NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

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

Zenon J. Czenze[1,2]* (iD), 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, Raumanga, Whangarei 0110, New Zealand
*Author for correspondence (Email: czenze@hotmail.com)

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 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, *Dacylanthus* 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 *Dacytlanthus*. 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: $rP = 0.77$, $t_{41} = 6.7$, $P < 0.001$), and daily minimum ($rP = 0.83$, $t_{41} = 9.55$, $P < 0.001$), 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; T_{mean}) 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, AIC_c = Akaike information criterion (small sample size), DeltaAIC = differences in AIC_cs.

Model*	Model Terms	df	AIC_c	DeltaAIC
Bats per night				
	Rain	2	162.6	0
	Rain+T_{mean}	3	164.9	2.31
	Rain*T_{mean}	4	167.3	4.62
	T_{mean}	2	168.3	5.71
Visits per night				
	Rain	3	311.1	0
	Rain+T_{mean}	4	312.7	1.55
	Rain*T_{mean}	5	315.0	3.83
	T_{mean}	3	318.9	7.76

*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), T_{mean} = daily mean temperature (°C). nf = model term not fitted in final model.

	Bats per night	Visits per night
Intercept	1.16 ± 0.09	2.73 ± 0.14
Rain	−0.03 ± 0.01	−0.05 ± 0.01
T_{mean}	nf	nf
Rain*T_{mean}	nf	nf

& Simpson 2006). However, increased bat activity during light rain may be a response to falling barometric pressure, which coincides with greater flying insect abundance, and may serve as a cue for increased foraging success (Park et al. 2000; Hope & Jones 2012; Czenze & Willis 2015). Unlike the periods of light rainfall Christie and Simpson (2006) reported, the heavier rainfall observed Pureora in 2017 likely limits an individual's energetic foraging returns and increases energetic costs due to greater heat loss when fur is wet (Withers et al. 2016). Alternatively, if individuals are active during the heavier rain, the lower visitation rates may be due to the reduced quality of *Dactylanthus* inflorescences.

Dactylanthus inflorescences will begin to rot less than a day after rain and this may be accelerated with heavy or consistent rain (Parker 2015; A. Holzapfel pers. comm.). Male inflorescences change with a rain-burst during anthesis as the entire inflorescence turns brown and disintegrates quickly, which is accelerated by a second rain burst (A. Holzapfel pers. comm.). Older male inflorescences have a different nectar scent from those that are just emerging, while those that are disintegrating have no discernible nectar scent (A. Holzapfel pers. comm.). Healthy *Dactylanthus* produce a sweet-smelling nectar, a trait that promotes bat visitation (Ecroyd et al. 1995; Ecroyd 1996b, a). The scent of healthy flowers may serve as a signal to bats about the nectar content and the potential energetic benefits associated with feeding from flowers. If heavy rainfall changes the scent and thus the attractiveness of *Dactylanthus,* which, in turn, reduces visitation by bats, it could partially explain the lower seed set of *Dactylanthus* during seasons with heavy rainfall (Parker 2015).

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 *Dacytlanthus* reproduction.

Author contributions

Acknowledgements

References

Adams RA 1996. Size-specific resource use in juvenile little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae): Is there an ontogenetic shift? Canadian Jounal of Zoology 74: 1204–1210.

Adams RA 1997. Onset of volancy and foraging patterns of juvenile little brown bats, *Myotis lucifugus*. Journal of Mammalogy 78: 239–246.

Arkins AM, Winnington AP, Anderson S, Clout MN 1999. Diet and nectarivorous foraging behaviour of the short-tailed bat (*Mystacina tuberculata*). Journal of Zoology 247: 183–187.

Burnham KP, Anderson DR 2002. A practical information-theoretic approach. Model selection and multimodel inference. 2nd ed. New York, Springer. 512 p.

Cameron AC, Trivedi PK 1990. Regression-based tests for overdispersion in the Poisson model. North-Holland. Journal of Econometrics 46: 347–364.

Christie JE, Simpson W 2006. Influence of winter weather conditions on lesser short-tailed bat *(Mystacina tuberculata)* activity in *Nothofagus* forest, Fiordland. New Zealand Journal of Zoology 33: 133–140.

Corbet SA 1990. Pollination and the weather. Israel Journal of Botany 39: 13–30.

Cummings G, Anderson S, Dennis T, Toth C, Parsons S 2014. Competition for pollination by the lesser short-tailed bat and its influence on the flowering phenology of some New Zealand endemics. Journal of Zoology 293: 281–288.

Cunningham SA 1995. Ecological constraints on fruit initiation by *Calyptrogyne ghiesbreghtiana* (Arecaceae): Floral herbivory, pollen availability, and visitation by pollinating bats. American Journal of Botany 82: 1527–1536.

Czenze ZJ, Thurley T 2018. Weather and demographics affect *Dactylanthus* flower visitation by New Zealand lesser short-tailed bats. New Zealand Journal of Ecology 42: 80–84.

Czenze ZJ, Willis CKR 2015. Warming up and shipping out: arousal and emergence timing in hibernating little brown bats (*Myotis lucifugus*). Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 185: 575–586.

Czenze ZJ, Brigham RM, Hickey AJR, Parsons S 2017a. Cold and alone? Roost choice and season affect torpor patterns in lesser short-tailed bats. Oecologia 183: 1–8.

Czenze ZJ, Brigham RM, Hickey AJR, Parsons S 2017b. Winter climate affects torpor patterns and roost choice in New Zealand lesser short-tailed bats. Journal of Zoology 303: 236–243.

Czenze ZJ, Brigham RM, Hickey AJR, Parsons S 2017c. Stressful summers? Torpor expression differs between high- and low-latitude populations of bats. Journal of Mammalogy 98: 1249–1255.

Czenze ZJ, Tucker JL, Clare EL, Littlefair JE, Hemprich-Bennett D, Oliveira HFM, Brigham RM, Hickey AJR, Parsons S 2018. Spatiotemporal and demographic variation in the diet of New Zealand lesser short-tailed bats (*Mystacina tuberculata*). Ecology and Evolution 8: 7599–7610.

Davis W, Hitchcock H 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. Journal of Mammalogy 46: 296–313.

Ecroyd CE 1996a. The ecology of *Dactylanthus taylorii* and threats to its survival. New Zealand Journal of Ecology 20: 81–100.

Ecroyd CE 1996b. *Dactylanthus* and bats: the link between two unique endangered New Zealand species and the role of the community in their survival. In: Saunders DA, Craig JE, Mattiske EM eds. Sydney, Surrey Beatty and Sons. Pp. 78–87.

Ecroyd CE, Franich RA, Kroese JHW, Steward D 1995. Volatile constituents of *Dactylanthus taylorii* flower nectar in relation to flower pollination and browsing by animals. Phytochemistry 40: 1387–1389.

Fleming TH, Sosa VJ 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. Journal of Mammalogy 75: 845–851.

Haisley Bossard C, Bossard CH 2015. Analysis of chemical constituents in the nectar of *Dactylanthus taylorii*. Unpublished BSc (Hons) thesis. University of Waikato, Hamilton, New Zealand.

Hamilton IM, Barclay RMR 1998. Diets of juvenile, yearling, and adult big brown bats (*Eptesicus fuscus*) in southeastern Alberta. Journal of Mammalogy 79: 764–771.

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.

de Lange PJ, Rolfe JR, Champion PD, Courtney SP, Heenan PB, Barkla JW, Cameron EK, Norton DA, Hitchmough RA 2013. Conservation status of New Zealand indigenous vascular plants, 2012. New Zealand Threat Classification Series 3, Department of Conservation, Wellington. 70 p.

Lloyd S, Ayre DJ, Whelan RJ 2002. A rapid and accurate visual assessment of nectar production can reveal patterns of temporal variation in *Banksia ericifolia* (Proteaceae). Australian Journal of Botany 50: 595–600.

Lobo JA, Quesada M, Stoner KE 2005. Effects of pollination by bats on the mating system of *Ceiba pentandra* (Bombacaceae) populations in two tropical life zones in Costa Rica. American Journal of Botany 92: 370–376.

McCartney J, Stringer IAN, Potter MA 2007. Feeding activity in captive New Zealand lesser short-tailed bats (*Mystacina tuberculata*). New Zealand Journal of Zoology 34: 227–238.

Memmott J, Craze PG, Waser NM, Price M V 2007. Global warming and the disruption of plant pollinator interactions. Ecology Letters 10: 710–717.

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. New Zealand Journal of Zoology 33: 113–124.

O'Donnell CFJ, Borkin KM, Christie JE, Lloyd B, Parsons S, Hitchmough RA 2018. Conservation status of New Zealand bats, 2017. Wellington, Department of Conservation. 4 p.

Park KJ, Jones G, Ransome RD 2000. Torpor, arousal and acivity of hibernating Greater Horseshoe Bats (*Rhinolophus ferrumequinum*). Functional Ecology 14: 580–588.

Parker CM 2015. Identifying host species of *Dactylanthus taylorii* using DNA barcoding. Unpublished MSc thesis. 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 of Ecology 30: 267–272.

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

Rolseth SL, Koehler CE, Barclay RMR 1994. Differences in the diets of juvenile and adult hoary bats, *Lasiurus cinereus*. Journal of Mammalogy 75: 394–398.

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 Change 12(3): 197–200.

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 strategies. Oxford University Press. Pp. 157–178.