl an Ektoparasiten und haben verschiedene Verhaltensstrategien entwickelt, um diese zu bekämpfen, z.B. Gefieder putzen, Sand- und Wasserbaden. Zusätzlich inkludieren viele Arten Insekten oder Teile von Pflanzen welche pharmazeutischen Wirkungen besitzen in ihr Putzverhalten. Jedoch sind Observationen von solchen Ereignissen anekdotisch. Darwinfinken inkludieren bei ihrer Gefiederpflege die Blätter eines endemischen Baumes (*Psidium galapageium*) welche Komponenten beinhalten die sowohl auf Mosquitos als auch auf die invasive parasitische Fliege *Philornis downsi* abweisend wirken. Die Larven von *P. downsi* saugen Blut von Nestlingen und brütenden weiblichen Darwinfinken und führen dadurch zu einer hohen Nestling Mortalität. In dieser Studie haben wir, mittels eines indirekten Ansatzes, die Hypothese getestet, dass das Inkludieren von *P. galapageium* Blättern bei der Gefiederpflege die oben genannten Parasiten abweist. Mosquitos und *P. downsi* beeinflussen ihre Wirte hauptsächlich während der Brutsaison, weiters beeinflusst *P. downsi* nur brütende Weibchen und keine ausgewachsenen Männchen. Um diese Hypothese zu testen haben wir quantitative Daten über das Putzverhalten mit Blättern in Darwinfinken während der Brut- und nicht Brutsaison gesammelt. Weiters haben wir die Einflüsse von Tageszeit und Feuchtigkeit auf das Putzverhalten untersucht, da feuchte Bedingungen die Freisetzung von volatilen organischen Komponenten erleichtern. Im Gegenteil zu unserer Erwartung, ist das Inkludieren von Blättern signifikant häufiger in der Nicht-Brutsaison vorgekommen, wo die Zahlen von Mosquitos und *P. downsi* geringer sind als in der Brutsaison. Vier Arten von Darwinfinken haben regelmäßig Blätter in ihre Gefiederpflege inkludiert. Während der Nicht-Brutsaison waren in 56% von allen Putzbeobachtungen Blätter inkludiert. Es gab keinen Einfluss von Geschlecht auf das Verhalten, aber das Inkludieren von Blättern zeigte sich überwiegend am Morgen, wenn diese feucht waren. Unsere Studie ist die Erste welche quantitative Daten über

das Inkludieren von sekundären Stoffen in Vögeln zeigt. Der hohe Prozentsatz von Inklusion von Blättern in der nicht Brutsaison legt nahe, dass dieses Verhalten einen adaptiven Gewinn erbringt. Jedoch sind weitere Studien benötigt, um zu testen, ob dieses Verhalten einen negativen Einfluss auf weitere Parasiten als Mosquitos und *P. downsi* hat.

Schlagwörter: Darwinfinken, Gefiederpflege, *Psidium galapageium*, *Philornis downsi*, Zoopharmakognosie

Keywords: Darwin's finches, preening, *Psidium galapageium*, *Philornis downsi*, self-medication

Introduction

Parasites can have strong detrimental effects on host fitness and are therefore a major selective force on various host traits (Clayton & Moore, 1997; Grenfell et al., 1995; Loye & Zuk, 1991; Rätti et al., 1993; Toft et al., 1991). Hosts have developed a wide array of defence mechanisms to counteract the effects of parasitic pressure on their fitness (reviewed in Clayton & Wolfe, 1993). Birds are hosts to various types of ectoparasites including arthropods, bacteria and fungi (reviewed in Bush & Clayton, 2018). To combat them, they have developed a range of nest and body maintenance behaviours such as nest sanitation, preening, allopreening, scratching, water bathing, dust bathing and sunning (reviewed in Bush & Clayton, 2018). In addition, a wide range of avian taxa supplement their behavioural strategies with self-fumigation, which is the application of substances to the body or their nests for the treatment or control of parasites or parasite vectors (reviewed in Bush & Clayton, 2018; Huffman, 2019). These substances include insects, plants or even human-made products, which may be pungent and/or have pharmaceutical properties. For instance,

common starlings (*Sturnus vulgaris*) and Eurasian blue tits (*Cyanistes caeruleus*) incorporate specific fresh herbs with antimicrobial properties into their nests (Costa-Neto, 2012; Gwinner, 2013; Lambrechts & Dos Santos, 2000), while house sparrows (*Passer domesticus*) and house finches (*Carpodacus mexicanus*) incorporate the fibres of cigarette butts into their nests (Suárez-Rodríguez et al., 2013). A taxonomically more widespread behaviour is the anointment of feathers and skin with insects (e. g. ants, millipedes; Ehrlich et al., 1986; Parkes et al., 2003) or aromatic plants (e. g. Maia & Moore, 2011; Moore et al., 2006; Weldon et al., 2011). “Anting” is a behaviour which involves the anointment of the feathers with ants and is performed habitually by over 200 bird species (Clayton et al., 2010). The formic acid that is released during anting is assumed to repel harmful parasites (Falótico et al., 2007; reviewed in Potter, 1970; Revis & Waller, 2004). Anointing with plant materials has been observed in only a few bird species and observations are rare or anecdotal (reviewed in Clayton & Wolfe, 1993). For instance, common grackles (*Quiscalus quiscula*) have been observed to preen with marigold flowers (genus *Tagetes*), which contain a natural insect repellent (Nero & Hatch, 1984), as well as with the pulp and rind of a lime fruit, which have insecticidal properties (Clayton & Vernon, 1993; Rodriguez & Wrangham, 1993). Additionally, the monarch flycatchers (*Chasiempis sandwichensis*) rub berries of Brazilian pepper (*Schinus terebinthifolius*), which has antibiotic properties, onto their feathers (VanderWerf, 2005).

The current study investigated anointing behaviour in Darwin’s finches. In 2012, a green warbler finch (*Certhidea olivacea*) and later four other species of Darwin’s finches were observed for the first time tearing off the leaves of the endemic tree *Psidium galapageium* and rubbing them onto their feathers (Cimadom et al., 2016). The authors observed two different methods of anointing: 1) the sponge method, in which the bird threads a piece of leaf through its feathers and 2) the lotion method, in which the bird chews the leaf

first and applies the mashed leaf to its feathers. Cimadom et al. (2016) hypothesised that the birds use these leaves to repel ectoparasites that negatively impact the fitness of Darwin's finches, namely the blood-sucking fly *Philornis downsi* and mosquitoes. Several mosquito species are native to the Galápagos Islands but others have been introduced (e.g. *Culex quinquefasciatus*, *Aedes aegypti*; Sinclair, 2013) and transmit novel mosquito-borne pathogens such as avian poxvirus (Parker et al., 2011). The avian poxvirus causes lesions on toes, legs, and the tissue around the bill. Individuals that survive often have deformed or missing digits (Parker et al., 2011). The introduced parasitic fly *P. downsi* has an even stronger effect on the fitness of Darwin's finches than the poxvirus: approximately 55% of Darwin's finch nestlings die annually due to parasitism by this species (Fessler et al., 2018; Kleindorfer & Dudaniec, 2016). The fly's first larval stage is mainly found in the nestlings' nostrils. The second and third larval stages live in the bottom of the nest where they penetrate the skin of the nestlings and consume their blood (Fessler et al., 2006) and also attack incubating females (Cimadom et al., 2016; Knutie et al., 2013). Cimadom et al. (2016) demonstrated a repellent effect of extracts of *P. galapageium* on mosquitoes and adult *P. downsi* and a growth inhibiting effect on *P. downsi* larvae in the laboratory. The abundance of both above-mentioned parasites varies seasonally. *P. downsi* affects Darwin's finches mainly during the birds' breeding season (January – April), which is when their parasitic larval stage occurs in the finches' nests (Fessler et al., 2006). Mosquito abundance is also higher during the warm and rainy breeding season, as it is only then that favourable temperatures (> 20 °C) and the availability of stagnant water pools stimulate mosquito breeding (Asigau et al., 2017; Khan et al., 2018). On the Galápagos islands, mosquito abundance increases with precipitation but decreases with altitude (Asigau & Parker, 2018; Bataille et al., 2010). Combined these factors result in very low abundance of mosquitoes in the highlands of the Galápagos Islands during the cool non-breeding season (Asigau et al.,

2017). The seasonality of *P. downsi* and mosquitoes' parasites provide an indirect approach to test whether Darwin's finches use *P. galapageium* leaves to repel them, which is why we focus on them even so Darwin's finches also suffer from other parasites. If *P. downsi* and mosquitoes are targeted by this behaviour, the frequency of preening with leaves should also match the abundance of the targeted organisms.

Furthermore, it has been suggested that time of day and humidity influence preening behaviour and could also influence preening with plants that release volatiles. Wet conditions of high humidity are known to facilitate the release of volatile organic compounds (VOC; Gouinguéné & Turlings, 2002; Salerno et al., 2017; Vallat et al., 2005). In several bird species, the frequency of preening peaked in the early morning (Henson et al., 2007; Robbins, 1981) and increased with increasing humidity (Brown, 1974; Henson et al., 2007).

In our study, we tested the hypothesis that preening with leaves by Darwin's finches serves to repel the invasive parasitic fly *P. downsi* and/or native and introduced mosquitoes. We predicted that if preening with *P. galapageium* serves to protect incubating females from *P. downsi*, the behaviour should be more frequently observed in females and more frequently during their breeding season. If preening serves to protect against mosquitoes, we expected the behaviour to be evenly distributed across both sexes and to increase with the high abundance of mosquitoes in the breeding season. To test these hypotheses, we gathered quantitative data on leaf-preening behaviour of Darwin's finches during the breeding and non-breeding season. We measured whether the occurrence of leaf-preening is influenced by season, time of day or wetness of leaves and whether it differs between the sexes.

Methods

Study area

This study was conducted in Los Gemelos (0°37'34" S, 90°23'10" W), at an elevation of around 600 m, in the humid "*Scalesia*" forest on the Island of Santa Cruz, Galapagos from

January 19–March 8, 2019 (main breeding season of Galápagos landbirds) and September 3–25, 2019 (non-breeding season). Some of the most prominent tree species in the forest are the endemic species *Scalesia pedunculata*, *Solanum cheesmaniae* and *Psidium galapageium*. The forest has been invaded by alien shrubs such as *Rubus niveus*, *Tradescantia fluminensis* and *Cestrum auriculatum* (Rivas-Torres et al., 2018).

The climate on the Galápagos Islands is highly seasonal. During the breeding season, from January to April, mean air temperatures in the humid highlands range between 16 and 28 °C and the skies are usually clear with occasional heavy rain showers. During the non-breeding season from June to December, the temperature is lower (ranging between 13 and 20 °C) and while there is hardly any precipitation in the lowlands, the highlands are continuously wet due to a consistent, dense mist (Causton et al., 2019; Jackson, 1993).

Behavioural observations

We selected 30 points for behavioural observations. Each point contained at least three medium-sized *P. galapageium* trees (>3 m high) and points were 100 m apart from each other (Figure S1). The distance between observation points was chosen to minimise possible overlaps of bird territories between points and was measured via GPS. At each point, we recorded the following habitat parameters: canopy height as well as the total number of and height of *P. galapageium* within a radius of 15 m (hereafter “point radius”). The point radius was measured with a laser range finder. Each point was visited five times per season between 6:00 and 11:00, which is the period of highest bird activity. On average, eight points were visited per day and routes between points were chosen so that each point was visited at different hours of the day. At each point, all behavioural observations were made within the 15 m point radius. After an initial training phase involving two observers (ST and TS), all behavioural observations were made by one person (TS). At the beginning of each visit, the observer noted the number and species identity of the passerines present within the point

radius. Then, for a duration of 30 min, preening events were recorded, along with the specification of whether preening was conducted with or without *P. galapageium*. The observer did not record whether birds that preened with leaves, used the sponge or lotion method because this would have required focal observation of preening individuals and would have increased the probability to miss preening individuals. The following parameters were recorded for each preening individual: species identity, life stage (adult vs. juvenile) and sex (male vs. female/immature male combined; see below for explanation of latter categorization). Adult males were identified using plumage characteristics, beak colour and song activity: small ground finch (*Geospiza fuliginosa*), medium ground finch (*Geospiza fortis*) and large ground finch males (*Geospiza magnirostris*) show a streaky plumage from crown to chin and their overall plumage darkens with every moult until they are completely black (Kleindorfer et al., 2019). Small tree finch (*Camarhynchus parvulus*) females and immature males have a light brown colouration. Mature males have black feathers on the head, starting at the beak and later forming a dark hood that extends down to throat and breast (Kleindorfer et al., 2019). Green warbler finch females and immature males have a grey-greenish colouration while males can be distinguished by their orange throat (Kleindorfer et al., 2019). In Darwin's finches, only males sing, thus any bird that sang was identified as male. However, yearling males of all Darwin's finches that do not sing cannot be distinguished from females and were therefore categorised as being in the female-immature male group (other). Juveniles were identified by pink beak colouration and begging behaviour. We distinguished individuals that were present at the same time and new arrivals based on species, sex and plumage colouration. Observations of individuals that looked the same and were not observed simultaneously were excluded from the data set.

At the start of each observation, leaves of *P. galapageium* at the observation point were scored as wet when the leaf surface exhibited visible dew or water droplets. Otherwise,

they were scored as dry. The initial time was noted as well as the weather conditions, which were categorised as rain vs. no rain and sun vs. fog. Temperature and humidity were recorded with two DS1923 hygchron temperature/humidity data loggers (iButton®).

Statistical analyses

For the statistical analyses, juveniles were excluded because they were not observed preening with leaves during the breeding season. Only data from four species (the green warbler finch, small ground finch, medium ground finch and small tree finch) were analysed. Observations of the woodpecker finch (*Camarhynchus pallidus*), large tree-finch (*Camarhynchus psittacula*), Galápagos flycatcher (*Myiarchus magnirostris*) and yellow warbler (*Setophaga petechial aureola*) were excluded because they were never or only once observed preening with leaves (Table 1).

Table 1: Observations of preening with and without leaves for the 8 observed species. Species in the four bottom rows were excluded from the analysis because they were never or only once observed to preen with leaves.

Species	preening without leaves	preening with leaves	total preening events	total observations, non-breeding season	total observations, breeding season
Medium Ground Finch	7	15	22	73	11
Small Ground Finch	61	30	91	263	151
Small Tree Finch	29	24	53	146	114
Green Warbler Finch	49	14	63	195	323
Galapagos Flycatcher	3	0	3	3	0
Large Tree Finch	1	0	1	0	1
Woodpecker Finch	14	1	15	5	10
Yellow Warbler	4	1	5	2	3

We fitted a generalised linear mixed regression model to the binary preening data (with leaves vs. without leaves) to test for effects of season (non-breeding vs. breeding season), sex (male vs. other), wetness of leaves (dry vs. wet), and time of day. Season, sex, and wetness of leaves were included as binary categorical predictors and time was treated as a numerical predictor (time of day at preening event, ranging from 6:00 to 11:00). To account for the fact that the observed preening events varied substantially between observation points, we included point ID, ranging from one to 30, as a random factor (random intercept) in our model. The statistical significance of coefficients was assessed using likelihood ratio tests.

We had no clear *a priori* hypotheses concerning which species might anoint with *P. galapageium* more or less than the others nor concerning how rain, sun or temperature would affect preening behaviour. We did not conduct hypothesis tests for these variables and did not include them in the regression model, but we explored their effects by visualising their associations with preening.

All statistical analyses were conducted in the statistical programming language R (version 4.0.1, R Core Team, 2020). R-package *janitor* (Firke, 2020) was used for data cleaning, package collection *tidyverse* (Wickham et al., 2019) and package *patchwork* (Pedersen, 2020) were used for analysis and plotting. Model fitting was done using the package *lme4* (Bates et al., 2015). Data and code are available on GitHub (Tebbich et al., 2020).

Results

We observed 229 preening events in total for the four species included in the analysis (the green warbler finch, small ground finch, medium ground finch and small tree finch). Of these observations, 146 were without leaves and 83 were with leaves.

The average temperature calculated over all preening events was 15.4 °C (STD=1.12) in the non-breeding season and 20.8 °C (STD=3.82) in the breeding season. It rained in 76% of all observations in the non-breeding season but only in 6% of all observations in the breeding season. The frequency of observations with sunshine was 2% in the non-breeding season and 52% in the breeding season. The average humidity was 99.9% (STD=0.98) in the non-breeding season and 96.5% (STD=5.50) in the breeding season.

Preening with leaves occurred predominantly in the non-breeding season and peaked in the early morning hours in all four observed species. Preening without leaves was more evenly distributed across the morning and occurred mainly in the breeding season (Figure 1A, B). In the non-breeding season, 56% of all preening events were with leaves, whereas in the breeding season only 10.8% were with leaves.

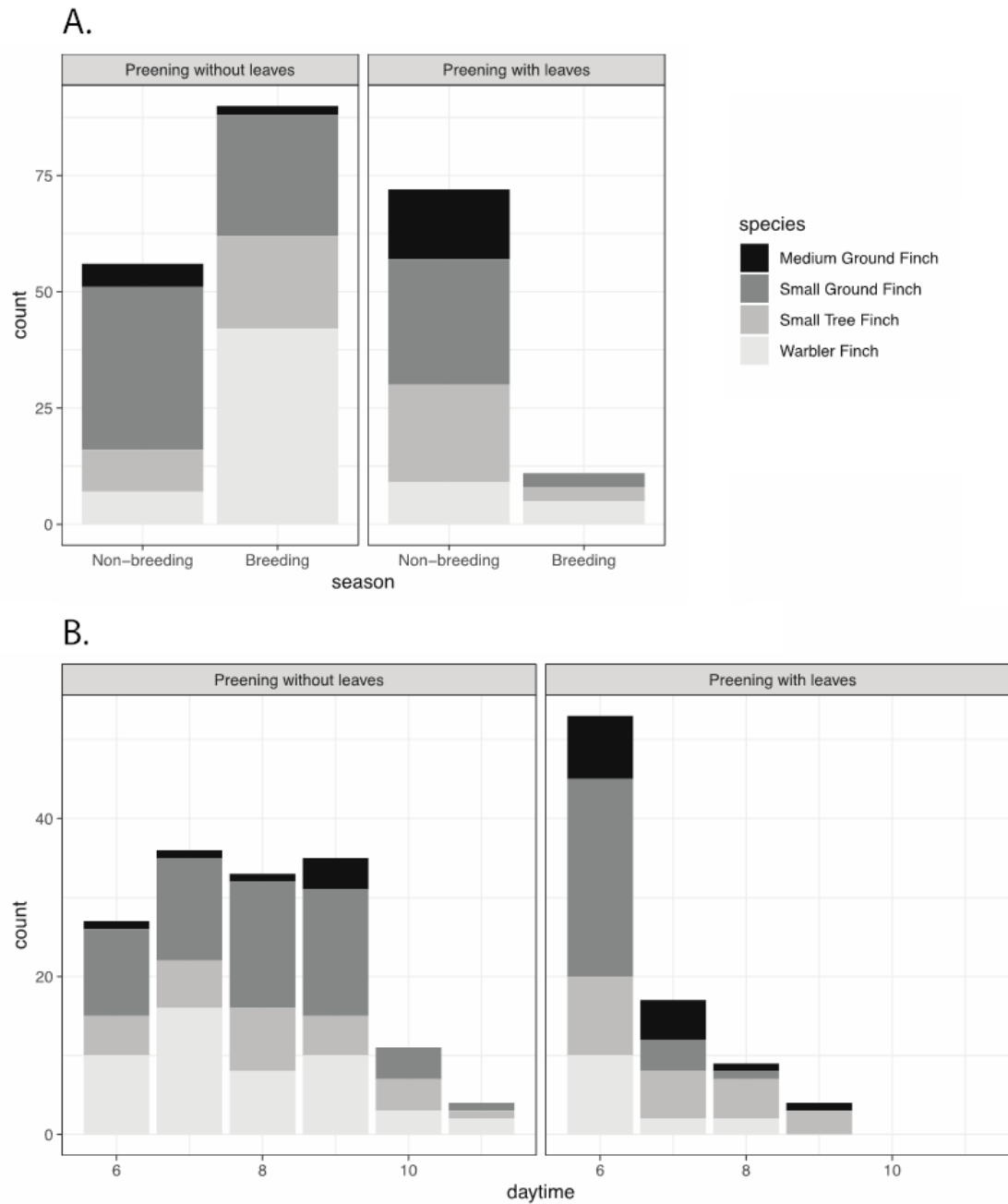


Fig. 1: Preening events without vs. with leaves, plotted against season (A.) and time of day (B.) for the four observed species.

The effects of season and time of day on the probability of preening with leaves were statistically significant ($p < 0.001$ for both). Effect size estimates derived from the model for season and time of day were similar with and without inclusion of sex and wetness of leaves as predictors. The estimated probabilities of preening with leaves in the breeding vs.

non-breeding season were 0.36 and 0.85 at 6:00; however, at 10:00, they were 0.01 and 0.09, respectively.

Both sexes preened with leaves at a similar frequency (effect of sex was not statistically significant in the model, $p = 0.16$; Figure 2).

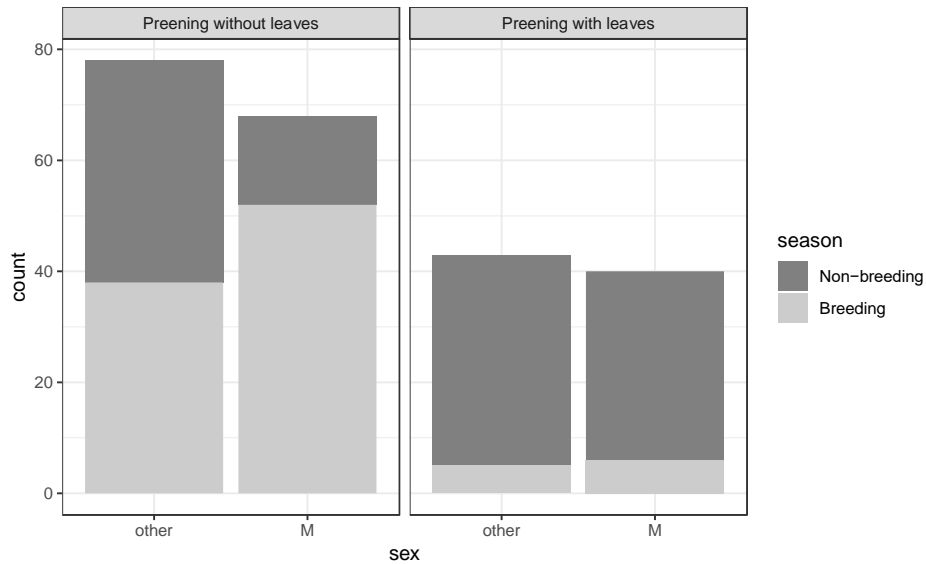


Fig. 2: Preening events without vs. with leaves, separately for males and other (females and immature males) and season.

There were species differences in the preening patterns between the seasons (Figure 1A). For example, medium ground finches preened predominantly in the non-breeding season and almost exclusively with leaves, whereas warbler finches preened mainly without leaves in the breeding season.

The behaviour of preening with leaves occurred when wet leaves were present in the non-breeding season (Figure 3) and both preening with leaves and occurrence of wet leaves showed the same decreasing daily trend (Figure 4). However, the effect of leaf wetness on preening with vs. without leaves was strongly correlated with season ($r = 0.66$) and therefore was itself not statistically significant in the model ($p = 0.10$). Humid conditions were ever-present in the non-breeding season, so the vegetation was frequently wet (correlation between

rain and presence of wet leaves was $r = 0.77$, correlation between season and rain was $r = 0.70$).

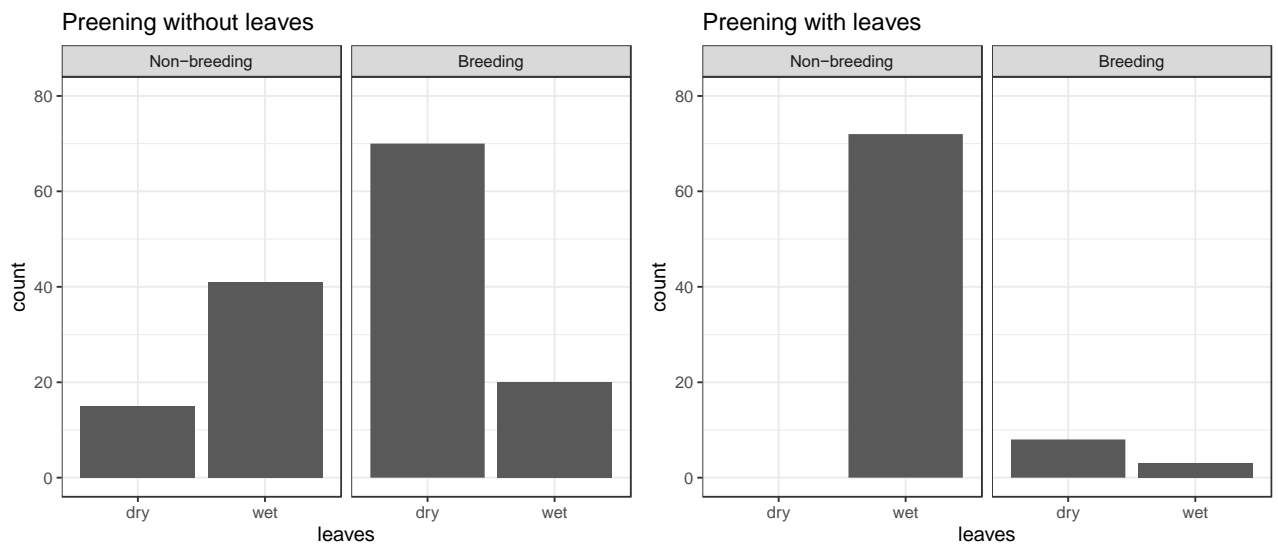


Fig. 3: Preening events with and without leaves, separately for breeding and non-breeding seasons and for dry vs. wet leaves.

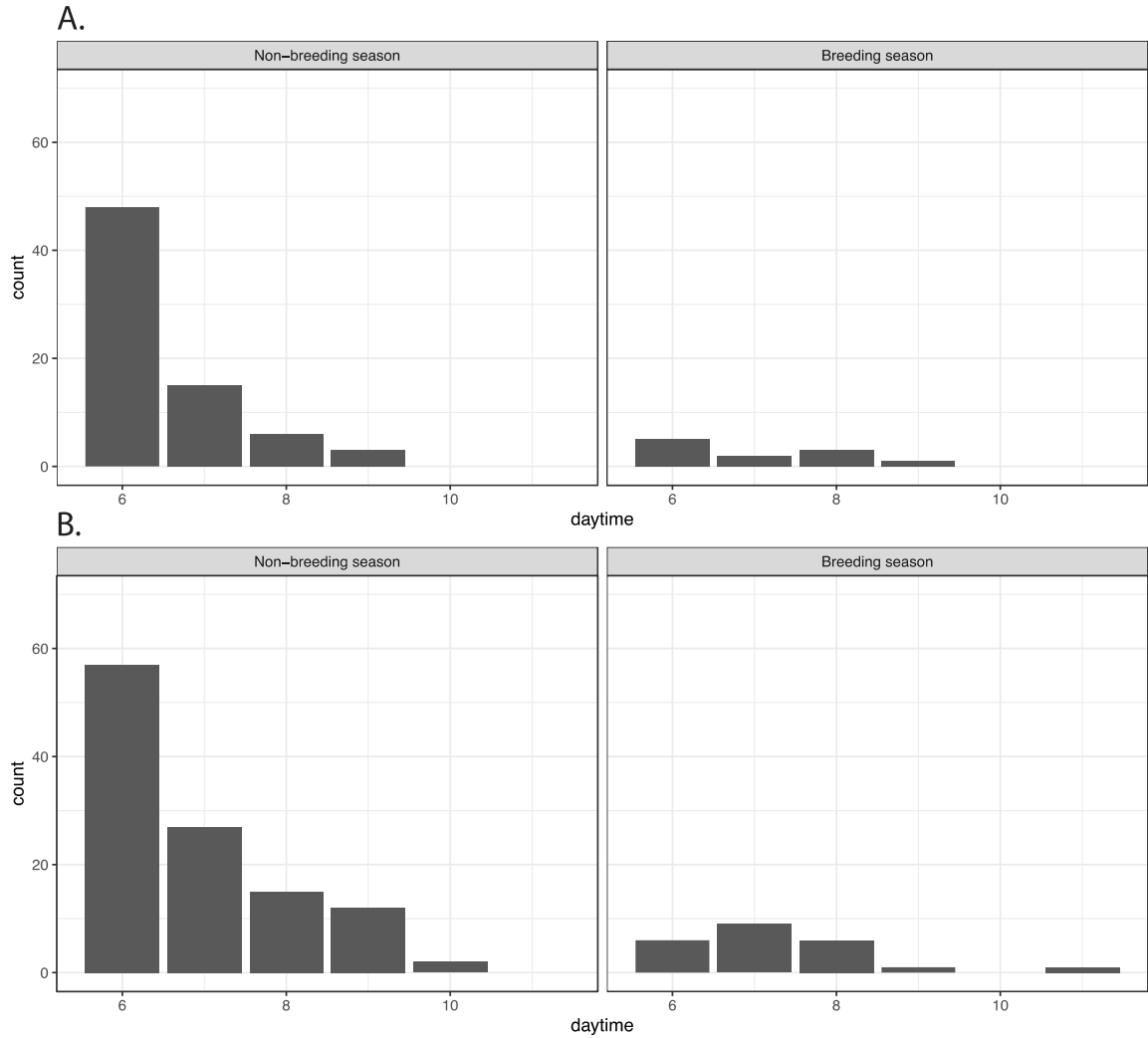


Fig. 4: Observations of preening events with leaves (A.) and observations of wet leaves (B.) plotted against time of day, separately for the non-breeding and breeding seasons.

Discussion

Contrary to our prediction, leaf preening occurred more frequently in the non-breeding season, when mosquito activity is low and Darwin's finches are not affected by *P. downsi* larvae. In addition, adult males preened as often as females and immature males. These findings suggest that preening with *P. galapageium* leaves does not primarily target mosquitos and *P. downsi* larvae, as mosquitos and *P. downsi* are not abundant during non-breeding season and only females are affected by the blood-sucking larvae of *P. downsi*.

The behaviour could, however, be important for repelling other ectoparasites such as feather mites, feather lice, feather degrading bacteria and fungi. Villa et al., 2013 recorded 8 genera of feather mites from the same Darwin's finch species in the same study area during the breeding season.. Seasonal patterns of their diversity, prevalence and intensity have not been studied to date. An experimental study on feather mites demonstrated that mites suffer from desiccation at relative humidity (RH) below 55% (Gaede & Knülle, 1987); however, in our study area, the RH was always well above this value in both seasons. In addition, most feather mites do not negatively impact birds (Dowling et al., 2001; Matthews et al., 2018), rather they have a mutualistic relationship with their host, cleansing the birds' feathers from fungi and bacteria (Doña et al., 2019). Villa et al. (2013) did find very small numbers of blood-feeding mites (*Pellonyssus* sp.) on Darwin's finches, but these numbers were too low to enable investigation of seasonal patterns. Given the small numbers found on Darwin's finches, it does not seem likely that the blood feeding mites are the main target of leaf preening behaviour.

In addition to mites, three genera of lice have also been found on Darwin's finches (*Brueelia*, *Myrsidea* and *Philopterus*; Palma & Peck, 2013). The feather louse (*Myrsidea rustica*) has indirect negative effects on flight performance of barn swallows (*Hirundo rustica*; Barbosa et al., 2002) and lice load increased with humidity in mourning doves (*Zenaida macroura*) and Inca doves (*Columbina inca*)(Moyer et al., 2002). However, dust ruffling of 26 Darwin's finches during the non-breeding season in 2020 revealed low prevalence (30.8% of birds with lice) and very low intensity (mean $2.0 \pm SE 0.42$ lice per infested bird; $n = 8$) of feather lice, making them an unlikely target (Courtney Pike unpublished data).

Keratinophilic fungi or feather-degrading bacteria have not yet been studied in Darwin's finches but are found in a wide range of avian taxa. They have been associated with

impaired flight performance and an increased risk of predation by raptors (Al Rubaiee et al., 2017; Møller et al., 2012). and in the northern United State l incidences of feather bacteria on house sparrows were highest in late fall and winter (Burt & Ichida, 1999) in ss The authors suggest that the higher incidence may be related to higher temperature and humidity but also to increased exposure to ultraviolet (UV) light, as it kills the vegetative cells of bacteria and their spores (Madigan et al., 1997). Humidity was always high at our study site, but temperature and the number of hours of sunshine were low during the non-breeding season. This combination of environmental factors could potentially lead to seasonality in feather-degrading bacteria.

The influence of climate conditions on feather-degrading fungi is less clear. A study in house sparrows (*Passer domesticus L.*) showed no overall seasonal pattern (Hubálek, 1976).

Analysis of the ethanolic extract and the essential oil of *P. galapageium* and its respective fractions (Cimadom et al., 2016) revealed that this plant not only contains insect repellent or insecticidal compounds but also compounds with antimicrobial properties (α - Pinene, Nerolidol, Eucalyptol, Terpinene, Guiaol; Chan et al., 2016; Choudhary et al., 2007; Gilles et al., 2010; Iacobellis et al., 2005; Maciel et al., 2010; Nissen et al., 2010). In addition, the closely related tree species, *Psidium guajava*, has antifungal and antibacterial properties (Morais-Braga et al., 2017; Padrón-Márquez et al., 2012; Pandey & Shweta, 2011). Combined, these findings raise the possibility that preening with *P. galapageium* reduces feather-damaging microbes. However, this needs to be tested in future studies with an experimental approach in which the incidence and seasonality of feather microbes is sampled. The antimicrobial properties of *P. galapageium* could be tested *in vitro* on the samples taken from the birds' feathers. *P. galapageium* also contains eucalyptol (Cimadom et al., 2016, Martina et al. submitted), which has skin soothing properties (Gilles et al., 2010). If parasites

cause itchy skin irritations, a soothing effect of *P. galapageium* could elicit the behaviour of preening with leaves.

As predicted, the behaviour of preening with leaves co-occurred with the presence of wet leaves in the non-breeding season. During the breeding season almost all of the few observations of preening with leaves occurred before 9:00. Both humidity and moistness of leaves decreased with time of day, which could explain why preening with leaves occurred more frequently during the early hours of the day. Wet conditions facilitate the release of volatile organic compounds (VOCs) by plants (Gouinguéné & Turlings, 2002; Salerno et al., 2017; Vallat et al., 2005) and thus more VOCs may be present in the early morning hours when humidity is high, making leaf preening at this time more effective. Whether time of day, rain, wetness of leaves or other factor such as the activity of herbivorous insects (Hare 2011) increases the release of VOCs needs to be tested. This could give greater insight into the possible function of this behaviour but also its annual pattern. For example, if any of the above mentioned factors triggers volatile emission, the effect on the fitness of the bird could be episodic and impact different ectoparasites at different times of the year but also lead to variation between years. On the Galápagos Islands climatic conditions vary strongly between years (Jackson 1993) and thus sampling of volatile emission and preening behaviour throughout the year and over several years would be necessary a comprehensive picture. An alternative explanation for the peak of leaf preening in the morning is that the preening pattern follows the activity of the parasites. For instance, amblyceran chewing lice but also the larvae of *P. downsi* instance have a diurnal feeding rhythm. (Stenkewitz et al 2017, O'Connor et al. 2010).

A higher concentration of volatiles could also be the mechanism by which preening with leaves is triggered. The ability to detect VOCs through olfaction (Amo et al., 2011; Krause & Caspers, 2012; Nelson Slater & Hauber, 2017) or taste (Berkhoudt, 1992; Niknafs

& Roura, 2018) has been demonstrated in several bird species, but not yet in Darwin's finches. Testing whether Darwin's finches are attracted to *P. galapageium* trees through olfaction or taste would be an important step in understanding how the behaviour of preening with this species' leaves is triggered in Darwin's finches at a proximate level. If Darwin's finches are able to detect the volatile compounds of *P. galapageium* leaves it seems plausible that they would also incorporate them into their nest as self-fumigation with medical plants may have beneficial effects on the health of the nestlings (reviewed in Gwinner 2013). However, although we dismantled over 600 warbler finch and small tree finch nests since 2012 (Cimadom et al. 2019), we never found any leaves in the nest material.

In our study area, six species of Darwin's finches are regularly present. Four of these species provided enough data for statistical analyses and they were all found to use *P. galapageium* leaves habitually in preening. Thus, it seems plausible that this behaviour is widespread among Darwin's finches, but currently there are no data from other islands and vegetation zones. The fact that preening with leaves occurs in several Darwin's finches suggests that this behaviour evolved before the niche specialisation of the Darwin's finches and probably has a strong genetic component. Darwin's finches are known for their wide range of unusual foraging techniques that are rare amongst passerines (reviewed in Tebbich et al., 2010). Tebbich et al. (2010) found high cognitive flexibility in species that show innovative techniques but also in species that do not. In line with the "flexible stem hypothesis" (West-Eberhard, 2003), this indicates that Darwin's finches derived from a highly flexible ancestor Tebbich et al. (2010). According to this theory high flexibility allowed the ancestors of the Darwin's finches to persist in a novel environment and behavioural adaptation would have been upheld by learning but later genetic accommodation (Weber & Depew, 2003) would have entrenched some or all components of this behaviour. In line with this scenario tool-use in the woodpecker finches has genetically fixed components

but also components which are developed in ontogeny through individual learning (Tebbich et al., 2001). A similar scenario can be envisaged for preening with leaves, but this needs to be tested experimentally. Alternatively, this behaviour could have been discovered by one or several individuals of one species and then passed on between species by way of a cross-species transfer of information (Avarguès-Weber et al., 2013; Krebs, 1973).

Additionally, our results show that juveniles apparently only start preening with leaves in the non-breeding season, which may indicate that this behaviour needs time to mature or that Darwin's finches need time to acquire this behaviour through social learning, as has been shown in other bird species (Slagsvold & Wiebe, 2011; Zentall, 2004). An alternative explanation is that juveniles suffer less from parasites and therefore show less leaf preening behaviour.

In conclusion, currently we can only speculate about the function of preening with leaves of *P. galapageium*, but our study is the first to quantify topical application of a plant species and to report this as a predictable, habitual behaviour that varies seasonally in a closely related species group. In the non-breeding season, the frequency of this behaviour was surprisingly high (56% of all preening events), which suggests that this behaviour has adaptive value. Anointing feathers with secondary products (ants, millipedes, beetles, caterpillars, plant materials and pesticides) is taxonomically widespread, but rare, which makes it hard to evaluate the significance of this behaviour to birds' fitness (reviewed in Bush & Clayton, 2018; reviewed in Potter, 1970). For instance, although anting has been observed in over 200 species, evidence that it reduces parasite load is scarce (reviewed in Bush & Clayton, 2018). This is probably attributable to methodological difficulties associated with measuring the effect of anointing and other forms of self-medication (Bush & Clayton, 2018; de Roode et al., 2013).

Clayton and Wolfe (1993) established three criteria for defining self-medication behaviour: (1) the medicinal substance must be deliberately contacted by the mediator; (2) the substance must be detrimental to one or more parasites when contacted and (3) the detrimental effect on parasites leads to an increase in host fitness. Preening with *P. galapageium* leaves already satisfies two criteria of self-medication, as the leaves are actively applied by the birds and Cimadom et al. (2016) have demonstrated repellent qualities against potential parasites. However, we were unable to identify which parasites the birds are targeting and cannot provide evidence for parasite-reducing or fitness-enhancing effects.

While we are not currently able to identify the function of anointing in Darwin's finches, this behaviour is another example of the incredible behavioural diversity of this species group and is one of several examples in which animal behaviour has led humans to the discovery of the pharmaceutical properties of an endemic plant species (Huffman, 2002). An international research group is currently investigating short and long-term measures to mitigate the effects of *P. downsi* and experiments with Nerolidol, one of the main compounds of *P. galapageium*, are yielding the first promising results showing that it is an effective repellent of adult flies.

Acknowledgments

I thank Erwin Nemeth for his advice on the study design and statistical analysis. I am further thankful for the team of the Charles Darwin foundation which gave me useful tips and support. Finally, I thank Sabine Tebbich for considering me for this project and enabling me to visit such a beautiful and far-off place, I am sure it wasn't always easy with me but I am glad she pulled through. Permission to conduct this study was granted by the Galápagos National Park Directorate (Project PC-35-19: Control of the Invasive Parasite, *P. downsi* and its Impact on Biodiversity). This work was funded by the University of Vienna (Interdisziplinäre Forschungsnetzwerke 2018 and KWA-Fellowship).

References

- Al Rubaiee, Z., Al Murayati, H., Nielsen, J. T., & Møller, A. P. (2017). Fungi, feather damage, and risk of predation. *Ecology and Evolution*, 7(24), 10797–10803. <https://doi.org/10.1002/ece3.3582>
- Amo, L., Visser, M. E., & Oers, K. van. (2011). Smelling out predators is innate in birds. *Ardea*, 99(2), 177–184. <https://doi.org/10.5253/078.099.0207>
- Asigau, S., Hartman, D. A., Higashiguchi, J. M., & Parker, P. G. (2017). The distribution of mosquitoes across an altitudinal gradient in the Galapagos Islands. *Journal of Vector Ecology*, 42(2), 243–253. <https://doi.org/10.1111/jvec.12264>
- Asigau, S., & Parker, P. G. (2018). The influence of ecological factors on mosquito abundance and occurrence in Galápagos. *Journal of Vector Ecology*, 43(1), 125–137. <https://doi.org/10.1111/jvec.12292>
- Avarguès-Weber, A., Dawson, E. H., & Chittka, L. (2013). Mechanisms of social learning across species boundaries. *Journal of Zoology*, 290(1), 1–11. <https://doi.org/10.1111/jzo.12015>
- Barbosa, A., Merino, S., De Lope, F., & Møller, A. P. (2002). Effects of feather lice on flight behavior of male Barn Swallows (*Hirundo rustica*). *The Auk*, 119(1), 213–216. <https://doi.org/10.2307/4090025>
- Bataille, A., Cunningham, A. A., Cruz, M., Cedeno, V., & Goodman, S. J. (2010). Seasonal effects and fine-scale population dynamics of *Aedes taeniorhynchus*, a major disease vector in the Galapagos Islands. *Molecular Ecology*, 19(20), 4491–4504. <https://doi.org/10.1111/j.1365-294X.2010.04843.x>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1). <https://doi.org/10.18637/jss.v067.i01>
- Berkhoudt, H. (1992). Avian taste buds: topography, structure and function. In R. L. Doty & D. Müller-Schwarze (Eds.), *Chemical signals in vertebrates 6* (pp. 15–20). Springer US. https://doi.org/10.1007/978-1-4757-9655-1_3
- Brown, N. S. (1974). The effect of louse infestation, wet feathers, and relative humidity on the grooming behavior of the domestic chicken. *Poultry Science*, 53(5), 1717–1719. <https://doi.org/10.3382/ps.0531717>
- Burt Jr, E. H., & Ichida, J. M. (1999). Occurrence of feather-degrading bacilli in the plumage of birds. *The Auk*, 116(2), 364–372. <https://doi.org/10.2307/4089371>
- Bush, S. E., & Clayton, D. H. (2018). Anti-parasite behaviour of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1751), 0–3. <https://doi.org/10.1098/rstb.2017.0196>
- Causton, C. E., Moon, R. D., Cimadom, A., Boulton, R. A., Cedeño, D., Lincango, M. P., Tebbich, S., & Ulloa, A. (2019). Population dynamics of an invasive bird parasite, *Philornis downsi* (Diptera: Muscidae), in the Galapagos Islands. *PLoS One*, 14(10), e0224125. <https://doi.org/10.1371/journal.pone.0224125>
- Chan, W.-K., Tan, L. T.-H., Chan, K.-G., Lee, L.-H., & Goh, B.-H. (2016). Nerolidol: a sesquiterpene alcohol with multi-faceted pharmacological and biological activities.

Molecules, 21(5), 529. <https://doi.org/10.3390/molecules21050529>

- Choudhary, M. I., Batool, I., Atif, M., Hussain, S., & fnm Atta-ur-Rahman. (2007). Microbial transformation of (–)-guaiol and antibacterial activity of its transformed products. *Journal of Natural Products*, 70(5), 849–852. <https://doi.org/10.1021/np068052a>
- Cimadom, A., Causton, C., Cha, D. H., Damiens, D., Fessl, B., Hood-Nowotny, R., Lincango, P., Mieles, A. E., Nemeth, E., Semler, E. M., Teale, SA & Tebbich, S (2016). Darwin’s finches treat their feathers with a natural repellent. *Scientific Reports*, 6(1), 1–9. <https://doi.org/10.1038/srep34559>
- Cimadom, A., Jäger H., Schulze, C.H., Hood-Nowotny, R., Wappl, C., & Tebbich, S. (2019) Weed management increases the detrimental effect of an invasive parasite on arboreal Darwin’s finches. *Biological Conservation*, (233), 93–101 <https://doi.org/10.1016/j.biocon.2019.02.025>
- Clayton, D. H., Koop, J. A. H., Harbison, C. W., Moyer, B. R., & Bush, S. E. (2010). How birds combat ectoparasites. *The Open Ornithology Journal*, 3(1). <https://doi.org/10.2174/1874453201003010041>
- Clayton, D. H., & Moore, J. (1997). Host-parasite evolution: general principles and avian models. In *Journal of Animal Ecology* (Vol. 14, Issue 2). Oxford [u.a.]: Oxford Univ. Press.
- Clayton, D. H., & Vernon, J. G. (1993). Common grackle anting with lime fruit and its effect on ectoparasites. *The Auk*, 110(4), 951–952. <https://doi.org/10.2307/4088657>
- Clayton, D. H., & Wolfe, N. D. (1993). The adaptive significance of self-medication. *Trends in Ecology & Evolution*, 8(2), 60–63. [https://doi.org/10.1016/0169-5347\(93\)90160-Q](https://doi.org/10.1016/0169-5347(93)90160-Q)
- Costa-Neto, E. M. (2012). Zoopharmacognosy, the self-medication behavior of animals. *Interfaces Científicas - Saúde e Ambiente*, 1(1), 61. <https://doi.org/10.17564/2316-3798.2012v1n1p61-72>
- de Roode, J. C., Lefèvre, T., & Hunter, M. D. (2013). Self-medication in animals. *Science*, 340(6129), 150–151. <https://doi.org/10.1126/science.1235824>
- Doña, J., Proctor, H., Serrano, D., Johnson, K. P., Oploo, A. O. van, Huguet-Tapia, J. C., Ascunce, M. S., & Jovani, R. (2019). Feather mites play a role in cleaning host feathers: New insights from DNA metabarcoding and microscopy. *Molecular Ecology*, 28(2), 203–218. <https://doi.org/10.1111/mec.14581>
- Dowling, D. K., Richardson, D. S., & Komdeur, J. (2001). No effects of a feather mite on body condition, survivorship, or grooming behavior in the Seychelles warbler, *Acrocephalus sechellensis*. *Behavioral Ecology and Sociobiology*, 50(3), 257–262. <https://doi.org/10.1007/s002650100360>
- Dvorak, M., Fessl, B., Nemeth, E., Kleindorfer, S., & Tebbich, S. (2012). Distribution and abundance of Darwin’s finches and other land birds on Santa Cruz Island, Galápagos: evidence for declining populations. *Oryx*, 46(1), 78–86. <https://doi.org/10.1017/S0030605311000597>
- Ehrlich, P. R., Dobkin, D. S., & Wheye, D. (1986). The adaptive significance of anting. *The Auk*, 103(4), 835.
- Falótico, T., Labruna, M. B., Verderane, M. P., De resende, B. D., Izar, P., & Ottoni, E. B.

- (2007). Repellent efficacy of formic acid and the abdominal secretion of carpenter ants (Hymenoptera: Formicidae) against *Amblyomma* ticks (Acari: Ixodidae). *Journal of Medical Entomology*, 44(4), 718–721. <https://doi.org/10.1093/jmedent/44.4.718>
- Fessl, B., Heimpel, G. E., & Causton, C. E. (2018). Invasion of an avian nest parasite, *Philornis downsi*, to the Galapagos Islands: colonization history, adaptations to novel ecosystems, and conservation challenges. In *Disease Ecology* (pp. 213–266). Springer. https://doi.org/10.1007/978-3-319-65909-1_9
- Fessl, B., Sinclair, B. J., & Kleindorfer, S. (2006). The life-cycle of *Philornis downsi* (Diptera: Muscidae) parasitizing Darwin's finches and its impacts on nestling survival. *Parasitology*, 133(6), 739–747. <https://doi.org/10.1017/S0031182006001089>
- Firke, S. (2020). *Janitor: Simple tools for examining and cleaning dirty data. R package version 2.0. 1*. <https://github.com/sfirke/janitor>
- Gaede, K., & Knülle, W. (1987). Water vapour uptake from the atmosphere and critical equilibrium humidity of a feather mite. *Experimental & Applied Acarology*, 3(1), 45–52. <https://doi.org/10.1007/BF01200412>
- Gilles, M., Zhao, J., An, M., & Agboola, S. (2010). Chemical composition and antimicrobial properties of essential oils of three Australian Eucalyptus species. *Food Chemistry*, 119(2), 731–737. <https://doi.org/10.1016/j.foodchem.2009.07.021>
- Gouinguéné, S. P., & Turlings, T. C. J. (2002). The effects of abiotic factors on induced volatile emissions in corn plants. *Plant Physiology*, 129(3), 1296–1307. <https://doi.org/10.1104/pp.001941>
- Grenfell, B. T., Dobson, A. P., & Moffatt, H. K. (1995). *Ecology of infectious diseases in natural populations* (Vol. 7). Cambridge University Press.
- Gwinner, H. (2013). Male European starlings use odorous herbs as nest material to attract females and benefit nestlings. In *Chemical signals in vertebrates 12* (pp. 353–362). Springer. https://doi.org/10.1007/978-1-4614-5927-9_28
- Hare, J. D. (2011). Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annual Review of Entomology*, 56, 161–180. <https://doi.org/10.1146/annurev-ento-120709-144753>
- Henson, S. M., Galusha, J. G., Hayward, J. L., & Cushing, J. M. (2007). Modeling territory attendance and preening behavior in a seabird colony as functions of environmental conditions. *Journal of Biological Dynamics*, 1(1), 95–107. <https://doi.org/10.1080/17513750601032679>
- Hubálek, Z. (1976). Seasonal distribution of fungi on house sparrows. *Transactions of the British Mycological Society*, 66(3), 509–516. [https://doi.org/10.1016/s0007-1536\(76\)80223-9](https://doi.org/10.1016/s0007-1536(76)80223-9)
- Huffman, M. A. (2002). Animal origins of herbal medicine. *From the Sources of Knowledge to the Medicines of the Future. IRD Editions, Paris*, 31–42.
- Huffman, M. A. (2019). *Self-medication: passive prevention and active treatment*. 696–702.
- Iacobellis, N. S., Lo Cantore, P., Capasso, F., & Senatore, F. (2005). Antibacterial activity of *Cuminum cyminum* L. and *Carum carvi* L. essential oils. *Journal of Agricultural and Food Chemistry*, 53(1), 57–61. <https://doi.org/10.1021/jf0487351>

- Jackson, M. H. (1993). *Galapagos, a natural history* (pp. 27–28). University of Calgary Press. https://doi.org/10.1163/_q3_SIM_00374
- Khan, M. A., Elhossary, S., Khan, I. A., Al Zahrani, M. H., Al Zahrani, F. S., & Al Bashri, F. M. (2018). The impact of climatic variables with GIS application on the abundance of medically important mosquitoes (Diptera: Culicidae) in Jeddah, Saudi Arabia. *Int. J. Mosq. Res*, 5(5), 12–18.
- Kleindorfer, S., & Dudaniec, R. Y. (2016). Host-parasite ecology, behavior and genetics: a review of the introduced fly parasite *Philornis downsi* and its Darwin's finch hosts. *BMC Zoology*, 1(1), 1–19. <https://doi.org/10.1186/s40850-016-0003-9>
- Kleindorfer, S., Fessl, B., Peters, K., & Anchundia, D. (2019). *Field guide: resident landbirds of Galapagos*. Charles Darwin Foundation. <https://doi.org/10.2307/j.ctvqc6gm3>
- Knutie, S. A., Koop, J. A. H., French, S. S., & Clayton, D. H. (2013). Experimental test of the effect of introduced hematophagous flies on corticosterone levels of breeding Darwin's finches. *General and Comparative Endocrinology*, 193, 68–71. <https://doi.org/10.1016/j.ygcen.2013.07.009>
- Krause, E. T., & Caspers, B. A. (2012). Are olfactory cues involved in nest recognition in two social species of estrildid finches? *PLoS ONE*, 7(5), 1–7. <https://doi.org/10.1371/journal.pone.0036615>
- Krebs, J. R. (1973). Social learning and the significance of mixed-species flocks of chickadees (*Parus spp.*). *Canadian Journal of Zoology*, 51(12), 1275–1288. <https://doi.org/10.1139/z73-181>
- Lambrechts, M. M., & Dos Santos, A. (2000). Aromatic herbs in Corsican blue tit nests: the 'Potpourri' hypothesis. *Acta Oecologica*, 21(3), 175–178. [https://doi.org/10.1016/S1146-609X\(00\)00122-3](https://doi.org/10.1016/S1146-609X(00)00122-3)
- Loye, J. E., & Zuk, M. (1991). Bird-parasite interactions: ecology, evolution and behaviour. In *Bird-parasite interactions: ecology, evolution and behaviour*. Oxford University Press; Ornithology Series, 2. Oxford University Press; Ornithology Series, 2.
- Maciel, M. V., Morais, S. M., Bevilaqua, C. M. L., Silva, R. A., Barros, R. S., Sousa, R. N., Sousa, L. C., Brito, E. S., & Souza-Neto, M. A. (2010). Chemical composition of Eucalyptus spp. essential oils and their insecticidal effects on *Lutzomyia longipalpis*. *Veterinary Parasitology*, 167(1), 1–7. <https://doi.org/10.1016/j.vetpar.2009.09.053>
- Madigan, M. T., Martinko, J. M., & Parker, J. (1997). *Brock biology of microorganisms* (Vol. 11). Prentice hall Upper Saddle River, NJ.
- Maia, M. F., & Moore, S. J. (2011). Plant-based insect repellents : a review of their efficacy , development and testing. *Malaria Journal*, 10(Suppl 1), 11. <https://doi.org/10.1186/1475-2875-10-S1-S11>
- Matthews, A. E., Larkin, J. L., Raybuck, D. W., Slevin, M. C., Stoleson, S. H., & Boves, T. J. (2018). Feather mite abundance varies but symbiotic nature of mite-host relationship does not differ between two ecologically dissimilar warblers. *Ecology and Evolution*, 8(2), 1227–1238. <https://doi.org/10.1002/ece3.3738>
- Møller, A. P., Peralta-Sánchez, J. M., Nielsen, J. T., López-Hernández, E., & Soler, J. J. (2012). Goshawk prey have more bacteria than non-prey. *Journal of Animal Ecology*,

81(2), 403–410. <https://doi.org/10.1111/j.1365-2656.2011.01923.x>

- Moore, S. J., Lenglet, A. D., & Hill, N. (2006). Plant-based insect repellents. In *Insect Repellents: Principles, Methods, and Uses* (pp. 393–417). <https://doi.org/10.1201/9781420006650.ch14>
- Morais-Braga, M. F. B., Carneiro, J. N. P., Machado, A. J. T., Sales, D. L., dos Santos, A. T. L., Boligon, A. A., Athayde, M. L., Menezes, I. R. A., Souza, D. S. L., Costa, J. G. M., & Coutinho, H. D. M. (2017). Phenolic composition and medicinal usage of *Psidium guajava* Linn.: Antifungal activity or inhibition of virulence? *Saudi Journal of Biological Sciences*, 24(2), 302–313. <https://doi.org/10.1016/j.sjbs.2015.09.028>
- Moyer, B. R., Drown, D. M., & Clayton, D. H. (2002). Low humidity reduces ectoparasite pressure: Implications for host life history evolution. *Oikos*, 97(2), 223–228. <https://doi.org/10.1034/j.1600-0706.2002.970208.x>
- Nelson Slater, M., & Hauber, M. E. (2017). Olfactory enrichment and scent cue associative learning in captive birds of prey. *Zoo Biology*, 36(2), 120–126. <https://doi.org/10.1002/zoo.21353>
- Nero, R. W., & Hatch, D. R. M. (1984). Common Grackles anting with marigold flowers. *Blue Jay*, 42(4), 3–5. <https://doi.org/10.29173/bluejay4382>
- Niknafs, S., & Roura, E. (2018). Nutrient sensing, taste and feed intake in avian species. *Nutrition Research Reviews*, 31(2), 256–266. <https://doi.org/10.1017/S0954422418000100>
- Nissen, L., Zatta, A., Stefanini, I., Grandi, S., Sgorbati, B., Biavati, B., & Monti, A. (2010). Characterization and antimicrobial activity of essential oils of industrial hemp varieties (*Cannabis sativa* L.). *Fitoterapia*, 81(5), 413–419. <https://doi.org/10.1016/j.fitote.2009.11.010>
- O'Connor, J., Robertson, J., & Kleindorfer, S. (2010). Video analysis of host–parasite interactions in nests of Darwin's finches. *Oryx*, 44(4), 588–594. doi:10.1017/S0030605310000086
- Padrón-Márquez, B., Viveros-Valdez, E., Oranday-Cárdenas, A., & Carranza-Rosales, P. (2012). Antifungal activity of *Psidium guajava* organic extracts against dermatophytic fungi. *Journal of Medicinal Plants Research*, 6(41), 5435–5438. <https://doi.org/10.5897/jmpr12.240>
- Palma, R. L., & Peck, S. B. (2013). An annotated checklist of parasitic lice (Insecta: Phthiraptera) from the Galápagos Islands. In *Zootaxa* (Vol. 3627, Issue 1). <https://doi.org/10.11646/zootaxa.3627.1.1>
- Pandey, A., & Shweta. (2011). Antibacterial properties of *Psidium guajava* leaves, fruits and stems against various pathogens. *International Journal of Pharmaceutical Research and Development (IJPRD)*, 3(11), 15–24.
- Parker, P. G., Buckles, E. L., Farrington, H., Petren, K., Whiteman, N. K., Ricklefs, R. E., Bollmer, J. L., & Jiménez-Uzcátegui, G. (2011). 110 years of Avipoxvirus in the Galapagos Islands. *Plos One*, 6(1), e15989. <https://doi.org/10.1371/journal.pone.0015989>
- Parkes, K. C., Weldon, P. J., & Hoffman, R. L. (2003). Polydesmidan millipede used in self-anointing by a strong-billed woodcreeper (*Xiphocolaptes promeropyrhincus*) from

- Belize. *Ornitologia Neotropical*, 14(2), 285–286.
- Pedersen, T. L. (2020). *patchwork: The Composer of Plots* (1.0.1).
- Potter, E. F. (1970). Anting in wild birds, its frequency and probable purpose. 87(4), 692–713. <https://doi.org/10.2307/4083703>
- Rätti, O., Dufva, R., & Alatalo, R. V. (1993). Blood parasites and male fitness in the pied flycatcher. *Oecologia*, 96(3), 410–414. <https://doi.org/10.1007/BF00317512>
- Revis, H. C., & Waller, D. A. (2004). Bactericidal and fungicidal activity of ant chemicals on feather parasites: an evaluation of anting behavior as a method of self-medication in songbirds. *The Auk*, 121(4), 1262–1268. <https://doi.org/10.1093/auk/121.4.1262>
- Rivas-Torres, G., Luke Flory, S., & Loiselle, B. (2018). Plant community composition and structural characteristics of an invaded forest in the Galápagos. *Biodiversity and Conservation*, 27(2), 329–344. <https://doi.org/10.1007/s10531-017-1437-2>
- Robbins, C. S. (1981). Effect of time of day on bird activity. *Studies in Avian Biology*, 6(3), 275–286.
- Rodriguez, E., & Wrangham, R. (1993). Zoopharmacognosy: the use of medicinal plants by animals. In K. R. Downum, J. T. Romeo, & H. A. Stafford (Eds.), *Phytochemical Potential of Tropical Plants* (pp. 89–105). Springer US. https://doi.org/10.1007/978-1-4899-1783-6_4
- Salerno, G., Frati, F., Marino, G., Ederli, L., Pasqualini, S., Loreto, F., Colazza, S., & Centritto, M. (2017). Effects of water stress on emission of volatile organic compounds by *Vicia faba*, and consequences for attraction of the egg parasitoid *Trissolcus basalis*. *Journal of Pest Science*, 90(2), 635–647. <https://doi.org/10.1007/s10340-016-0830-z>
- Sinclair, B. J. (2013). CDF checklist of Galapagos flies. In *Charles Darwin Foundation Galapagos Species Checklist*.
- Slagsvold, T., & Wiebe, K. L. (2011). Social learning in birds and its role in shaping a foraging niche. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 969–977. <https://doi.org/10.1098/rstb.2010.0343>
- Snow, D. W. (1966). Molt and the breeding cycle in Darwin's finches. *Journal Für Ornithologie*, 107(3–4), 283–291. <https://doi.org/10.1007/BF01677899>
- Stenkewitz, U., Nielsen, Ó. K., Skírnisson, K., & Stefánsson, G. (2017). Feather holes of rock ptarmigan are associated with amblyceran chewing lice. *Wildlife Biology*, 2017(SP1) <https://doi.org/10.2981/wlb.00255>
- Suárez-Rodríguez, M., López-Rull, I., & Macias Garcia, C. (2013). Incorporation of cigarette butts into nests reduces nest ectoparasite load in urban birds: new ingredients for an old recipe? *Biology Letters*, 9(1), 20120931. <https://doi.org/10.1098/rsbl.2012.0931>
- Tebbich, S., Schwemhofer, T., Barbara, F., & Pike, C. (2020). Data and code for ‘Darwin’s finches habitually anoint their feathers with leaves of the endemic tree *Psidium galapageium* during the non-breeding season’.
- Tebbich, S., Sterelny, K., & Teschke, I. (2010). The tale of the finch: adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1543), 1099–1109. <https://doi.org/10.1098/rstb.2009.0291>

- Tebbich, S., Taborsky, M., Fessl, B., & Blomqvist, D. (2001). Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1482), 2189–2193. <https://doi.org/10.1098/rspb.2001.1738>
- Toft, C. A., Aeschlimann, A., & Bolis, L. (1991). *Parasite-Host associations: coexistence or conflict?* Oxford University Press (OUP).
- Vallat, A., Gu, H., & Dorn, S. (2005). How rainfall, relative humidity and temperature influence volatile emissions from apple trees in situ. *Phytochemistry*, 66(13), 1540–1550. <https://doi.org/10.1016/j.phytochem.2005.04.038>
- VanderWerf, E. A. (2005). ‘Elepaio “anting” with a garlic snail and a Schinus fruit. *Journal of Field Ornithology*, 76(2), 134–137. <https://doi.org/10.1648/0273-8570-76.2.134>
- Villa, S. M., Le Bohec, C., Koop, J. A., Proctor, H. C., & Clayton, D. H. (2013). Diversity of feather mites (Acari: Astigmata) on Darwin’s finches. *The Journal of Parasitology*, 99(5), 756–762. <https://doi.org/10.1645/12-112.1>
- Weber, B. H., & Depew, D. J. (2003). *Evolution and learning: The Baldwin effect reconsidered*. Mit Press.
- Weldon, P. J., Carroll, J. F., Kramer, M., Bedoukian, R. H., Coleman, R. E., & Bernier, U. R. (2011). Anointing chemicals and hematophagous arthropods: responses by ticks and mosquitoes to Citrus (Rutaceae) peel exudates and monoterpene components. *Journal of Chemical Ecology*, 37(4), 348–359. <https://doi.org/10.1007/s10886-011-9922-7>
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., ... Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, 4(43), 1686. <https://doi.org/10.21105/joss.01686>
- Zentall, T. R. (2004). Action imitation in birds. *Learning and Behavior*, 32(1), 15–23. <https://doi.org/10.3758/bf03196003>