Foraging Ranges of Insectivorous Bats Shift Relative to Changes in Mosquito Abundance

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Abstract

The need to develop effective management strategies for insectivorous bat populations requires an understanding of factors influencing habitat use. Availability of pest prey, such as mosquitoes, is likely to be one such factor. To assess whether this is the case, we radio-tracked Vespadelus vulturnus Thomas (little forest bat), a predator of Aedes vigilax Skuse (saltmarsh mosquito), in saltmarsh and adjacent coastal swamp forest during periods of high and low Ae. vigilax abundance. When mosquito abundance in structurally-open saltmarsh was similar to the more clutered coastal swamp forest, use of saltmarsh by V. vulturnus was disproportionally greater than its availability, with saltmarsh selected preferentially for foraging. However, at times of low Ae. vigilax abundance in saltmarsh, use of saltmarsh by V. vulturnus was reduced and all habitats were used in proportion to availability in the study area. This is the first radio-tracking study to demonstrate a shift in foraging range by an insectivorous bat species correlated with fluctuations in the distribution and abundance of a particular prey resource. The shift in foraging range by V. vulturnus, corresponding with a spatio-temporal variation in abundance of Ae. vigilax highlights the importance of mosquitoes as a dietary item. Broadscale pest control of Ae. vigilax may have ecological implications for the diet and habitat use of V. vulturnus. An adaptive management approach is proposed, whereby careful monitoring of insectivorous bat populations is recommended before and after any application of broadscale mosquito control measures. We also suggest a precautionary approach is taken such that broadscale control of mosquitoes avoids the lactation period of bats, a time when their energetic demands are greatest and when there is reduced risk of contracting mosquito-borne diseases transmitted by Aedes vigilax.

Introduction

Conservation of insectivorous bats requires appropriate management of habitats in which bats forage as well as any prey resources that sustain these habitats. To assist policy-makers, greater knowledge of factors influencing habitat use by foraging bats is required. While vegetation clutter is known to influence mobility and foraging activity of many bat species [1,2,3], availability of prey is also a key factor [4,5]. Many studies have investigated the influence of prey availability on bat activity using prey abundance as a proxy for prey availability. However, it has been shown that vegetation clutter also can reduce access to these prey resources for bats [5,6]. This may suggest that habitats with high insect abundances may not always be suitable foraging habitats for bats as acoustic complexity restricts access to abundant prey resources.

Mosquitoes can be an abundant locally and have been identified as prey items for many bat species worldwide [7,8,9]. Aedes vigilax Skuse (saltmarsh mosquito) is an estuarine species that is a serious nuisance biting pest and has been identified as an important vector of mosquito-borne pathogens such as Ross River virus (RRV) and Barmah Forest virus (BFV) [10]. Notwithstanding potentially significant public health risks, this species can cause substantial nuisance-biting impacts and broadscale mosquito control programs have been implemented in many Australian coastal regions [11]. Although there is evidence that Aedes vigilax may be an important dietary item for insectivorous bats foraging within saltmarshes [12,13,14,15], no study has specifically investigated the importance of the mosquito to insectivorous bats. Population abundances of Aedes vigilax are influenced strongly by tidal and rainfall inundation of larval habitats (i.e., coastal saltmarsh and mangrove communities) and, as a consequence, can be highly variable spatially and temporally. However, general patterns such as peaks in abundances can be predicted [16]. Generally, more abundant populations tend to be present approximately two weeks after inundation of saltmarshes by spring tides and/or heavy rainfall, representing a more plentiful prey resource for insectivorous bats. Given that Aedes vigilax can disperse >5 km from larval habitats [17], adjacent coastal swamp forests are likely to provide refuge for this mosquito species as well as providing sources of blood meals, sustaining high abundances for longer periods.

Vespadelus vulturnus Thomas (little forest bat) is a small insectivorous bat closely associated with forest and woodland habitats in coastal and inland regions of south-eastern Australia [18]. This species feeds opportunistically on flying insects with a diet composed of locally abundant prey items including moths and beetles. [18]. With a high frequency modulated echolocation call (end frequency 50-33 kHz) capable of detecting small prey items,
矾鸟（学名：V. vulturnus）已被观察到在河口栖息地捕猎蚊子[14]。它也被认为会在蚊子数量丰富时，特别在河口栖息地，它们是矾鸟饮食中占很大一部分的双翅目昆虫[19]。

在河口栖息地，11只来自沿海地区，蚊子（学名：Ae. vigilax）的DNA在收集的20只矾鸟粪便中被检测到[20]。超声波探测器显示，小而高频的回声定位蝙蝠种类（包括矾鸟V. vulturnus）的活动量与蚊子的密度呈正相关[13]。然而，探测器只能记录群体响应，需要无线电追踪来记录个体的对策并确定它们的觅食范围有何变化。我们假设矾鸟V. vulturnus的觅食范围的变化会与蚊子Ae. vigilax在声学简单的盐沼中的空间-时间变化紧密相关。为了测试这种假设，我们在两个预测会拥有较大和较小蚊子Ae. vigilax种群的时期内，研究了矾鸟V. vulturnus在盐沼中的栖息地使用情况。栖息地使用通过无线电追踪V. vulturnus在盐沼中觅食来评价，那里是成年蚊子Ae. vigilax的发源地，以及邻近的但声学较复杂的沿海沼泽森林提供了庇护所的栖息地，用于寻找宿主的蚊子。同时，蚊子和其它空中昆虫的调查在两个栖息地进行。

**Materials and Methods**

**Ethics statement**

所有工作均在科学许可（S12771）下进行，并由新南威尔士州国家公园和野生动物服务处提供。动物福利许可（TRIM no. 09/7861）为进行网捕和无线电追踪所获得，由新南威尔士州总督的动物护理和伦理委员会获得。

**Study site**

研究区域位于帝国湾地区（33°29′57″S, 151°21′40″E）的中央海岸，新南威尔士州，澳大利亚。该地区位于悉尼以北50公里，体验着温暖的亚热带气候。

在研究区域内，一个大型国家公园和一些较小的自然保护区维持着洞穴栖息的和岩洞栖息的捕食性蝙蝠种群，包括六个被新南威尔士州受威胁物种保护法1995年[21]所列的物种。在回声定位探测调查中经常记录到的物种包括Chalinolobus gouldii Gray（Gould’s wattled bat），Mormopterus sp. 2 Peters（东部大耳蝠），和V. vulturnus。后者被选中进行这项研究，因为它是一种小蝙蝠（4克），能够通过其高频回声定位（末频率50-53 kHz）来区分小型猎物，且在研究区域内被发现会吃蚊子[20]。

海岸盐沼和沿海沼泽森林是两个受威胁的植被群落（NSW Threatened Species Conservation Act 1995）在该区域内，提供重要的幼虫和庇护所的栖息地对于许多河口和淡水蚊子物种包括Ae. vigilax。在潮汐影响较小的沿海沼泽森林中，蚊子易受到潮汐冲刷的植物，主要是耐盐的低矮耐盐的草本植物[23]，包括Sarcocornia quinqueflora（Bunge ex Ung.-Sternb.）A.J.Scott（萨福克），Samolus repens（J.R.Forst. and G.Forst.）Pers.（匍匐牛膝草）。树木和灌木相互依存。沿海沼泽森林位于排水不畅的洼地。它有一个典型的高13米的冠层，由Melaleuca quinquenervia（Cav.）Blake（阔叶纸皮树），Eucalyptus robusta Anon（红皮木麻树）和Casuarina glauca Sieber ex Spreng（沼泽木麻属）占据。下层植被有湿地或半湿的灌木[24]。

一个小型自然保护区（Cockle Bay）包含大约18公顷的沿海沼泽和20公顷的沿海沼泽森林。所有节肢动物的样本在这些植被群落在自然保护区进行，而蝙蝠网捕是在沿海沼泽森林的飞行区进行的。大约300米南面是上坡的森林，而一个较小的湿地沼泽森林位于它附近。沿海沼泽森林的环境为许多河口和淡水蚊子物种提供了庇护所，包括Ae. vigilax。气候在低于沿海森林和高于红树林[22]，沿海沼泽是在有过度的降水情况下，由沙生的植物，主要是低矮耐盐的草本植物[23]，包括Sarcocornia quinqueflora（Bunge ex Ung.-Sternb.）A.J.Scott（萨福克），Samolus repens（J.R.Forst. and G.Forst.）Pers.（匍匐牛膝草）。树木和灌木相互依存。沿海沼泽森林位于排水不畅的洼地。它有一个典型的高13米的冠层，由Melaleuca quinquenervia（Cav.）Blake（阔叶纸皮树），Eucalyptus robusta Anon（红皮木麻树）和Casuarina glauca Sieber ex Spreng（沼泽木麻属）占据。下层植被有湿地或半湿的灌木[24]。

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Figure 1. Study area. Map of study area (inset: map of Australia indicating relative location of Empire Bay). Stars represent harp trapping locations within coastal swamp forest habitat (dark grey). Saltmarsh and mangrove habitats (light grey) are visible around Cockle Bay.
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low density (2.5 dwellings ha⁻¹) residential areas are located 200 m to the east and 1 km west of the nature reserve.

**Harp trapping of bats, attachment of radio-transmitters and radio-tracking methods**

Habitat use by *V. vulturnus* was investigated by radio-tracking in two periods during the austral late summer (February 2010) and early autumn (March 2010). Bats were trapped in harp traps along flyways in coastal swamp forest adjacent to saltmarsh. In February 2010, 10 *V. vulturnus* individuals were radio-tracked while six were radio-tracked three weeks later (March 2010), with three individuals tracked in both periods (see Methods S1).

Each trapped individual was fitted with a LB-2N radio-transmitter (Holohill, Carp, Canada), attached between the shoulder blades with Vetbond (3M, Pymble NSW). Each transmitter had an aerial length of 10 cm and weighed 0.31 g, representing 7.93% of *V. vulturnus* mean mass. While the radio-transmitters exceeded the guideline of 5% of body mass suggested by [25], heavier transmitters have been used to study the same species as well as other similar sized bats and have not been reported to restrict the mobility of individual bats significantly [26,27]. Additionally, pregnant females can weigh 6.5 g and are therefore capable of carrying at least 42% extra body mass.

Estimated locations for bats fitted with transmitters were recorded at least 10 min apart on foot throughout the night by bisecting or triangulating the signal direction (see Methods S1). Location data only were obtained over a maximum of 10 consecutive nights each tracking period as it was predicted that mosquito population abundances after the 10th night would not be consistent with preceding nights due to the time lag from inundation of saltmarsh and the resulting egg hatches. To provide data about distances travelled by bats to foraging sites, day roosts of bats fitted with radio-transmitters were located (see Methods S1).

**Analysis of radio-tracking data**

Successful triangulated or bisected locations (see Methods S1) were plotted in ArcMap 9.0 (ESRI, Redlands, USA) and overlaid onto a vegetation layer of the study area [24]. For each tracking period, ≥15 foraging locations (see Methods S1) were used to calculate foraging ranges (95% fixed kernel density estimator (KDE)) in ArcMap 9.0 using the HRT extension [28].

Compositional analysis [29] was used to determine if bats were using habitats proportional to availability or whether they preferentially selected habitats, and whether this changed between tracking periods. While the analysis can be undertaken at two scales (population and the individual), roost locations of two individuals tracked in February 2010 were located >1.8 km from roosts of other tracked individuals, suggesting foraging data were likely to be representative of more than one population/social group. Use of foraging data collected from individuals of multiple social groups has the potential to confound foraging preferences at the population scale, since habitats available to members of one social group may not be available to members of another social group. For this reason, compositional analysis only was undertaken at the individual scale. For the analysis, the proportion of bisected/triangulated locations within each habitat was treated as a measure of habitat use, while available habitats were considered to be those that made up an individual’s foraging range (95% KDE) (Fig. 2).

Habitats assessed in compositional analyses were coastal floodplain wetlands, coastal swamp forest, mangroves, saltmarsh, open water and a forest complex consisting of wet sclerophyll forest, dry sclerophyll forest, and subtropical rainforest. (Given calculated transmitter error and average error ellipse, it was deemed appropriate to pool these forest habitats together into the one complex).

A chi-squared goodness-of-fit test was used to assess whether habitat selection was non-random and whether each habitat was used in a similar proportion to its availability. Differences between log-transformed relative proportions of both used and available habitats were used to rank habitats according to whether they were being used more than other habitats after accounting for each habitat’s availability. A Wilcoxon-pairwise comparison was used to ascertain the significance of these ranks.

**Surveillance of available prey**

In each habitat, mosquito abundance was surveyed nightly using two CO₂—baited encephalitis virus surveillance (EVS) traps [30] (Australian Entomological Supplies, Bangalow, NSW, Australia), while other flying insects were sampled using a single light trap (Australian Entomological Supplies, Bangalow, NSW, Australia). Traps were set in forest gaps within the coastal swamp forest, while in coastal saltmarsh, traps were set along the interface of the saltmarsh habitat and a stand of encroaching mangroves. Captured mosquitoes were keyed to species [31] and the abundance of each was recorded. All light trap specimens <2 mm in size were pooled together while all other specimens were sorted into three insect orders (Lepidoptera, Coleoptera, Diptera), with any other specimens pooled into an ‘other’ category. Insects then were oven dried at 60 °C for a minimum of 48 h and until a constant mass could be recorded (to nearest 1 x 10⁻² g) and used as a measure of biomass. Log-linear analysis was used to compare *Ae. vigilax* abundance and nightly insect biomass between habitats (saltmarsh/coastal swamp forest) and tracking period (February/March 2010).

**Results**

**Prey abundance**

In all, 13 243 mosquitoes representing 13 species were collected over both tracking periods (Table 1). *Aedes vigilax* was the most abundant species in each habitat irrespective of tracking period, representing ≈74% of specimens trapped in both habitats during February 2010 and ≈56% and ≈85% of specimens trapped in saltmarsh and coastal swamp forest, respectively during March 2010. Other commonly collected mosquito species were *Ae. altipennis* Westwood (Hexham grey), *Culex sitiens* Wiedemann (saltmarsh culex) and *Cx. annulirostris* Skuse (common banded mosquito).

During February 2010, 4 387 mosquitoes representing all 13 species were trapped in the coastal swamp forest, while 5 481 mosquitoes representing 12 of the 13 species were collected from saltmarsh. In March 2010, 2 391 and 984 mosquitoes representing 10 of the 13 species were sampled in coastal swamp forest and saltmarsh, respectively. During both tracking periods, lepidopterans and coleopterans provided the greatest biomass to saltmarsh light trap collections, while coleopterans and lepidopterans provided the greatest biomass to coastal swamp forest light trap collections.

Mean nightly insect biomass did not differ significantly between habitats or tracking periods (L.R. χ²(5) = 0.874, P = 0.832), with
0.93 g and 1.01 g collected from saltmarsh and coastal swamp forest, respectively in February 2010, and 0.97 g and 1.02 g collected in March 2010 (Figs. 4a & 4b). The biomass of lepidopterans, dipterans, other insects and insects <2 mm in size did not differ significantly between tracking periods or habitats (L.R. χ²(1) = 0.019, P = 0.991; L.R. χ²(1) = 0.097, P = 0.953; L.R. χ²(1) = 0.463, P = 0.793; L.R. χ²(1) = 2.479, P = 0.290; Figs. 4a &

Figure 2. Spread of habitats in study area. Typical GIS output illustrating spread of habitats in the study area and the foraging locations ('used habitat') used to construct foraging ranges ('available habitat').
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4b). Coleopteran biomass, however, was significantly greater in coastal swamp forest (L.R. $\chi^2(1) = 6.597$, $P = 0.037$; Figs. 4a & 4b).

Radio-tracking of, and habitat use by, *Vespadelus vulturnus*

In all, 422 triangulation attempts were undertaken for 10 bats during February 2010. Of these, 188 (45%) were successful (at least two triangulated bearings intersected one another). Bats were tracked for a mean of $6.50 \pm 2.95$ ($\pm 1$ SE) nights per bat, with 42 triangulation attempts, of which 45% were successful.

Bat #2 and Bat #10 only were tracked for one and two nights, respectively. An active signal from Bat #2 was only detected for one hour after the release of this bat suggesting that the radiotruemitter had probably been removed by the bat. An active signal for Bat #10 was still present on the last night of the tracking session, but only two nights of foraging data were collected since this bat only had been trapped on the penultimate night. Foraging ranges were not calculated for these two individuals.

During March 2010, 327 triangulation attempts were made with 149 of these successful (46%). Bats were tracked for a mean of

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**Table 1.** Mosquito species and their total abundances in saltmarsh and coastal swamp forest during February 2010 and March 2010.

| Species              | FEBRUARY 2010 (n = 10) | MARCH 2010 (n = 8) |
|----------------------|------------------------|-------------------|
|                      | Saltmarsh | Coastal swamp forest | Saltmarsh | Coastal swamp forest |
| Aedes alternans      | 564 (10.29) | 56 (1.28) | 243 (24.70) | 23 (0.96) |
| Ae. imperfectus      | 16 (0.29)  | 7 (0.16)   |                 |              |
| Aedes multiplex      | 49 (0.89)  | 219 (4.99) | 7 (0.71)      | 92 (3.83)   |
| Aedes notoscriptus   | 68 (1.24)  | 49 (1.12)  | 18 (1.83)     | 50 (2.08)   |
| Aedes procax        | 46 (0.84)  | 499 (11.37)| 3 (0.30)      | 24 (1.00)   |
| Aedes vigilax        | 4051 (73.91)| 3243 (73.92)| 555 (56.40)  | 2035 (84.83)|
| Anopheles annulipes  | 6 (0.11)   | 20 (0.46)  | 2 (0.20)      | 12 (0.50)   |
| Coquillettidia linealis | 2 (0.05)  |                 |              |              |
| Culex annulirostris | 291 (5.31) | 155 (3.35) | 48 (4.88)     | 67 (2.79)   |
| Cx. molestus         | 1 (0.02)   | 3 (0.07)   | 2 (0.20)      | 42 (1.75)   |
| Cx. quinquefasciatus| 15 (0.27)  | 8 (0.18)   | 8 (0.81)      | 41 (1.71)   |
| Cx. sitiens          | 350 (6.39) | 116 (2.64) | 98 (9.96)     | 13 (0.54)   |
| Verrallina funerea   | 24 (0.44)  | 10 (0.23)  |              |              |
| Total                | 5481       | 4387       | 984           | 2391        |

NB. Values in brackets represent percent of total mosquito abundance in each habitat.

**Figure 3.** Nightly *Aedes vigilax* abundance. Mean nightly abundance of the *Ae. vigilax* in saltmarsh and coastal swamp forest during February 2010 and March 2010. * Indicates interaction effect.

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**Figure 3.** Nightly *Aedes vigilax* abundance. Mean nightly abundance of the *Ae. vigilax* in saltmarsh and coastal swamp forest during February 2010 and March 2010. * Indicates interaction effect.

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months (February 2010 – which 46
nights. A foraging range was not calculated for this individual.

forest complex (Z = 2
greater than use of coastal floodplain wetlands (Z =
and mangrove forests (Table 3). Use of saltmarsh was significantly

saltmarsh ranked highest of all habitats followed by coastal swamp

open water ranked highest of all habitats used by

Discussion

5.67±2.25 nights per bat, with 55±11 triangulation attempts, of
which 46.25% were successful. Bat #6 was trapped on the
penultimate night of the tracking session and only tracked for
two nights. A foraging range was not calculated for this
individual.

Foraging ranges (95% KDE) of *V. vulturnus* individuals were
larger in February 2010 (35±4 ha) than in March 2010 (14±7 ha).
Habitat use by *V. vulturnus* individuals was non-random in both
months (February 2010 – χ²(5) = 28.802, P < 0.001; March 2010 –
χ²(5) = 36.480, P < 0.001). In February 2010, use of saltmarsh was
significantly greater than availability of the habitat (χ²(1) = 3.846,
P = 0.05), while all other habitats were used in similar proportions
to their availability (Fig. 3). Compositional analysis revealed that
saltmarsh ranked highest of all habitats followed by coastal swamp
forest, coastal floodplain wetlands, open water, the forest complex
and mangrove forests (Table 3). Use of saltmarsh was significantly
greater than use of coastal floodplain wetlands (Z = -2.380,
P = 0.017), mangrove forests (Z = -1.960, P = 0.050) and the
forest complex (Z = -2.380, P = 0.017).

In March 2010, all habitats were used in similar proportions to
their availability (Fig. 6). Compositional analysis revealed that
open water ranked highest of all habitats used by *V. vulturnus*
individuals, followed by coastal swamp forest, mangrove forests,
saltmarsh, the forest complex and coastal floodplain wetlands
(Table 3). The use of open water was significantly higher than the
use of the forest complex (Z = -2.023, P = 0.043).

With the exception of one night in March 2010, all radio-
tracked bats roosted outside the coastal swamp forest. Most
individuals roosted in eucalypt vegetation on an escarpment 300–
400 m away adjacent to the coastal swamp forest. Additionally,
triangulated bearings for these individuals indicated that these
roosts were located <200 m from each other. Three individuals
(two in February 2010 and one in March 2010) roosted beneath
the metal caps of telegraph poles in urban areas. The two
individuals in February 2010 (male and female) only roosted on
telephone poles, roosting on three poles separated by a maximum
distance of 670 m. These roost locations were 1.82±0.16 km from
the site of capture, while the roost location for all other bats was
<600 m from the site of capture.

**Table 2. Total insect biomass (g) collected in light traps in saltmarsh and coastal swamp forest during February 2010 and March 2010.**

| Taxa/class          | FEBRUARY 2010 (n = 10) | MARCH 2010 (n = 8) |
|---------------------|------------------------|--------------------|
|                     | Saltmarsh | Coastal swamp forest | Saltmarsh | Coastal swamp forest |
| Lepidoptera (moths) | 4.82 (47.05) | 3.63 (32.51) | 4.01 (51.96) | 4.71 (57.88) |
| Coleoptera (beetles)| 1.27 (12.43) | 5.46 (48.94) | 0.25 (3.20) | 2.07 (25.44) |
| Diptera (flies)     | 0.43 (4.24)  | 0.19 (1.75)   | 0.15 (1.94)  | 0.22 (2.71)   |
| Other               | 0.69 (6.73)  | 0.81 (7.26)   | 0.20 (2.59)  | 0.38 (4.67)   |
| <2 mm               | 3.03 (29.54) | 1.06 (9.55)   | 3.11 (40.31) | 0.76 (9.29)   |
| Total               | 10.24      | 11.15         | 7.22        | 8.14          |

NB. Values in brackets represent percent of total insect biomass in each habitat.
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Prey biomass

*Aedes vigilax* was the most abundant mosquito species in
saltmarsh and coastal swamp forest during February and March
2010. This trend has been observed during long-term mosquito
surveillance in the study area with *Ae. vigilax* representing 41.2%
of all mosquitoes trapped over nine consecutive trapping seasons
(unpublished data – L. Gonsalves and C. Webb). While population
abundances of this mosquito species can be variable, its consistent
presence in the study area provides *V. vulturnus* and other small-
sized bats with a reliable prey resource during the austral summer.

As expected, the abundance of *Ae. vigilax* during March 2010
was significantly lower in saltmarsh than in February 2010. This
result was in line with expectations as the lack of extensive tidal
flooding of saltmarsh in the weeks preceding the March 2010
radio-tracking period did not provide suitable conditions for
mosquito development [33]. However, there was no significant
difference in the mean abundance of *Ae. vigilax* in coastal swamp
forest between the two radio-tracking periods. Mark-release-
recapture experiments have shown that *Ae. vigilax* can disperse >5
km from larval habitats [17] and coastal swamp forest is likely to
provide a humid refuge as well as a source of blood meals for this
species, sustaining high population abundances for longer periods
than exposed saltmarsh environments.

Since the trapping techniques used to survey mosquitoes and
other insects were not the same, any comparison of mosquito
abundance with abundance of other insects must be interpreted
with caution. The mosquito traps collect a subset of the extant
mosquito population as over a short range they specifically target
host-seeking female mosquitoes as those mosquitoes are most
attracted to the carbon dioxide-baited traps. A comparison of
*Ae. vigilax* biomass with the biomass of other insect fauna revealed
that in February 2010, *Ae. vigilax* biomass in saltmarsh (8.02 g) and
coastal swamp forest (6.42 g) was similar to the biomass of all other
insect taxa combined (assuming one adult mosquito weighs
0.00198 g). In March 2010, *Ae. vigilax* biomass in saltmarsh
(1.10 g) and coastal swamp forest (4.02 g) was within the range of
biomass contributed by other aerial nocturnal insect fauna. This
emphasises the potentially important contribution of *Ae. vigilax* as a
food source for *V. vulturnus*.

While average nightly insect biomass did not differ between
habitats or tracking periods, the biomass of particular taxa did.
Coleopteran biomass was significantly greater in coastal swamp
forest than in saltmarsh during both radio-tracking periods. While few studies investigating distribution of beetles in saltmarsh [34,35] have identified elevation and associated saltmarsh vegetation gradients as variables closely associated with beetle distribution, no studies have specifically investigated beetle distribution along a saltmarsh-adjacent forest gradient. Other studies investigating beetle distribution and abundance in forested areas and more open habitats have reported higher abundances of coleopterans in forests and forest fragments than in adjacent clear cuts [36], forest clearings [37], and open pastures [38]. With relatively few comparative studies of beetle abundances in different structural vegetation associations, it is difficult to compare our results directly to previous investigations.

Habitat use by *Vespadelus vulturnus*

Given the error associated with radio-tracking, it is often difficult to elucidate habitat use at fine spatial scales and this may result in the use of particular habitats being under- or over-estimated. Many of the foraging locations classified as open water in this study were located close to mangroves that fringe saltmarsh on the seaward side. While some individuals were recorded to commute (>1.8 km) across open water from roosts to foraging areas, it is quite possible that some of these locations were in fact in saltmarsh edge zones (saltmarsh-mangrove interface), where ultrasonic detectors have found bats to be more active than in the interior of the saltmarsh [39]. Additionally, light-tagged *V. vulturnus* individuals released in the saltmarsh interior have been observed commuting to edge vegetation before leaving saltmarsh.
[20], further supporting the view that these vegetation interfaces provide an edge for bats to forage along. Despite the potential for underestimation of small portions of habitat, compositional analysis revealed that after accounting for availability of habitats within the foraging range, saltmarsh was the most preferred habitat for foraging *V. vulturnus* individuals in February 2010. While *V. vulturnus* has been recorded echolocating and feeding in saltmarsh previously [13,39], this is the first study to identify the preferential use of saltmarsh for foraging by an insectivorous bat species. *Chalinolobus gouldii* was the species most commonly recorded by ultrasonic detectors in saltmarsh [40], yet radio-tracking of this medium-sized bat (14 g) with a low echolocation frequency (29 kHz), revealed that saltmarsh was used in proportion to its availability [40]. In March 2010, use of saltmarsh by *V. vulturnus* decreased, with greater use of open water and coastal swamp forest. However, continued use of both threatened vegetation communities reaffirms that they are important foraging patches for *V. vulturnus*.

### Relationships between prey biomass and habitat use

If prey abundance is influencing habitat use by foraging *V. vulturnus* individuals, one would expect that a change in prey abundance in one habitat from February 2010 to March 2010 would also be reflected in a shift in foraging range over this time. During this study, while *Ae. vigilax* populations were abundant in both saltmarsh and coastal swamp forest in February 2010, *V.*

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**Figure 5. Habitat availability and use in February 2010.** Percentage of available and used habitat in February 2010. doi:10.1371/journal.pone.0064081.g005

**Table 3.** Ranking matrices for *V. vulturnus* in February 2010 and March 2010, based on comparisons of the proportions of locations for each bat in each habitat type with the proportion of each habitat type available within the bat’s foraging range (95% KDE).

| Habitat                  | Coastal floodplain wetlands | Coastal swamp forests | Forest complex | Mangrove forests | Saltmarsh | Open water | Rank |
|--------------------------|-----------------------------|-----------------------|----------------|------------------|-----------|------------|------|
| **February 2010**        |                             |                       |                |                  |           |            |      |
| Coastal floodplain wetlands | 0                           | −1.06                 | 0.21           | 0.39             | −1.38     | −0.17      | 3    |
| Coastal swamp forest      | 1.06                        | 0                     | 1.27           | 1.45             | −0.32     | 0.90       | 2    |
| Forest complex            | −0.21                       | −1.27                 | 0              | 0.18             | −1.59     | −0.37      | 5    |
| Mangrove forests          | −0.39                       | −1.45                 | −0.18          | 0                | −1.77     | −0.56      | 6    |
| Saltmarsh                 | 1.38                        | 0.32                  | 1.59           | 1.77             | 0         | 1.21       | 1    |
| Open water                | 0.17                        | −0.90                 | 0.37           | 0.56             | −1.21     | 0          | 4    |
| **March 2010**            |                             |                       |                |                  |           |            |      |
| Coastal floodplain wetlands | 0                           | −1.43                 | −0.96          | −1.37            | −0.96     | −1.59      | 6    |
| Coastal swamp forest      | 1.43                        | 0                     | 0.47           | 0.06             | 0.46      | −0.16      | 2    |
| Forest complex            | 0.96                        | −0.47                 | 0              | −0.41            | 0.00      | −0.63      | 5    |
| Mangrove forests          | 1.37                        | −0.06                 | 0.41           | 0                | 0.40      | −0.22      | 3    |
| Saltmarsh                 | 0.96                        | −0.46                 | 0.00           | −0.40            | 0         | −0.63      | 4    |
| Open water                | 1.59                        | 0.16                  | 0.63           | 0.22             | 0.63      | 0          | 1    |

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**Figure 6. Habitat availability and use in March 2010.** Percentage of available and used habitat in March 2010. doi:10.1371/journal.pone.0064081.g006

*V. vulturnus* preferentially foraged in saltmarsh. However, when the abundance of *Ae. vigilax* was significantly lower in saltmarsh, habitat use by foraging *V. vulturnus* individuals shifted with greater use of coastal swamp forest. This trend was not observed for any other prey taxa measured in this study.

While prey may be abundant in a given habitat, the ability of bats to access these resources can be inhibited by other physical characteristics of the habitat such as vegetation clutter, indicating that prey abundance does not always equate to availability [5,6]. Preferential use of saltmarsh for foraging in February 2010 may reflect this principle – it is energetically less demanding and perhaps more efficient to locate prey in an open habitat such as saltmarsh than in a cluttered forest environment [41].

A shift to foraging in coastal swamp forest in March 2010 when *Ae. vigilax* was more abundant in this habitat than the neighbouring saltmarsh may indicate that *V. vulturnus* preferentially seeks *Ae. vigilax* as a dietary resource. Alternatively, use of coastal swamp forest by *V. vulturnus* suggests that this species chooses to forage in a habitat that, while being energetically more demanding due to clutter, sustains prey items that are energetically more profitable, mitigating the cost of foraging in this clutter. Lepidopterans and coleopterans contributed the greatest amount of biomass in coastal swamp forest in March 2010. Lepidopterans and coleopterans provide about 25.5 kJ g⁻¹ [42] and 21.3 kJ g⁻¹ [43] of energy, respectively. Mosquitoes, however, provide lower levels of energy to predators, representing 6.3–14.8 kJ g⁻¹ [44]. However, the ‘hardness’ of prey items also influence the net energy gained from ‘energy rich’ prey items that may require more extensive processing times (mastication and digestion) and thus increased energy expenditure [45]. Handling time (time taken to capture prey) associated with each prey item, presumably, will also influence the habitats in which bats choose to forage [46].

It is possible that other factors may be influencing which habitats *V. vulturnus* selects for foraging. An artefact of the design of this study, based around tidal activity, is the potential influence of lunar illumination on habitat use by *V. vulturnus*. During the March 2010 radio-tracking period (commencing with a waning crescent moon phase and concluding on a full moon), the level of lunar illumination was greater than the February 2010 radio-tracking period (commencing on the night of a new moon and concluding on the night following the first quarter moon phase). It is possible that *V. vulturnus* foraged in the more sheltered coastal swamp forest during March 2010 to mitigate the risk of predation associated with foraging in open habitats [47]. However, we did not observe any nocturnal predators (e.g., owls) while radio-tracking (L. Gonsalves pers. obs.).

With the exception of one roost, bats were roosting outside the confines of the coastal swamp forest, sometimes >1.8 km away and separated by a water body. Despite this, all radio-tracked individuals were trapped in the coastal swamp forest and foraged there or in the neighbouring saltmarsh each night of the study, further highlighting that these two threatened vegetation communities are important foraging areas for *V. vulturnus*, at least in the study area. Individuals travelled distances greater than previously reported for this species [1370 m from trapping location to roost: [27]], with some individuals travelling >1.8 km from roosts to foraging habitats. Foraging ranges observed during this study were also greater than predicted in a banding study [48] and foraging ranges in forest estimated for the similar-sized *V. pumilus* Gray (eastern forest bat) [26].

**Implications for broadscale mosquito control**

Appropriate management of *Ae. vigilax* populations requires consideration of the potential impacts of broadscale mosquito control on the diets of insectivorous bats. A threatening process for bats worldwide is the loss or reduction of prey items due to pesticide use [49]. However, the impact of pesticides on local insect populations is dependent on the type and delivery method of those insecticides. The most commonly used mosquito control agents in Australia (e.g., *s*-methoprene and *Bacillus thuringiensis israelensis*) are generally mosquito-specific and target the aquatic immature stages [11]. While broadscale insecticide use against mosquito populations in Australia is generally only undertaken during periods of epidemic disease activity, use of early season treatment to assist in suppression of irruptions of mosquito populations later in the season is gaining acceptance by authorities undertaking control programs [50]. Given that such control programs can substantially diminish larval mosquito populations, in some cases reducing larval populations by up to 98.2% [50], use of broadscale mosquito control will diminish the important prey
resource that *Ae. vigilax* represents to *V. vulturnus* [20]. Use of such mosquito control measures has indirectly been linked to bird declines [32], while declines in bat populations have previously been attributed to deteriorating feeding conditions [31].

Conclusions

Our study demonstrates a short-term shift in foraging range by *V. vulturnus* correlated with fluctuations in *Ae. vigilax* distribution and abundance, indicating that this mosquito is an important dietary resource for this bat species. Consequently, appropriate management of *Ae. vigilax* populations requires consideration of potential impacts of broadcast mosquito control on the diet of at least one insectivorous bat species. To assess the impact of mosquito control on insectivorous bats more adequately, an adaptive management process should be followed where careful monitoring of bats before and after an application of broadcast mosquito control is required. However, in the interim, control programs should avoid the lactation period of bats, when energetic demands are greatest [32], and risk of contracting mosquito borne disease is reduced [53].

Supporting Information

Methods S1 Methods used for radio-tracking and calculation of foraging ranges. (DOCX)

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Author Contributions

Conceived and designed the experiments: LG BL VM. Performed the experiments: LG. Contributed reagents/materials/analysis tools: LG BL VM. Wrote the paper: LG BL VM.

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