**Dactylanthus** flower visitation by New Zealand lesser short-tailed bats appears to be influenced by daily rainfall

Zenon J. Czenze\(^1,2\)*, Tertia Thurley\(^3\)

\(^1\)School of Biological Sciences, Private Bag 92019, Auckland Mail Centre, Auckland 1142, New Zealand
\(^2\)Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, NSW, Australia
\(^3\)Department of Conservation, 2 South End Avenue, Whangarei 0110, New Zealand

*Author for correspondence (Email: czenze@hotmail.com)

Published online: 17 February 2021

**Abstract:** The unique relationship between *Dactylanthus taylorii* and its pollinator, the New Zealand lesser short-tailed bat (*Mystacina tuberculata*), is poorly understood despite both species being threatened. We used data collected over two summers (2016 and 2017) to determine if mean ambient temperature and total daily rainfall during the flowering period affected flower visitation by bats. We placed dataloggers around *D. taylorii* inflorescences to monitor bats with implanted passive integrated transponders (PIT-tags). We determined that flower visitation and bat activity was negatively correlated with daily rainfall but not temperature. Further, we found that juveniles and adult males were much more common visitors, with only four visits from adult females in two years. There is still much to learn about the unique and vulnerable relationship between these two New Zealand species, but it appears that rainfall may play a larger role than previously thought.

**Keywords:** *Dactylanthus taylorii*, *Mystacina tuberculata*, nectarivory, pollination, rainfall, wood rose

**Introduction**

Plant metabolism and primary production varies with temperature, moisture, and light availability with reduced productivity associated with inclement weather (Zimmerman 1988; Corbet 1990; Lloyd et al. 2002). The relationship between flowering plants and their pollinators can also be influenced by environmental factors (Corbet 1990; Memmott et al. 2007).

*Dactylanthus taylorii* (henceforth *Dactylanthus*) is New Zealand’s only fully parasitic flowering plant, and the only ground-flowering plant pollinated by a bat (Ecroyd et al. 1995; Ecroyd 1996a, b). *Dactylanthus* inflorescences emerge from under the soil during late February to early May and secrete copious amounts of glucose-rich nectar that contains chemicals typical of bat-pollinated plants (Ecroyd et al. 1995; Ecroyd 1996a, b; Haisley Bossard & Bossard 2015). Unfortunately, this nectar also attracts invasive mammals—possums (*Trichosurus vulpecula*), rats (*Rattus sp.*), and mice (*Mus musculus*)—that can destroy flowers and, as a result, *Dactylanthus* only occupies a fraction of its former range (Ecroyd 1996).

The New Zealand lesser short-tailed bat (*Mystacina tuberculata* henceforth *Mystacina*) feeds on a variety of insects, as well as fruit, nectar, and pollen from several plants (Arkins et al. 1999; Peterson et al. 2006; McCartney et al. 2007; Cummings et al. 2014; Czenze et al. 2018), and it is the primary pollinator of *Dactylanthus* (Ecroyd 1996b). Bats are effective pollinators and the frequency of their visits to flowers can positively influence plant reproduction and fruit production (Fleming & Sosa 1994; Cunningham 1995; Lobo et al. 2005). Both *Mystacina* and *Dactylanthus* are threatened (de Lange et al. 2013; O’Donnell et al. 2018), and, despite the likely reproductive consequences, only one study has quantified the visitation patterns of *Mystacina to Dactylanthus* (Czenze & Thurley 2018).

*Mystacina’s* mating season coincides with the flowering period of *Dactylanthus* and during late summer males spend a third of the night singing to attract females (Toth 2016). Juveniles, born earlier in the year, become volant during summer and may be under greater energy constraints compared to adults due to naïve foraging behaviour (Rolseth et al. 1994; Adams 1996, 1997; Hamilton & Barclay 1998). Perhaps to mitigate these increased energetic costs or augment energy reserves, both adult males and juvenile bats visit *Dactylanthus* more often than adult females (Czenze & Thurley 2018).

Previous work, using rotten inflorescences as a proxy for rainfall, contends that more rainfall/rotten influences negatively affects yearly seed production by *Dactylanthus* (Parker 2015). The author advocates that future work should quantify rainfall conditions during the flowering season to help understand its effect on *Dactylanthus*. Activity patterns of *Mystacina* are broadly related to environmental variables with higher activity during warmer evenings (Czenze et al. 2017a, b; but see, O’Donnell et al. 2006; Czenze et al. 2017c) and in one case rain (Christie & Simpson 2006). Our previous work suggests that flower visitation during a single flowering period positively correlated to temperature, but not rain (Czenze & Thurley 2018). Therefore, the goal of this study was to quantify the variation in ambient temperature and...
rainfall during two flowering seasons of Dactylanthus and determine if these environmental conditions affected visitations by bats. We predicted that flower visitation would correlate positively with overnight ambient temperature and negatively with precipitation. Additionally, we predicted that if juveniles and adult males are under predictable and seasonal energetic shortfalls then the demographic differences in visitation we recorded in 2016 should be retained between years.

Methods

Our study was conducted over two years (February–March 2016 and 2017) in the Pikiariki Ecological Area of Pureora Forest Park (38°26′S, 175°39′E), central North Island, New Zealand. Pikiariki is approximately 450 ha of native, mature podocarp-hardwood forest. Half of the Pikiariki bat population are estimated to have been marked with passive integrated transponder tags (PIT-tags) as part of ongoing monitoring that started in 2012. Untagged adult and juvenile bats are PIT-tagged each year in February just prior to the Dactylanthus flowering season and during the two-year study period 977 individuals were recorded at roost trees. Juvenile bats were distinguished from adults by the lack of ossification of the metacarpal-phalangeal joint on the third digit (Davis & Hitchcock 1965).

From 2016–2017, during the peak Dactylanthus flowering period (i.e. 21 February–15 March), 15 of the most accessible clumps of Dactylanthus inflorescences, which bats were known to visit, were fitted with PIT-tag ring antennae (Biomark HPR Plus automatic PIT-tag reader, Biomark, Idaho, USA). Antennae completely encircled inflorescences to ensure detection of visiting bats, and data loggers stored an individual’s unique PIT-tag number and the time of visit (sensu Czenze & Thurley 2018). We recorded daily (24 hr) ambient temperature (°C) variables (e.g. daily maximum, daily minimum, daily mean) and total daily (24 hr) rainfall (mm) in Pikiariki from a central weather station approximately 2 km from roosts and feeding areas (CliFlo: NIWA National Climate Database, http://cliflo.niwa.co.nz/). However, since both daily maximum (Pearson product–moment correlation: \( r_P = 0.77, t_{11} = 6.7, P < 0.001 \)) and daily minimum (\( r_P = 0.83, t_{11} = 9.55, P < 0.001 \)) were correlated with daily mean ambient temperature, we restricted analysis to only include daily mean as it was the strongest predictor.

For all analyses we combined data collected from both 2016 (Czenze & Thurley 2018) and 2017. We used separate generalised linear mixed models (R version 3.4.2; R Development Core Team 2017) (R Core Team 2018) to assess the effect of daily mean ambient temperature and total daily rainfall on (1) total number of nightly flower visits (visits per night) and (2) total number of individuals that visited plants each night (bats per night). Due to low sample in some demographics we did not include age or sex in our models. To determine if our data were overdispersed, we used an overdispersion test (Cameron & Trivedi 1990) in the package AER v 1.2.5. We determined that the parameter visits per night was overdispersed and was best fit by a negative binomial distribution; however, we determined bats per night was best fit by a Poisson distribution. We used AIC (Akaike Information Criteria) for model selection, choosing the best fitting models to characterise visitation and activity patterns (Burnham and Anderson, 2002). All analyses were conducted in R 3.4.2 (R Development Core Team 2017) and values are reported as the mean ± SD. We assessed significance at the \( P < 0.05 \) level.

Results

From 21 February–15 March 2017 we recorded 15 tagged individuals at nine inflorescences (0 adult females, 6 juvenile females, 1 adult male, 8 juvenile males). We recorded the most visits by juvenile males (\( n = 108 \)) followed by juvenile females (\( n = 97 \)), and adult males (\( n = 18 \)), and did not record any visits from adult females. We combined these data with those from 2016 (24 individuals; 4 adult females, 6 juvenile females, 6 adult males, and 8 juvenile males; Czenze & Thurley 2018) when we recorded the most visits by adult males (\( n = 197 \)), followed by juvenile females (\( n = 149 \)), juvenile males (\( n = 64 \)), and adult females (\( n = 4 \)). In 2017, we recorded an average of 11.8 ± 2.4 visits per night, and 14.8 ± 12.2 in 2016 and a maximum of 35 visits per night from 5 individuals in 2017, and 44 visits from 6 individuals in 2016.

During the sampling seasons, the mean ambient temperature in 2016 (15.4 ± 1.8°C) was similar to 2017 (15.2 ± 2.1°C). However, the average daily rainfall in 2016 (0.6 ± 1.4 mm) was c. 8.9-fold lower than in 2017 (5.3 ± 12.7 mm). In 2016 we recorded four days with daily rainfall > 1 mm compared to 11 days in 2017. Further, in the 2016 season we did not record any rainfall events that exceeded 6 mm of daily rainfall; however, during the 2017 season there were 6 rainfall events that exceeded a daily total of 10 mm.

Both bats per night (df = 42, \( z = -2.21, P = 0.03 \)) and visits per night (df = 42, \( z = -3.18, P < 0.01 \)) were best explained by total daily rainfall (Table 1), with fewer visits to flowers during days with heavier rainfall (Table 2).

Discussion

The interannual variation in Dactylanthus seed production suggests that environmental conditions affect aspects of Dactylanthus reproduction (Parker 2015), but the author laments the fact that no direct environmental measurements were made. Although the sampling seasons in 2016 and 2017 were similar in all ambient temperature conditions, 2017 was wetter compared to 2016. If we assume that, like in other bat species (Fleming & Sosa 1994; Cunningham 1995), increased flower visitation by Mystacina positively affects Dactylanthus reproduction, then wetter years may yield fewer reproductively successful Dactylanthus.

Plant primary production can be negatively affected by heavy rainfall (Rosenzweig et al. 2002). For Dactylanthus, a greater proportion of rotting male inflorescences can be observed during rainy flowering periods (A. Holzapfel pers. comm.), which likely negatively affects yearly seed production (Parker 2015). Anecdotally, we observed a similar pattern with more rotted flowers during the wetter 2017 than the previous year (T. Thurley pers. obs.; D. Mudge pers. comm.). Unfortunately, it is still unclear whether the increased rainfall of 2017 directly influenced flower survival as we were not able to quantify the survival duration of flowers or seed production in Pureora between years. Future research should, during the flowering period, aim to quantify seed production, weather conditions, and Mystacina activity concurrently to tease apart the most influential variables and thus aid in Dactylanthus conservation.

During winter in the South Island, the population of Mystacina do not appear to be rain averse and were actually more likely to be active when there was > 1 mm of rain (Christie
Table 1. Best fit models describing the effect of daily mean temperature (°C; Tmean) and total daily rainfall (mm; Rain) on the total number of lesser short-tailed bats (Mystacina tuberculata) recorded at Dactylanthus taylorii per night (bats per night), and total number of visits recorded per night (visits per night) in Pureora, New Zealand, during February–March, 2016 and 2017. In both models only total daily rainfall was retained in the final model. df = degrees of freedom, AICc = Akaike information criterion (small sample size), DeltaAIC = differences in AICc-s.

<table>
<thead>
<tr>
<th>Model*</th>
<th>Model Terms</th>
<th>df</th>
<th>AICc</th>
<th>DeltaAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bats per night</td>
<td>Rain</td>
<td>2</td>
<td>162.6</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Rain+Tmean</td>
<td>3</td>
<td>164.9</td>
<td>2.31</td>
</tr>
<tr>
<td></td>
<td>Rain*Tmean</td>
<td>4</td>
<td>167.3</td>
<td>4.62</td>
</tr>
<tr>
<td></td>
<td>Tmean</td>
<td>2</td>
<td>168.3</td>
<td>5.71</td>
</tr>
<tr>
<td>Visits per night</td>
<td>Rain</td>
<td>3</td>
<td>311.1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Rain+Tmean</td>
<td>4</td>
<td>312.7</td>
<td>1.55</td>
</tr>
<tr>
<td></td>
<td>Rain*Tmean</td>
<td>5</td>
<td>315.0</td>
<td>3.83</td>
</tr>
<tr>
<td></td>
<td>Tmean</td>
<td>3</td>
<td>318.9</td>
<td>7.76</td>
</tr>
</tbody>
</table>

*Visits per night was best fit by a negative binomial distribution and bats per night was best fit by a Poisson distribution.

Table 2. The estimated coefficients ± 1 SE for the outputs from the models shown in Table 1. Rain = total daily rainfall (mm), Tmean = daily mean temperature (°C). nf = model term not fitted in final model.

<table>
<thead>
<tr>
<th></th>
<th>Bats per night</th>
<th>Visits per night</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.16 ± 0.09</td>
<td>2.73 ± 0.14</td>
</tr>
<tr>
<td>Rain</td>
<td>−0.03 ± 0.01</td>
<td>−0.05 ± 0.01</td>
</tr>
<tr>
<td>Tmean</td>
<td>nf</td>
<td>nf</td>
</tr>
<tr>
<td>Rain*Tmean</td>
<td>nf</td>
<td>nf</td>
</tr>
</tbody>
</table>

Czenze and Thurley (2018) contend that during the flowering season adult females are under comparatively lower energetic pressure than adult males (due to costs associated with singing) or juveniles (due to naïve foraging behaviour). Here we confirm, and indeed strengthen, the findings of Czenze and Thurley (2018) as we recorded no visits from adult females in 2017 and found that visitations were dominated by juveniles and adult males. Juveniles and adult males may visit Dactylanthus more often to help recoup energetic losses as carbohydrate-rich nectar can be easily digested and mobilised. Since we monitored inflorescences nearest communal roosts, and thus also near many male singing trees, males may have been feeding from flowers closest to their singing trees and skewing the results. Additionally, the high proportion of juvenile bats we recorded may be explained by young bats remaining near communal roosts due to underdeveloped flying ability. However, if proximity to inflorescences is driving the greater visitation by males and juveniles, it raises the question why are hundreds of adult females occupying the nearby communal roosts virtually absent from our records? Future studies, where feasible, should attempt to outfit Dactylanthus further away from communal roosts to determine if females have patches in different areas of their home-range which they frequent.

Admittedly, there are several factors that constrained our study, and the results presented must be interpreted with caution. First, our data are limited to only two years of visitation data from one population; obviously it would be ideal to continue this type of study in multiple populations over the course of several years. Second, we were unable to quantify other potential environmental correlates like windspeed or operative temperature at the inflorescence, which would have made our models more robust and potentially changed our results. However, our results suggest that Dactylanthus visitation by bats is more strongly influenced by rainfall than temperature and help to elucidate how environmental conditions can affect the unique mutualistic relationship between Dactylanthus and Mystacina. For Dactylanthus conservation to continue to be successful, more work is required to determine the specific effects of environmental conditions and their ecological correlates to Dactylanthus reproduction.
Author contributions

TT collected data in the field, ZJC analysed the data. ZJC and TT wrote the manuscript.

Acknowledgements

We thank D. Mudge for the upkeep of equipment and endless enthusiasm, A. Hozapfel for useful insight, and S. Parsons for editorial advice. We also thank two reviewers whose input on an earlier version of the manuscript greatly improved its quality. Finally, we acknowledge the New Zealand Department of Conservation at the Pureora Field Base for housing and logistical support.

References


Hope PR, Jones G 2012. Warming up for dinner: Torpor and arousal in hibernating Natterer’s bats (Myotis nattereri) studied by radio telemetry. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 182: 569–578.


O’Donnell CFJ, Christie JE, Simpson W 2006. Habitat
use and nocturnal activity of lesser short-tailed bats 
(*Mystacina tuberculata*) in comparison with long-tailed 
bats (*Chalinolobus tuberculatus*) in temperate rainforest. 

O’Donnell CFJ, Borkin KM, Christie JE, Lloyd B, Parsons S, 
Hitchmough RA 2018. Conservation status of New Zealand 

and acivity of hibernating Greater Horseshoe Bats 
(*Rhinolophus ferrumequinum*). Functional Ecology 14: 
580–588.

Parker CM 2015. Identifying host species of *Dactylanthus* 
The University of Waikato, Hamilton, Auckland.

Peterson PG, Robertson AW, Lloyd B, McQueen S 2006. 
Non-native pollen found in short-tailed bat (*Mystacina* 
tuberculata) guano from the central North Island. 
New Zealand Ecological Society. New Zealand Journal 

R Core Team 2018. R: A language and environment for 
statistical computing. R Foundation for Statistical 
Computing, Vienna, Austria.

in the diets of juvenile and adult hoary bats, *Lasiurus* 

Rosenzweig C, Tubiello FN, Goldberg R, Mills E, Bloomfield 
J 2002. Increased crop damage in the US from excess 
precipitation under climate change. Global Environmental 

Toth CA 2016. Lek breeding in the lesser short-tailed 
bat (*Mystacina tuberculata*): male courtship, female 
selection, and the determinants of reproductive strategies. 
Unpublished PhD thesis. University of Auckland, 
Auckland, New Zealand.

Zimmerman M 1988. Nectar production, flower phenology, 
and strategies for pollination. In: Lovett Doust J, Lovett 
Doust L eds. Plant reproductive ecology: patterns and 

Received: 4 April 2018; accepted 1 October 2020

Editorial board member: Colin O’Donnell