TONGAN FLYING FOX (*PTEROPUS TONGANUS*) ACTIVITY PATTERNS & ASSOCIATING COVER TYPES IN AMERICAN SAMOA

by

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Dedicated to my mother, Miriama Ve'e.

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ABSTRACT

Globally bats provide ecological services including pollination and natural pest removal. In American Samoa, the Tongan flying fox (*Pteropus tonganus*) is one of the primary animal species contributing to the success and regrowth of native forests. Trees used to create Samoan artifacts and cuisines benefit from the seed dispersal and pollination provided by these bats. However, habitat loss and human disturbance have caused population declines since the 1980s.

The American Samoa Department of Marine & Wildlife Resources (AS-DMWR) is using GPS tags to study flying fox movement and ecology. Information obtained from this research program aids bat conservation and contributes knowledge regarding understudied *Pteropus spp*. My thesis used these data from AS-DMWR to answer several important questions about Tongan flying fox ecology. The first objective of my research was to identify and quantify the diel patterns of Tongan flying fox commuting, foraging, and roosting activities. I used tri-axial acceleration data from the GPS tags to classify observations of bats to these specific activities. Then, I compared the percentage of time bats allocate to each activity during day and night using a one-tailed t-test. Results showed a significant difference in roosting only, with a p-value = 0.04 and t t_{0.05(1)4} = 2.95. Approximately 25% of roosting activities for tagged Tongan flying foxes occurred during the night and 75% occurred during the day. These results are consistent with the description of Tongan flying foxes as a nocturnal species. My second objective evaluated cover types in Tutuila, American Samoa where bats frequently perform these activities. Accelerometer and locational data obtained from GPS tags were used to identify segments of Tongan flying fox movement associated with the activities, roosting, foraging and commuting. Step-Selection Function (SSF), from the AMT (Animal Movement Tracking) R package determined cover type covariates that statistically

correlated with segments of bat movement associated with specific activities. My results showed that Tongan flying foxes were likely to select locations within lowland forests for all three activities. Locations within coastal forests were also likely to be selected by Tongan flying foxes for commuting and roosting, while foraging was more likely to occur at locations near buildings and plantations.

In conclusion, the information presented in my thesis regarding Tongan flying fox activity patterns and associated cover types can help land managers and farmers develop efficient and effective management plans that reduce human and bat conflicts. Such plans could include delineating wind farm sites where risks of turbine strikes are low, identifying ways farmers could include flying foxes in their agricultural practices, and designating reserve areas needed to preserve this critical species.

CHAPTER 1. REVIEW OF TONGAN FLYING FOX (P. TONGANUS) IN AMERICAN SAMOA

1.1 Introduction

Bat species around the globe have experienced population declines (Jones et al. 2009) from factors including habitat loss, diseases, and over harvest (Verbroom 1998). The diminishing numbers of bats worldwide makes their conservation and management important. Unfortunately, such efforts are challenging for most bat species because we lack necessary knowledge (Jones et al. 2009). As a consequence, obtaining information concerning habitat requirements and behavior is a critical first step to the effective conservation and management of most bat species (Mickleburg et al. 1992; Hancock et al. 2004). However, detailed movement and habitat studies for flying foxes are limited due to the high mobility and low body weight of these bats making observational and remote sensing studies difficult to conduct (De Jong et al. 2013). Generalizing habitat requirements for *Pteropus* species could be misleading because of the wide range of ecosystems occupied by these bats (Olesky et al. 2015). Therefore, it is important to collect movement and habitat information for many flying foxes for conservation purposes (Jones et al. 2009).

The important ecological services provided by bats make the conservation and management of their populations critical in many ecosystems (Tideman 1987). Bats of the genus *Pteropus* provide an excellent example of this. These large flying foxes (or fruit bats) are commonly found in tropical, subtropical, and temperate regions of Asia, Australia, East Africa, and islands across the Pacific Ocean (Yupadee et al. 2017). Many of these flying foxes disperse seeds and pollinate plants (Borkin et al. 2011). For example, Tongan flying foxes in the Vavau archipelago of Tonga were the sole effective disperser of 57% of the plant species whose fruits they consume (McConkey & Drake 2015). These ecological services provided by flying foxes are essential to maintaining

community diversity and the health of native forests through the regeneration of trees and plants (Fujita & Tuttle 1991). *Pteropus* species potentially disperse seeds over large distances to remote locations (Olesky et al. 2015). Flying foxes also provide important economic services. For example, bananas (*Musa* spp.) provide an important contribution to the economy of countries like Costa Rica (Nur 1976). Farmers depend heavily on natural pollinators such as bats, to cultivate bananas (Nur 1976). Yet, these bats suffer from population loss and the lack of information pertaining to their ecology constrains our ability to understand and ideally mitigate such losses (Fujita & Tuttle 1991, Plotwright et al. 2011).

American Samoa is an archipelago located in the south Pacific Ocean, occupied by two flying fox species whose populations have suffered from habitat loss as well as facing challenges from past over harvesting. These islands contain only three native terrestrial mammal species including the previously mentioned Tongan flying fox (*P. tonganus*), Samoan flying fox (*P. samoensis*), and a non-flying fox species the Pacific sheath-tailed bat (*Emballonura semicaudata*) (Amerson et al. 1982). Tongan flying foxes can be found in American Samoa, Cook Islands, Fiji, New Caledonia, Niue, Papua New Guinea, Samoa, Solomon Islands, Tonga, and Vanuatu (Cox 1983, Cousins & Compton 2005).

Tongan flying foxes are important pollinators of many native tree and plant species found in the Pacific islands (Cox 1983). Tongan flying foxes are medium-sized flying foxes, weighing between 400-600 g with a forearm length of 130-150 mm (Brooke 2001). Peak birthing of Tongan flying foxes occurs from May to July annually (Scanlon et al. 2014). They are commonly found at feeding sites in parts of the forests containing large quantities of small fruits and flowers such as *Ficus obliqua* and *Syzygium inophylloides* (Brooke et al 2000). In American Samoa, Tongan flying foxes are main pollinators and dispersers of the Polynesian chestnut (*Inocarpus fagifer*), which is used to create traditional Samoan carvings and canoes (Medeiros et al. 2019). Tongan flying foxes are nocturnal and social roosters (Cox 1983). They roost in colonies of thousands of bats and forage in native forests, agricultural plantations, villages, and houses near the forests (Pierson et al. 1992).

Successful management of populations of Tongan fly foxes in American Samoa is constrained by both legacies of past human activity as well as lack of critical local knowledge. For example, during the 1990s two hurricanes caused an 80% decline in Tongan flying fox population in American Samoa (Banack & Grant 2003). Following these disasters, laws and regulations promoted the management and conservation of bats in American Samoa (Brooke et al 2000). However, data are needed to assess the effectiveness of these actions. Furthermore, a search of Web of Science using the key words: *Pteropus tonganus*, Tongan flying fox (and fruit bat), American Samoa, Tutuila, and Manu'a, identifies only four studies (Morrel & Craig 1995; Grant et al 1997; Brooke et al 2000; Banack & Grant 2002). These studies describe baseline habitat requirements and behaviors of this species in American Samoa and provide the basis of the hypotheses evaluated in this thesis regarding the activity patterns: commuting, foraging, and roosting. My tests of these hypotheses will provide the in-depth understanding of these bats' ecology and behaviors needed for effective management benefiting both landowners and flying foxes (Jones et al. 2009).

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CHAPTER 2. USING TRI-AXIAL ACCELERATION DATA TO IDENTIFY TONGAN FLYING FOX (P. TONGANUS) ACTIVITIES AND ASSESS NOCTURNALITY

2.1 Introduction

Studies of animal behavior and activities are crucial for conservation, understanding life history, and land management (Sutherland 1998). Animal behavior can elucidate the influence of wide range of exogenous and endogenous factors on an animal's fitness (Nathan et al. 2008). For example, Cid et al. (2020) compared activity range—the amount of time spent active per day— with body mass amongst 128 mammalian species and found general patterns showing large carnivores needing more time active in a day to meet energetic demands. Barclay (1985) studied African insectivorous bat foraging behavior and found that these bats exhibited short foraging periods due to dry conditions and low insect abundance. Hengjan et al. (2017) investigated the golden-crowned flying fox daytime behavior and activity budget using focal sampling and found that the most frequent activity was sleeping. Ultimately, knowledge gained from such studies can help inform decision making by local government and land managers (Kinzik et al. 2005). For example, information from Henghan et al.'s (2018) study on nighttime behavior and habitat utilization of large flying foxes (*Pteropus vampyrus*) was used in the development of landscape management, species conservation, and disease prevention in regions of Southeast Asia.

Bat commuting, foraging, and roosting behaviors have been studied to develop effective conservation strategies. The U.S. Department of Agriculture (USDA) created a conservation assessment for five forest bat species in eastern U.S. based on studies regarding their roosting and foraging behaviors (USDA 2006). Law (1993) studied Queensland blossom bat (*Syconucteris* australis) roosting and foraging behaviors and concluded that unless feeding sites are also protected,

protecting roosting sites alone is not an adequate conservation measure. Olesky et al.'s (2015) study on Madagascan flying fox (*Pteropus rufus*) commuting behavior and seed dispersal emphasized the importance of understanding flying fox habitat requirements when traveling long distances. As these bats travel from roost to feeding site and vice versa, they are defecating seeds from the fruits they consumed contributing to the growth of native forests (McConkey & Drake 2006).

Behavior and activities vary amongst flying fox species. Bats of *Pteropus spp*. inhabit places that differ in ecological communities and contain varying habitats, which is mainly why generalizing movement and associating habitat requirements for *Pteropus spp*. could be misleading (Olesky et al. 2015). Some species roost, forage, and commute in large groups and others forage alone. For example, Australian black flying foxes are social mammals. They forage and roost in colonies of thousands of bats. Courtship and mating behaviors of this species occur during the daytime (Nicola 2002). In contrast, Samoan flying foxes, found in the Samoan islands, roost and forage in solitude and most of their flight behaviors (ex: commuting, soaring) occur during the daytime (Thomson et al. 1998).

Flying foxes are relatively diverse in their roosting ecology and behavior. De Jong et al. (2013) defines a roost as a location where the last morning and the first evening data points for one or more individuals overlap on ≥ 1 day(s) and where bats rest or sleep (Palmer 1999). Some have adapted to roost in cover types near roads and houses, and others roost in remote habitats. The *Pteropus livingstonei* in Comoro Islands and *P. leucopterus* in the Philippines roost in native montane forests (Heaney et al. 1987), whereas *P. phaeocephalus* in Chuuk and *P. howensis* in Ontong Java roost on emergent coral atolls (Sandborn & Nicholson 1950). Flying foxes commonly show fidelity to traditional roost sites. Wiles (1982) reported that *Pteropus mariannus* used the

same roosting site in Guam for hundreds of years. In Australia, a traditional roosting site was used for at least 60 years (Tidemann 1985). *Pteropus spp.* roost in habitats with food sources and emerging trees that provide shelter and easy exits for upward flight (Palmer and Woinarski 1999). The Tongan flying fox roosts in large colonies during the daytime (Cousins & Compton 2005) in both secluded and human dominated areas. However, most roosting sites are far from human disturbance and difficult to access. Tongan flying foxes utilize roosting sites for a long period of time unless those sites are disturbed (Morrell & Craig 1995). For example, the two hurricanes that occurred during the 1990s in American Samoa caused Tongan flying foxes to split into smaller groups and move to different roosting locations (Cousins & Compton 2005). Tongan flying foxes gathered and returned to traditional roosting sites once affected habitats recovered, however, abundance of Tongan flying fox was reduced (Russel et al 2006). Important information concerning roosting habitats of *Pteropus spp.* is key for conservation considering that roosting sites are crucial to the survival and reproductive success of bats (Kunhert et al. 2016).

Common flight activities for flying foxes include commuting and foraging. Commuting movements can be characterized as long distances traveled by a bat between roosting and foraging sites (Law 1993) using their advanced navigational capabilities that allow them to adjust their speed and direction when flying (Vebroom 1998). Sapir et al. (2014) observed nine straw-colored fruit bats (*Eidolon helvum*) traveling 42.5 \pm 17.5 km (mean \pm s.d.) to and from their roost near Accra, Ghana. Foraging movements of flying foxes can be characterized as low flights in and out of trees or plants in search for food (Paez et al. 2018). During foraging activities, these bats forage in areas containing abundant food sources that primarily comprise their diet (Mickleburg & Houston 1992). Tongan flying foxes forage from dusk to dawn and feed in distant areas including coastal and upland forests, peninsulas, and hillsides protruding out into the ocean (Morrell & Craig

1995). Commuting and foraging play important roles in two of the ecological services flying foxes provide: seed dispersal and pollination. During flight activities, Tongan flying foxes pollinate nearly 80% of canopy trees in Samoa (Banack 1998). However, such flight activities and associated habitat features used by flying foxes are poorly documented. Palmer & Woinarski (1999) found only 3% of foraging movements of black flying fox (*P. Alecto*) in Australia occurred on conservation reserve lands. Like most *Pteropus spp.*, there is a lack of information concerning Tongan flying fox behavior. Such knowledge is essential for developing conservation methods.

With the help of technology, researchers are able to conduct animal behavior studies at a level that was once unattainable (Halsey et al. 2009) thereby providing insights into previously poorly understood behaviors like commuting and foraging. Accelerometer data has been used in numerous studies to identify, monitor and understand the behavior of free-ranging wildlife (Shepard et al 2010; Brown et al. 2012; Mathie et al. 2004) allowing wildlife biologists to observe daily activities of many species. Accelerometers are devices that measure acceleration and sense static and dynamic forces (Murchie et al. 2010). They measure acceleration along three axes: x, y, and z to sense the orientation and activity of an object. The three-dimensional axes collect data on two factors: accelerometer waveform patterns and accelerometer waveform variations (Brown et. Al 2013). Accelerometer data has allowed researchers to accurately identify unknown animal behaviors (Watanabe et al. 2005). For example, Nathan et al. (2012) used tri-axial acceleration data to identify behavior modes of free-ranging griffon vultures.

The objectives of this study were to 1) identify Tongan flying fox commuting, foraging and roosting activities using tri-axial acceleration data and 2) determine time allocations for each identified activity and the percentage of each activity spent during day and night. Based on previous studies, I hypothesized that Tongan flying foxes in American Samoa will be nocturnal. I

predicted that if my hypothesis was true, the average number of minutes spent foraging and commuting will be significantly higher at night than during the day while the average number of minutes spent roosting will be significantly higher during the day than at night.

2.2 Methods

I conducted bat mist-netting at the Olovalu crater in Futiga and the Tuimalefano family land in Malaeloa in June 2019. During October 2016 and 2017, American Samoa Department of Marine and Wildlife Resources (AS-DMWR) conducted mist-netting at the Olovalu crater as well. Data obtained from tags deployed in 2016 and 2017 were also analyzed in this study. Olovalu crater contains traditional roosting sites for both Samoan and Tongan flying foxes. I used several net sizes: 18X30m (propped on poles and trees), 9X30m, and 9X10m. Nets were usually set up at 1700 hr and taken down at 0100 hr. I checked the nets every 15 minutes to reduce stress on bats and their time caught in the nets. Thirty-four bats total (1 *P. samoensis, 33 P. tonganus*) were caught during mist-netting. I weighed each bat, measured forearm length, recorded gender and age, and checked for any injuries. I also fed them mango juice to compensate for missed feeding during captivity.

AS-DMWR and I tagged 6 Tongan flying foxes altogether using e-obsGmbH GPS bird tags (e-obs Digital Telemetry; Gruenwald, Germany). All GPS tags deployed were <3% of the bat's weight (O'Shea & Bogan 2003). To attach tag to bat, I trimmed the fur from the area on the bat's back, between its wings, and used fabric glue to adhere the GPS tag to skin. Starting the morning after tag deployment, I returned to the netting site to download data from the tag using the GPS base station receiver. This was repeated daily until data demonstrated a continuous resting state overnight and into the next morning thereby indicating tag loss from the bat. The data I obtained from GPS tags using the base station receiver included longitude and latitude coordinates,

timestamps, and accelerometer (ACC) values. I uploaded these observations to Movebank (Kranstauber et al. 2011), a free online database of animal tracking data. Movebank makes the data accessible to the public upon request.

I classified observation from each bat into the activity categories of commuting, foraging or roosting. This classification was accomplished using the accelerometer data from the bat tags in combination with preexisting data. The preexisting data included assessments of ACC values from experimentally manipulated tags, an understanding of where Tongan flying foxes typically perform certain behaviors, landcovers of American Samoa wildlife habitats, and a python-based web application called AcceleRater (Hebrew University of Jerusalem, Minerva Center for Movement Ecology 2014). Before classifying accelerometer data across all tags, AcceleRater requires a sampled dataset to learn how to classify ACC values to behavioral classes. To accomplish this, I annotated a sampled dataset of 240 ACC data segments (48 from each bat and broken down into 16 segments for each activity type from each bat) using the Movebank Accelerometer Viewer web application. I assigned each ACC data segment to one of the three activity states based upon the bat's speed of movement, its location, and the associated cover types. I plotted GPS locations reported around the same time as the ACC segment, on a landcover GIS layer of Tutuila (Meyer et al. 2017) to identify the associated habitat. I then evaluated the bat's location and speed to better describe each bat's specific activity during each segment. Finally, I refined classification of points for the sample segments by evaluating accelerometer data from handheld tags moved in ways analogous to bat behavior (Ieremia 2018). These tag calibration values from Ieremia (2018) used the positioning and wavelengths of the 3 axes: x (red axis), y (green axis), z (blue axis) to characterize each activity type. Foraging and commuting were indicated by high peaks in wavelengths for the z-axis (blue). Commuting consisted of longer distances between locations and typically occurred in areas not containing food sources. Roosting was characterized by all three axes at rest. Each ACC data segment contained at least 78 consecutive tri-axial values (x, y, and z) that were visually assigned as either continuous commuting, foraging, or roosting activity. I then used the AcceleRater web application (The Hebrew University of Jerusalem, Minerva Center for Movement Ecology 2014) to classify the entire dataset into behavioral states of commuting, foraging, and roosting for all bats using the following machine learning algorithms or models: artificial neural network (ANN), decision tree, support vector machines (SVMs), nearest neighbor, and random forest. SVMs applied include linear SVM and radial basis function (RBF) SVM. I computed standard deviations using a 10-fold cross validation procedure to ensure robustness in the performance of each model. The 5 selected models are common algorithms used for various pattern recognition and classification tasks (Nathan et al. 2008). I compared the models using weighted averages of precision, recall, and accuracy for each model across all activities.

After all of the data from the tags for each bat were classified into one of the three activities, I summarized and analyzed information statistically to test my main hypothesis regarding the proportion of each activity type bats exhibited during daylight and at night. I classified each observation as occurring during day or night based upon when it was recorded. Observations with times >0600 hr and <1800 hr were classified as during the day, and those with times <0600 hr and <1800 hr were classified as during the day, and those with times <0600 hr and <1800 hr were classified as during the night. I calculated the proportions of time spent performing a specific activity by dividing the time each bat spent in each activity by the total time spent conducting all 3 activities during day/night. For example, if a bat spent 8 of the 12 hr during the day roosting, it spent ~67% of the day roosting. Similarly, if it spent 2 of the 12 night time hours roosting, it spent only ~17% of the night roosting. Next, I calculated the difference between the

proportion of time each bat spent engaged in each activity time at day and during the night. I used a one-tailed t-test to compare these differences across all 5 bats to a null hypothesis of no difference as indicative of bats not being more likely to engage in any of these specific activities at a particular time of the day. All analyses were conducted in R version 1.3.1093 (R Development Core Team 2020) and Microsoft Excel (Version 16.2; 2020).

2.3 Results

Thirty-four (34) flying foxes were captured during bat mist-netting. All captured bats were caught at the Olovalu crater site and none at the Tuimalefano family land in Malaeimi. Six (6) GPS tags were deployed on 6 out of the 34 captured flying foxes, however, only 5 tags were analyzed in this study. I excluded data from tagged Bat 5096 because it only reported 4 sets of GPS locations due to tag loss shortly after deployment. All tagged bats were Tongan flying foxes (see Table 2.4 in Appendix A) because only 1 Samoan flying fox was captured and did not have the appropriate body weight for the GPS tag. Bat 5100 had 17190 locations and was tracked for 2 weeks; bat 5101 had 4062 locations and was tracked for 11 days; bat 5102 had 13052 locations and was tracked for 8 days; bat 5103 had 5039 locations and was tracked for 5 weeks; and bat 5104 had 5628 locations and was tracked for 5 days. All tagged bats were tracked during fall except bat 5104 which was tracked during summer. Bats 5100, 5101, and 5103 were tracked during the month of October (and into November for bat 5103) in 2016; bat 5102 was also tracked during Cotober but in the following year of 2017; bat 5104 was tracked during June and into July in 2019. In average across all tags, bats were tracked for about 15 days at 8994 locations.

Using AcceleRater, I classified a total of 52,500 ACC data segments as a specific activity: commuting, foraging, and roosting. Acceleration for all 5 tags were measured at 10Hz. Three-thousand five hundred of those segments were classified as commuting, 15037 as foraging, and

33963 as roosting (see Figure 2.1 and 2.2). The specific recall was on average 95-99% for each model and 98-99% for each activity across models (Table 2.1). The precision of assignment was also relatively high on average 93-98% for the different models and 88-99% for each activity across models (Table 2.2). The accuracy of assignment was on average 94-98% for each model and 80-99% for each activity across models (Table 2.3). All implemented models had a percentage of correctness of assignment > 95% except for nearest neighbor and ANN which had 94.7% and 94.9%, respectively (see Table 2.4).

Bat 5104 differed from the other four bats regarding time spent performing each activity during diurnal and nocturnal periods. This bat spent more time (65%) foraging during the daytime than nighttime (57%). The other 4 bats spent > 65% foraging during nighttime and < 57% during daytime. The other four bats also spent approximately 20-30% commuting daytime and < 20% commuting during nighttime. Bat 5104 was the only bat that spent more time commuting during the nighttime (29%) and less during the daytime (16%) (see Table 2.5). Bats 5100, 5102, 5103, and 5104 all spent more time roosting during the day than at night. However, the difference between Bat 5104's proportion of time spent roosting during the day and at night was not statistically significantly ($t_{0.05(1)4} = 6.6$; p-value = 0.09). In contrast, Bat 5101 spent more time roosting during the day than the night with a statistically significant difference between time proportions ($t_{0.05(1)4} = 23$; p-value = 0.03). All bats spent the most time foraging, followed by roosting, with the least time spent commuting (see Table 2.5).

Among the three activities I investigated only roosting was significantly ($t_{0.05(1)4} = 2.95$; P-value = 0.04192) different according to the t-tests (see Table 2.6). P-values for commuting and foraging were 0.31 and 0.12 respectively. The average across all five bats of the difference between proportion of each activity at night and during the day were all close to zero (Table 2.6).

Commuting and resting have positive mean values (0.07 and 0.09, respectively). Foraging had a negative mean value of -0.13. Because the mean of each activities was calculated based on subtracting time spent conducting specific activities during the nighttime from that of during the daytime, the negative mean value indicates that foraging was the only activity where a higher proportion occurred during the night than day. The positive mean values indicated that commuting and roosting occurred during the day more frequently than night.

2.4 Discussion

My results provided mixed support for my hypothesis that Tongan flying foxes would be nocturnal. Roosting was the only activity with statistically significant support for bats to engage in it during the day than night. Similarly, Brooke et al. (2000) found that Tongan flying foxes roost during the day while more active behaviors occur during the night. However, contrary to my hypothesis, I detected no significant difference between day and night time proportions for commuting and foraging activities. It is worth noting that the negative mean value for foraging in my results was in the direction I expected in terms of foraging time proportions being greater in night than day; however, the mean was not statistically significant (Table 2.6).

Unlike the other 4 tagged Tongan flying fox, Bat 5104 was the only bat to spend most of its time commuting during the night and foraging during the day. This may be due to the change in its temporal and spatial habitats. Bat 5104 was the only bat tagged during Summer 2019 after 2 years since the last bat mist-netting was conducted on Olovalu crater. During the years of no mist netting, American Samoa experienced a tropical cyclone Gita in February 2018 causing serious damage to homes and habitats. Tropical cyclones exert a major impact on foraging behavior and ecology of flying foxes in regards of depleting food sources (Grant et al 1997). Wildlife habitats on Olovalu crater were in fact negatively affected by Tropical Cyclone Gita (pers. comm. AS-

DMWR). Our first day mist netting at Olovalu crater since 2017 revealed that many trees had fallen and the pathway that was once used as an access point into the crater for vehicles was completely blocked by debris. Past netting sites where previous successful captures occurred were no longer accessible.

Several aspects of my data collection and analysis may have impacted my conclusions. Previous statements regarding Tongan flying fox activity patterns were based upon scan samples of large numbers of bats (Brooke et al. 2006; Cousins & Compton 2005). In contrast, my work was based on continuous monitoring of five individual bats. The continuous activity data provided by the GPS tags avoided numerous potential biases associated with scan sampling of unmarked individuals, such as only collecting more data on readily observed individuals of a group, to estimate activity patterns of the larger group (Altmann 2014). However, the intense focus my work placed on five individual bats limited my sample size which in turn constrained the relevance of several analytical approaches. Furthermore, the statistically insignificant trends that were in the expected direction for most of the bats in my study suggests that sampling additional individuals may have provided more significant results. Tracking a small number of individuals also introduces biases associated with variation in the time of year when each of these bats were tracked and variation associated with such biases across a small number of individuals may also have impacted my ability to draw statistically significant conclusions.

Constraints associated with the use of accelerometer data and the AcceleRater machine learning tool may also have impacted insights from my analysis. No significant differences in foraging and commuting between day and night time proportions can be due to Accelerater overlapping certain characteristics of x, y, and z axis positioning and wavelength for the 3 activities during classification across all bat tags. For example, the positioning and wavelength of x, y, z axis of a bat foraging from one feeding site to another could appear similar to a bat commuting from one roosting site to another. Gonzalez et al. (2015) stated the importance of conducting direct visual behavioral observations before implementing behavior classification techniques. Nathan et al. (2012) deployed tags on 2 captive vultures to observe ground-truth accelerometer data and behaviors happening at the exact same time. This dataset was used to train the learning algorithms implemented to classify behaviors across all deployed tags. Unlike Nathan et al.'s (2012) study, I used observations from handheld tags being moved in ways analogous to bat behavior (Ieremia 2018). Observations of accelerometer data (such as the positioning and wavelength of x, y, z axis) from handheld tags (Ieremia 2018), and timestamps and GPS locations from deployed tags were used to refine bat activity classification for the sampled dataset. However, activities labeled across all bat tags in AcceleRater were based on ACC values only and not time and location like the sampled dataset. AcceleRater requires input data consisting only of x, y, and z accelerometer values from GPS tags.

In my study, roosting had the greatest number of labeled segments across all tagged bats, which suggests that this activity occurs the most with Tongan flying foxes. Similarly, Hengjan et al. (2017) found that the most frequent activity for golden-crowned flying foxes was resting (76.3%). Kunhert et al. (2016) emphasize the importance of understanding what occurs during roosting because it has a large impact upon *Pteropus spp*. reproductivity and survival. For example, winter colonial roosts play an important role in mating for Bonin flying foxes, which reinforces the importance of understanding flying fox roosting behavior when studying the reproductive cycle of these bats (Sugita et al. 2009). Bats exhibit a range of thermoregulatory strategies when they enter a state of torpor making roosting even more important to these animals (Stawski et al. 2014). While the prevalent view suggests subtropical and tropical bat species do not express torpor, studies have

indeed reported bat species in these regions entering torpor to reduce requirements for energy and water under warm conditions (Stawski et al. 2009; Cory Toussaint et al. 2010; Liu & Karasov 2011).

Despite the majority of Tongan flying fox activities involving roosting, it is still important to understand foraging and commuting behavior and ecology of these bats to interpret the ecological services they provide. During foraging and commuting, bats perform pollination and seed dispersal as they move between food patches or travel long distances (Flemming 1982; Shilton et al. 1999). Flying foxes are especially important for large-seeded fruits and depositing seeds away from the parent canopy (Scanlon et al. 2014). Oceanic island ecosystems are often characterized by low species diversity resulting in low flying fox functional redundancy as seed dispersers (Brooks et al. 2002). McConkey & Drake (2015) concluded that there is almost no redundancy in the seed dispersal function of Tongan flying fox in islands they inhabit given that alternative consumers (e.g. birds, rodents, land crabs) were unable to compensate as dispersers. This emphasizes the ecological importance of Tongan flying foxes on these islands and their role in maintaining native forests biological diversity (Meehan et al. 2002; McConkey & Drake 2006).

In early 2019, the American Samoa Power Authority (ASPA) signed a contract for a wind power generating project (Sagapolutele 2019). As plans for this project are being developed, it is important to understand bat activity patterns to manage wind energy while effectively conserving their population. My results suggest that Tongan flying fox mortality caused by wind turbines can be reduced using temporal management strategies. Wellig et al. (2018) conducted a study concluding that nocturnal operation of tall wind turbines should be restricted above 5 ms⁻¹ to decrease bat fatalities. Given that a Tongan flying fox's time proportion spent commuting is mostly during the day than night, wind turbines should be set at a specific speed during a specific time to reduce bat mortality. However, foraging time proportions must also be considered in management strategies despite it being greater at night than day and foraging mostly consisting of short distances between food sources. For effective wind farm management strategies, cover types associated with foraging and commuting activities of *P. samoensis* should also be evaluated to select potential sites for wind farms. Including information on activity patterns and associating cover types for *P. samoensis* in management plans is also crucial given that this species is known to be diurnal, unlike Tongan flying fox, and is endemic to the Samoan islands (Thomson et al 1998).

In conclusion, understanding activities conducted by flying foxes is important to their conservation and management. Tongan flying foxes spend most of their time roosting during the day followed by foraging during the night, making them nocturnal animals. Knowledge in Tongan flying fox roosting, foraging, and commuting activities is crucial when studying their survival, reproductive cycle, interaction with surroundings (e.g. cover types, humans), and ecological services for these aspects of a bat's life are impacted by what occurs during specific activities. Information from this study provides knowledge on Tongan flying fox activities and contributes to effective and efficient land management and species conservation.

2.5 Figures and Tables



Figure 2.1 Total count of identified accelerometer segments for all three activities across all 5 tagged Tongan flying foxes (*P. tonganus*). GPS tags were deployed and data was collected from tags at the Olovalu crater on October 2016 and 2017, and June 2019. Data from all bats contain 3500 segments of commuting (COMM), 15037 foraging (FORG), and 33963 roosting (ROOST).



Figure 2.2 Representative acceleration plots for the three different activities: commuting (COMM), foraging (FORG), and roosting (ROOST), obtained by AcceleRater using datasets of Tongan flying foxes tagged in October 2016 and 2017, and June 2019 at the Olovalu crater. Each plot represents a single activity segment (made up of 78 consecutive sets of x,y,z ACC values).

Table 2.1 Number of GPS locations reported for each bat and number of days each bat was tracked for. All tagged bats were captured, tagged, and released at the Olovalu crater during October 2016 & 2017 and June 2019. Bats are no longer tracked once data obtained from base station receiver shows continuous resting state indicating that the tag has fallen off the bat.

Bat	# of Locations	# of Days Tracked
5100	17190	14
5101	4062	11
5102	13052	8
5103	5039	35
5104	5638	5

Table 2.2 Recall of assignment to a specific activity (commuting, foraging, or roosting) for each model and each activity across models. Recall is the probability that a segment with a particular activity in the dataset will be correctly classified as this activity (Resheff et al. 2014). Weighted averages for each model 'weighted average' (column) and means for each activity across models 'mean' (row) are also presented. The 5 selected models generated in the AcceleRater web application recognized patterns and classified accelerometer segments of tagged Tongan flying foxes to a specific activity. Tags were deployed and data from tags were obtained in October 2016 and 2017, and June 2019 at the Olovalu crater.

RECALL (%)								
MODEL	COMM	FORG	ROOST	weighted average				
Nearest Neighbors	71.95	88.71	98.8	94.1				
Linear SVM	81.24	95.09	99.14	96.77				
RBF SVM	87.43	95.43	99.03	97.22				
Random Forest	86.34	95.17	98.95	97.02				
ANN	77.41	98.58	99.35	97.65				
mean	80.87	94.6	99.05	96.55				

Table 2.3 Precision of assignment to a specific activity for each model and each activity across models. Precision is the probability that an assigned behavior in the dataset is indeed this particular activity (Resheff et al. 2014). Weighted averages for each model 'weighted average' (column) and means for each activity across models 'mean' (row) are also presented. The 5 selected models generated in the AcceleRater web application recognized patterns and classified accelerometer segments of tagged Tongan flying foxes to a specific activity. Tags were deployed and data from tags were obtained in October 2016 and 2017, and June 2019 at the Olovalu crater.

PRECISION (%)							
MODEL	COMM	FORG	ROOST	weighted average			
Nearest Neighbors	84.76	92.83	95.42	93.96			
Linear SVM	81.68	94.88	99.18	96.77			
RBF SVM	85.87	96.3	98.82	97.22			
Random Forest	85.41	95.26	99.03	97.03			
ANN	97.7	94.51	99.09	97.68			
mean	87.08	94.76	98.31	96.53			
Table 2.4 Accuracy of assignment to a specific activity for each model and each activity across models. Accuracy is the probability of a sample in the dataset to be assigned correctly to the specific activity (Resheff et al. 2014). Weighted averages for each model 'weighted average' (column) and means for each activity across models 'mean' (row) are also presented. The 5 selected models generated in the AcceleRater web application recognized patterns and classified accelerometer segments of tagged Tongan flying foxes to a specific activity. Tags were deployed and data from tags were obtained in October 2016 and 2017, and June 2019 at the Olovalu crater.

ACCURACY (%)								
MODEL	COMM	FORG	ROOST	weighted average				
Nearest Neighbors	97.23	94.81	96.16	95.84				
Linear SVM	97.5	97.13	98.92	98.31				
RBF SVM	98.18	97.65	98.61	98.3				
Random Forest	98.08	97.26	98.69	98.24				
ANN	98.35	97.95	98.99	98.65				
mean	97.87	96.96	98.27	97.87				

Table 2.5 Precision-recall plot generated by AcceleRater for all bats. Standard deviation computed using a 10-fold cross validation procedure. Percentage (%) of correctness for each model. The 5 selected models generated in the AcceleRater web application recognized patterns and classified accelerometer segments of tagged Tongan flying foxes to a specific activity. Tags were deployed and data from tags were obtained in October 2016 and 2017, and June 2019 at the Olovalu crater.

	%	
Model name	Correct	Std
Nearest neighbors	94.7	0.14
Linear SVM	97.04	0.18
RBF SVM	97.82	0.13
Random Forest	97.6	0.19
ANN	94.9	0.67

Table 2.6 Time calculations for each activity during the day and night, of each tagged Tongan flying fox. Tags were deployed and data from tags were obtained in October 2016 and 2017, and June 2019 at the Olovalu crater. Units for all time spent values are in minutes. Total time spent during the day and night is the sum of commuting (Com), foraging (For), and roosting (Rest) time spent during the day and night, respectively. Proportions are quotients of time spent of a specific activity during day/night and total time spent during day/night.

			D	AY	NIGHT				
Bat	Value	Total	Com	For	Rest	Total	Com	For	Rest
5100	Time spent	6221.23	1778.62	2852.15	1509.47	6411.03	515.98	5024.57	870.48
	Proportion		0.29	0.46	0.26		0.08	0.78	0.14
5101	Time spent	3510.58	1130.95	1991.5	388.13	3651.72	737.97	2469.43	444.32
	Proportion		0.32	0.57	0.11		0.2	0.68	0.12
5102	Time spent	5148.2	1066.95	2805.58	1275.67	5250.8	969.68	3252.05	1029.07
	Proportion		0.21	0.54	0.35		0.18	0.62	0.2
5103	Time spent	4585.67	905.22	2369.18	1311.27	3502.33	346.23	2644.77	511.33
	Proportion		0.2	0.52	0.29		0.1	0.76	0.15
5104	Time spent	3549.55	571.2	2309.48	668.87	3199.57	933.82	1825.18	440.57
	Proportion		0.16	0.65	0.19		0.29	0.57	0.14

Table 2.7 One sample t-test was conducted in Program R, on each activity using mean values from Table 3 in Appendix. Roosting is the only activity with a p-value less than 0.05. The t-test statistic value (T-VALUE), degrees of freedom (DF), p-value, confidence interval (CONF INT), and mean values of samples (SAMP EST) are presented.

ACTIVITY	T-VALUE	DF	P-VALUE	CONF INT	SAMP EST
СОМ	1.162	4	0.3098	-0.09169622, 0.22369622	0.066
FOR	-1.943	4	0.1239	-032547409, 0.05747409	-0.134
REST	2.9512	4	0.04192	0.005329804, 0.174670196	0.09

2.6 Appendix A



Figure 2.3 Box plots illustrating summary data for each activity across all tagged Tongan flying foxes based on mean values from Table 2.8. Tags were deployed and data from tags were obtained in October 2016 and 2017, and June 2019 at the Olovalu crater.

Table 2.8 List of tagged bats and their information. Date and time bats were captured and tagged, tag ID assigned to deployed tags, bat species, sex, age, reproductive status, weight, forearm, and site where bat was captured are presented. 'PT' stands for *Pteropus tonganus*, whereas 'PS' would stand for *Pteropus samoensis* if any were captured. Reproductive status is indicated by 'NR' non-reproductive, 'NA' not applicable, 'PREG' if pregnant, and 'POST' if bat just gave birth.

Date	Time	Tag	Species	Sex	Age	Rep	Weight	Forearm	Site
10/20/16	0445	5101	РТ	F	А	NR	360g		Olovalu
10/20/16	0450	5100	РТ	М	А	NA	460g		Olovalu
11/16/16	1930	5103	РТ	М	А	NA	610g	147mm	Olovalu
6/26/17	1845	5096	РТ	М	А	NA	285g		Olovalu
10/19/17	0515	5102	РТ	F	А	POST	300g	136mm	Olovalu
6/15/19		5104	РТ	М	А	NA			Olovalu

Table 2.9 Differences between proportion values of each activity during the day and night across all tagged Tongan flying foxes (Ex: proportion commuting in day – proportion commuting in night). Tags were deployed and data from tags were obtained in October 2016 and 2017, and June 2019 at the Olovalu crater.

ВАТ	СОМ	FOR	REST
5100	0.21	-0.32	0.12
5101	0.12	-0.11	-0.01
5102	0.03	-0.08	0.15
5103	0.1	-0.24	0.14
5104	-0.13	0.08	0.05

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CHAPTER 3. COVER TYPES ASSOCIATED WITH COMMUTING, FORAGING, AND ROOSTING ACTIVITIES OF TONGAN FLYING FOXES (*P. TONGANUS*) IN AMERICAN SAMOA

3.1 Introduction

Understanding habitat selection is fundamental to the development of effective conservation and management plans (Naussauer & Opdam 2008). Definitions of 'habitat' vary from classic niche dimension estimation through resources and conditions (Hutchison 1957; Sinclair et al 2005). For all definitions, habitat is organism-specific and more than vegetation and vegetation structure' (Hall et al. 1997; Krausman & Morrison 2016). The study of habitat-use and selection in mammals provides more understanding of an animal's behavior and environmental processes. It also describes the distribution of individuals across habitat types (Jones 2001). Habitat changes influenced by humans increase landscape complexity and thus the need for studies concerning animal distribution and habitat selection (Carrasco et al. 2014).

Habitat selection studies can be done at multi scales ranging from landscapes to microhabitats with each providing different insights. Mehrabi et al. (2014) measured soil type, leaf litter, and vegetation cover at dung beetle trapping sites to illustrate the importance of microhabitat responses when assessing the consequences of human activity on biodiversity loss. Similarly, Bogoni et al. (2013) studied habitat selection at microhabitat-scale by measuring vegetation (ex: canopy coverage, exposed soil) to determine how fine-scale characteristics influence the richness and dynamics of mammals in Inpumirim, Brazil. At the other extreme, Jin et al. (2020) investigated the foraging habitats of scaly-sided mergansers (*Mergus* squamatus) using remote sensing images and Global Positioning System (GPS) locations from birds carrying transmitters finding that foraging habitat is important for bird survival and breeding. Hinton et al. (2020) used cropland

data layers from the United States Department of Agriculture (USDA) to estimate habitat selection by female elk (*Cervus* canadenis) during Minnesota's agricultural season. They concluded that agricultural crops increase their reproductive success and promote population growth. Shilton et al. (2008) used a rainforest landcover of north-east Queensland, Australia to monitor roosting ecology and population dynamics of spectacled flying foxes (*Pteropus* conspicilattus) postcyclone.

Technological progress has created new opportunities to investigate animal habitat selection (Tomiewicz et al. 2010). A great example of this comes from the use of Global Positioning System (GPS) locations obtained from tracking devices to model habitat selection (Manly et al. 2002). GPS data can be combined with landscape-level habitat characteristics using a Geographical Information System (GIS) to reveal environmental characteristics at locations used by animals (Dedele et al. 2018). Roever et al. (2010) used GPS radiotelemetry to investigate grizzly bear (*Ursus* arctos) movements relative to roads. Similarly, Olesky et al. (2015) used high-resolution GPS tracking to determine habitat selection for long distance seed dispersal by Madagascan flying foxes (*Pteropus rufus*).

Many studies explaining and predicting spatial population distribution patterns are based on underlying habitat attributes or resources (Ehrlen & Morris 2015; Jones & Tonn 2004; McNitt et al. 2020). Typically, such studies use resource selection functions (RSFs) to estimate the probability of a habitat or resource being selected by an animal (Manly et al. 2002). There are different variations of RSFs including Step-Selection Functions (SSFs) (Zeller et al. 2012). SSFs link consecutive animal locations that are defined as steps and contrast them with random steps that characterize resources available to the animal while it moves through the environment (Forester et al. 2009; Turchin 1998). SSFs are relatively powerful for studying resource selection by animals moving through the landscape at multiple spatial and temporal scales (Thurfjell et al. 2014). Environmental variables and parameters calculated from tracking data such as step lengths, turning angles, and random steps are fitted in SSF models to determine which environmental variable is selected by an animal during movement. Given that bats of *Pteropus spp*. fly long distances and provide important ecosystem services during such activities (e.g., seed dispersal), it is desirable to analyze tracking and environmental data at larger scales (Corlett 2009).

Despite their ecological importance, bats of *Pteropus spp.* remain understudied (Walsh et al. 2017). Information on flying fox behavior, movement and ecology can provide an improved understanding of seed dispersal and other ecological services in their native ranges. Luskin (2010) studied the foraging behavior of flying foxes in Fiji to examine the impact of fragmented landscapes on seed dispersal. It is important to note that habitat preferences vary between flying fox species because these species are found in different ecological systems. For example, Australia's little red flying fox (Pteropus scapulatus) can be found in habitats like swamps mangroves, and bamboo stands (Sinclair et al. 1996). Madagascar's Rodrigues flying fox (Pteropus rodricensis) once inhabited dense rainforests; however, deforestation restricted their activity to small wooded valleys (O'Brien et al. 2007). Furthermore, habitat preference also varies between bat behaviors and activities within species. Roosting Indian flying foxes (Pteropus medius) prefer areas with less human disturbance and areas that provide shelter and protection from rainfall and prey (Hahn et al. 2013). However, Indian flying foxes forage in areas containing abundant food sources and while doing so are not restricted to places far from human activity (Sudhakaran & Doss 2012). The Queensland blossom bat roosts along rainforest edges during winter and in interior rainforest during spring. This allows the avoidance of cold temperatures within rainforests during winter and hot temperatures at the exterior of forests during Spring (Law 1996).

The Tongan flying fox's (*P.* tonganus) typical habitat includes tropical wet forests, mangrove forests, and plantations (Luskin 2010). Roosting sites are commonly found in undisturbed forests located in lowland areas and on steep slope and ridges (Cousins & Compton 2005). Tongan flying fox forage in areas of forests, farmlands, and plantations containing abundant food sources such as bananas, mangoes, and breadfruits (Luskin 2010; Cousins & Compton 2005). In contrast, Tongan flying foxes commute across most habitat types (Brooke et al. 2000) and have been observed flying near coasts, and over roads, buildings, and in open areas.

The objective of this study is to evaluate cover types associated with commuting, foraging, and roosting activities of Tongan flying foxes in Tutuila, American Samoa. I hypothesized that Tongan flying foxes will use different cover type conditions for different activities. Based upon published studies I predict that Tongan flying foxes will use the broadest range of cover types while commuting, foraging will occur in or near lowland forests and agroforests containing abundant food sources, and roosting will occur in or near lowland and upland forests with high canopy coverage.

3.2 Methods

I conducted bat mist-netting at the Olovalu crater in Futiga and the Tuimalefano family land in Malaeloa in June 2019. In October 2016 and 2017, American Samoa Department of Marine and Wildlife Resources (AS-DMWR) conducted mist-netting at the Olovalu crater as well. Data obtained from tags deployed in 2016 and 2017 were also analyzed in this study. Olovalu crater contains traditional roosting sites for both Samoan and Tongan flying foxes. I used several net sizes: 18X30m (propped on poles and trees), 9X30m, and 9X10m. Nets were usually set up at 1700 hr and taken down at 0100 hr. I checked the nets every 15 minutes to reduce stress on bats and their time caught in the nets. Thirty-four bats total (1 *P. samoensis, 33 P. tonganus*) were caught during mist-netting. I weighed each bat, measured their forearms, recorded their gender and age, and checked for any injuries. I also fed them mango juice to compensate for missed feeding during captivity.

AS-DMWR and I tagged 6 Tongan flying foxes altogether using e-obsGmbH GPS bird tags (e-obs Digital Telemetry; Gruenwald, Germany). All GPS tags deployed were <3% of the bat's weight (O'Shea & Bogan 2003). To attach tag to bat, I trimmed the fur from the area on the bat's back, between its wings, and used fabric glue to adhere the GPS tag to skin. Starting the morning after tag deployment, I returned to the netting site to download data from the tag using the GPS base station receiver. This was repeated daily until data demonstrated a continuous resting state overnight and into the next morning thereby indicating that the tag fell off.

I used a layer package from AS-DMWR containing American Samoa's wildlife habitats (Meyer et al. 2017) to create a raster of specific cover types. The layer package consisted of 1x1 meter pixels with 51 values representing habitat type. Using ArcGIS Pro, I extracted environmental variables used in this study from the layer package to create a raster. Then, I used Program R (R Studio Team 2020) to aggregate and reclassify extracted environmental variables from the raster into categories relevant to Tongan flying fox movement. Categories or cover types used are agroforests, buildings, coastal forests, developed spaces, fresh water, lowland forests, ocean, and plantations (see Table 2.1). The roads layer combined major and secondary roads. Agroforests consisted of mango, breadfruit, coconut and mixed agroforests. Lowland forests combined low, intermediate and high canopy lowland forests. By contrast coastal forests was defined as pandanus, casuarina, and mixed plantations. The resulting raster was used in step-selection function to evaluate cover types associated with identified Tongan flying fox activities from chapter 2. Cover

types were coded as indicator variables ("1" if activity occurred on the specific cover type, "0" if not).

Location and accelerometer data were obtained from deployed GPS tags. I identified Tongan flying fox commuting, foraging, and roosting activities in chapter 2 using accelerometer data. The resulting activity datasets from chapter 2 for each bat contained labeled activities and timestamps. I cross-referenced a total of 2600 activity segments, consisting of the first 520 activity segments from each bat, with GPS locations that were reported around the same timestamp as the identified activity. Commuting had 495 activity segments with GPS locations and timestamps, foraging had 1173, and roosting had 932. I filtered the cross-referenced activity and GPS data by activity then cleaned and examined it using the AMT R package. I used AMT to calculate observed and random step lengths, tracks, and turning angles for each activity used to fit in SSF models with environmental predictor variables (see Table 3.1). Estimated coefficients and exponential coefficients of models calculated in SSF were evaluated to determine cover types preferred by Tongan flying foxes for commuting, foraging, and roosting activities. In addition, I estimated Akaike information criterion (AIC) (Akaike, 1974) for SSF models using Program R to determine parsimonious model. I ranked fitted SSF models by ΔAIC values calculated Program R.

3.3 Results

Commuting, foraging, and roosting activities occurred on 8 of the 9 cover types altogether (see Table 3.6 in Appendix B). The Tongan flying foxes did not use freshwater cover types during commuting, foraging, and roosting activities. Only commuting occurred over 6 cover types with 256 locations on agroforests, 43 on developed spaces, 33 on lowland forests, 9 over plantations, 6 over buildings and 1 over coastal forests. No commuting activities were observed over ocean and road cover types. Observations of foraging also occurred in 6 cover types with 248 locations in

developed spaces, 106 in lowland forests, 27 in plantations, 23 over buildings, 5 in agroforests, and 1 over the ocean. No foraging activities were conducted over roads and coastal forests. Roosting is the only activity that occurred within all cover types except freshwater, with 65 locations in developed spaces, 62 in lowland forests, 13 over buildings, 7 in plantations, 4 in agroforests, 2 over the ocean, 2 in coastal forests, and 1 over roads.

Inspecting the fitted SSF models and the estimated coefficients for each model supported the following observations: 1) lowland forests was the only cover type feature with positive coefficients across all 3 activities, 2) other cover types with positive coefficients include coastal forests when commuting and roosting, and buildings and plantations when foraging; and 3) lowland forests for foraging and roosting were the only cover types statistically significant (Table 3.2). We can infer from the positive and negative coefficients for each cover type across all activities that Tongan flying fox is likely to select and avoid locations on these cover types, respectively. Coastal forests had the largest estimated coefficient of 1.20 with a standard error of 1.27, followed by lowland forest 1.04 with a standard error of 0.57 for commuting. Buildings had the largest estimated coefficient of 0.96 with a standard error of 0.57 for foraging. Followed by lowland forests and plantations with coefficients of 0.61 and 0.12, with standard errors of 0.29 and 0.55, respectively. Coastal forests had the largest coefficient of 0.75 with a standard error of 0.86, followed by lowland forests 0.64 with a standard error of 0.28 for roosting. The exponential coefficient values calculated by SSF for each model across all activities are indicative of how likely an animal is to use a specific cover type or quantify relative selection strength as a function of availability of each cover type (Fieberg et al. 2020; Signer et al. 2019; Table 3.2). Assuming that all cover types are equally available to Tongan flying fox, coastal forests had the greatest exponential coefficient for commuting (3.33) and roosting (2.11), and buildings had the greatest

exponential coefficient (2.60) for foraging. As mentioned, lowland forest was the only cover type with a p-value <0.05 for foraging (0.03) and roosting (0.02), hence the low standard error values. Other cover types with positive coefficients, including lowland forest for commuting, had p-values >0.05 meaning that these preferences are not statistically significant.

In evaluating model structure, developed spaces had a Δ AIC of 0 for commuting and roosting, and ocean had a Δ AIC of 0 for foraging (see Table 3.3-3.5). Buildings, developed spaces, and lowland forests ranked second for commuting, foraging, and roosting, respectively. However, lowland forest was the only 2nd ranking model for roosting with a Δ AIC <2 (1.73). For commuting buildings had a Δ AIC of 7.79 and for foraging developed spaces had a Δ AIC of 5.86. The most parsimonious models based upn Δ AIC values of 0 were consistent with the observatin that Tongan flying foxes do not commute, forage, or roost in locations classified as developed spaces and ocean. This was supported by the negative coefficients calculated by SSF of developed spaces when commuting and roosting, and ocean when foraging.

3.4 Discussion

Tongan flying foxes used fewer cover types during commuting than foraging. Tongan flying fox was likely to select locations on lowland and coastal forests for commuting. Understanding Tongan flying fox commuting activities is important to gain knowledge on how to manage wind energy while effectively preserving this bat species' population. As the footprint of wind farms expands (U.S. Department of Energy 2008), there are many locations where flying fox activities need to be understood to enhance conservation with respect to wind energy management (Smales 2018). My results suggest that Tongan flying fox mortality caused by wind farms can be reduced using temporal and spatial management strategies. In Northwestern Europe, bat mortality at wind turbines differed between cover types (Rydell et al 2010). Wind turbines located along

the coast and within forests experienced higher bat mortality rates than wind turbines located in complex agricultural cover types (Rydell et al. 2010). Because lowland and coastal forests were likely selected by Tongan flying fox for commuting (and roosting), locations on these cover types are not appropriate wind turbine sites. In addition, cover types associated with foraging should also be considered in wind farm management strategies considering that commuting distances between foraging sites increase when resources are scarce. Although other cover types containing few to no locations associated with commuting and foraging activities may be appropriate for wind farm sites, temporal restrictions mentioned in chapter 2 should still be applied in wind farm management strategies since Pteropus spp. habitats change when disturbed (Morrell & Craig 1995). Overall, lowland forests, coastal forests, and plantation cover types associated with Tongan flying fox foraging and commuting activities are not appropriate for wind farms sites. Locations on roads, would not be suitable for wind energy development not only because my data suggests that Tongan flying foxes may forage there but also because also because vehicular traffic is incompatible with wind turbines. For more effective wind farm management strategies, cover types associated with foraging and commuting activities of *P. samoensis* should also be evaluated given that this species is known to be diurnal (unlike *P. tonganu*), and endemic to the Samoan islands (Thomson et al 1998). To do so, similar accelerometer and GPS data on Samoan flying foxes is needed. Using information concerning only Tongan flying fox movement and ecology for wind farm management strategies will protect only this species and threaten P. samoensis.

Tongan flying foxes are likely to select locations on lowland forests, plantations and buildings for foraging. Although these bats are known to disperse from colonies and primarily forage in natural forests (Cox 1991), agricultural forests and residential areas are also used as foraging sites (Wilson & Engbring 1992). Luskin (2010) found that Tongan flying fox showed no adaptation to transformed cover types in Fiji, except foraging in farmland trees. He also stated that Tongan flying foxes would feed mainly on fruits from farmlands and flowers from native forests (Luskin 2010). The relative unproductiveness of natural forests contrasted with cultivated fruit trees resulted in Tongan flying fox preference to forage in farmland (Keppel 2005; Luskin 2010). During data collection from the deployed GPS tag on Bat 5104, we observed the bat leaving its roosting site on Olavalu crater and foraging in the same area outside of the crater for two consecutive nights. We visited this area for ground-truth observations and found that Bat 5104 was foraging in trees next to homes and a church. In Indonesia, Hengjan et al. (2017) detected *Pteropus vampyrus* foraging in fruit trees near people's homes. In Sri Lanka, Yapa et al. (1999) claimed that pteropdid bats (*Cynopterous sphinx, Rousettus leschenaultia, Pteropus giganteus*) damaged fruit trees in plantations and home gardens. These situations are common when increased availability of food resources in human-dominated areas attract bats of *Pteropus spp*. (Parry-Jones and Augee 2001; Sheema et al 2017).

Results for foraging and commuting suggest that areas near or on lowland forests, coastal forests, buildings, and plantations are where seed dispersal and pollination services provided by Tongan flying fox occur. Flying foxes perform seed dispersal and pollination during long-distance movements and foraging flights between feeding sources (Scloesing et al. 2020). However, my results do not show how effective these ecological services performed by Tongan flying fox are especially since fragmented cover types are involved (e.g. buildings and plantations). Luskin (2010) found that fragmented cover types in Fiji resulted in Tongan flying fox's preferential foraging in farmland and low foraging densities in forests. This led to the contribution of less effective seed dispersal services in significant decrease in intraspecies competition for forest resources (Luskin 2010). To further understand the effectiveness of seed dispersal by Tongan flying fox, more

information such as gut retention and captive studies for ground-truth movement and behavior data are needed.

Similar to commuting, locations on lowland and coastal forests were also likely selected by Tongan flying fox for roosting. Commuting and roosting sharing similar associating cover types may be due to Tongan flying fox finding suitable roosting sites containing abundant resources resulting in reduced commuting cost between foraging and roosting sites. Traveling distances have shown to decrease in other Pteropus spp. when resources were abundant and increase when resources were scarce (Palmer and Woinarski 1999). Roosting sites for Tongan flying fox are mainly found in lowland native forests along cliffs, islets, inland swamps, i.e., in relatively inaccessible sites (Miller & Wilson 1997). However, Cousins & Compton (2005) observed Tongan flying foxes move from traditional roosting sites to different roosting locations due to the impact of two hurricanes. Tongan flying fox utilize roosting sites for a long period of time unless those sites are disturbed (Morrell & Craig 1991). Tongan flying foxes selecting locations on coastal forests for roosting is consistent with Brooke et al.'s (2000) findings of 21 roosting sites in coastal forests on cliffs or steep slopes immediately above the ocean. In this study, 2 roosting locations were identified with the ocean cover type. These two locations may have been reported when the bat was roosting on a coastal forest immediately above the ocean or it was leaving this resting location and flew over the ocean. This is a similar situation with the 1 roosting location on roads cover type. The Tongan flying fox may have been roosting on a tree next to the road or the GPS location was reported when it left its resting spot on a tree near and flew over the road. As mentioned, activity segments were matched with GPS locations that were reported around the same timestamp as the identified activity, and not the exact same time.

In conclusion, foraging was the activity associated with the most cover types while roosting and commuting were associated with lowland and coastal forests. Understanding habitats associated with Tongan flying fox activities is important for the development of efficient and effective management plans that reduce human and bat conflicts. My results, including those from chapter 2, contribute information needed for effective wind farm management strategies while conserving Tongan flying fox populations. They also suggest that farmers need to find ways to include these bats in their agricultural practices given that plantations contain Tongan flying fox foraging locations. In addition, my results also provide some information for potential designated reserve areas for Tongan flying fox in American Samoa.

3.5 Figures and Tables

Table 3.1 Categories for environmental variables and descriptions. Environmental variables were extracted from a GIS layer package of American Samoa's wildlife habitats. The 'Category' column contains the names given to groups of environmental variables aggregated to create specific cover types. 'Code in AMT' contains the abbreviations of cover type categories in AMT and SSF R code. 'Cover types' lists the environmental variables that make up a specific cover type.

Cover type	Code in AMT	Environmental variable
Agroforest	ag.fors	Mango, breadfruit, coconut, and mixed agroforests
Buildings	build	Buildings
Coastal forests	co.fors	Pandanus, casuarina, and mixed coastal forests
Developed space	dev.space	Open developed space
Fresh water	f.water	Lakes and ponds
Lowland forest	low.fors	Low, intermediate, and high canopy lowland forests
Ocean	ocean	Ocean
Plantations	plant	Banana, papaya and mixed plantations
Roads	road	

Table 3.2 Step lengths, turning angles, random steps, and distances calculated using the animal movement tracking (AMT) R package along with extracted cover types were fitted in step-selection function (SSF) models. SSF calculated the coefficients (coef), exponential values (exp(coef)), standard errors (se(coef)), and p-values (Pr(>|z|)) for each fitted SSF model. Positive coefficients (coef) indicates animal's preference and negative coefficients (coef) indicates avoidance.

		CO	OMM			FC	ORG			RO	OST	
Cover types	coef	exp(coef)	se(coef)	Pr(> z)	coef	exp(coef)	se(coef)	Pr(> z)	coef	exp(coef)	se(coef)	Pr(> z)
Developed space	-1.25	0.29	1.11	0.26	-1.32	0.27	1.03	0.20	-1.65	0.19	1.03	0.11
Buildings	-0.04	0.96	0.72	0.95	0.96	2.60	0.57	0.09	-16.31	0.00	2157.61	0.99
Roads	-12.72	0.00	10650.09	1.00	-15.28	0.00	2647.57	1.00	-13.02	0.00	2206.29	1.00
Lowland forests	1.04	2.84	0.57	0.07	0.61	1.84	0.29	0.03	0.64	1.89	0.28	0.02
Coastal forests	1.20	3.33	1.27	0.35	-15.28	0.00	1715.31	0.99	0.75	2.11	0.86	0.39
Agroforests	-13.35	0.00	2555.82	1.00	-14.23	0.00	1472.33	0.99	-15.15	0.00	2253.99	0.99
Fresh water	-14.41	0.00	3229.31	1.00	-13.76	0.00	2068.00	0.99	-13.50	0.00	2208.42	1.00
Ocean	-17.02	0.00	3822.44	1.00	-17.11	0.00	1500.50	0.99	-16.71	0.00	2092.14	0.99
Plantations	-14.53	0.00	2591.54	1.00	0.12	1.12	0.55	0.83	-16.23	0.00	1906.37	0.99

Table 3.3 Akaike information criterion (AIC) rankings for SSF models for commuting. The number of variables (K), log likelihood (LL), Akaike difference (Δ AIC), and Akaike weight (AICcWt) are presented. Variables fitted in each SSF model include specific cover type, step lengths, turning angles, random steps, time of day, and logarithm of step lengths. Models were ranked by Δ AIC indicating that developed spaces is the most parsimonious model ranking 1 st with a Δ AIC of 0.

	a) COMM							
Modnames	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt	
Developed spaces	6	807.38	0.00	1.00	0.98	-397.67	0.98	
Buildings	6	815.17	7.79	0.02	0.02	-401.56	1.00	
Ocean	6	822.32	14.94	0.00	0.00	-405.14	1.00	
Fresh water	6	822.63	15.26	0.00	0.00	-405.29	1.00	
Coastal forests	6	827.61	20.23	0.00	0.00	-407.78	1.00	
Lowland forests	6	827.90	20.53	0.00	0.00	-407.93	1.00	
Plantations	6	831.04	23.66	0.00	0.00	-409.50	1.00	
Agroforests	6	833.79	26.41	0.00	0.00	-410.87	1.00	
Roads	6	836.16	28.78	0.00	0.00	-412.06	1.00	

Table 3.4 Akaike information criterion (AIC) rankings for SSF models for foraging. The number of variables (K), log likelihood (LL), Akaike difference (Δ AIC), and Akaike weight (AICcWt) are presented. Models were ranked by Δ AIC. Variables fitted in each SSF model include specific cover type, step lengths, turning angles, random steps, time of day, and logarithm of step lengths. Models were ranked by Δ AIC indicating that developed spaces is the most parsimonious model ranking 1st with a Δ AIC of 0.

b) FORG							
Modnames	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt
Developed spaces	6	3124.25	0.00	1.00	0.95	-1556.12	0.95
Buildings	6	3130.11	5.86	0.05	0.05	-1559.05	1.00
Ocean	6	3138.22	13.97	0.00	0.00	-1563.10	1.00
Fresh water	6	3138.28	14.02	0.00	0.00	-1563.13	1.00
Coastal forests	6	3148.48	24.23	0.00	0.00	-1568.23	1.00
Lowland forests	6	3149.14	24.89	0.00	0.00	-1568.57	1.00
Plantations	6	3149.30	25.05	0.00	0.00	-1568.64	1.00
Agroforests	6	3153.49	29.24	0.00	0.00	-1570.74	1.00
Roads	6	3154.19	29.94	0.00	0.00	-1571.09	1.00

Table 3.5 Akaike information criterion (AIC) rankings for SSF models for roosting. The number of variables (K), log likelihood (LL), Akaike difference (Δ AIC), and Akaike weight (AICcWt) are presented. Models were ranked by Δ AIC. Variables fitted in each SSF model include specific cover type, step lengths, turning angles, random steps, time of day, and logarithm of step lengths. Models were ranked by Δ AIC indicating that developed spaces is the most parsimonious model ranking 1st with a Δ AIC of 0.

c) ROOST							
Modnames	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt
Developed spaces	6	1781.95	0.00	1.00	0.56	-884.96	0.56
Buildings	6	1783.67	1.73	0.42	0.23	-885.83	0.79
Ocean	6	1784.84	2.90	0.24	0.13	-886.41	0.92
Fresh water	6	1786.73	4.79	0.09	0.05	-887.36	0.97
Coastal forests	6	1789.01	7.07	0.03	0.02	-888.49	0.99
Lowland forests	6	1790.30	8.36	0.02	0.01	-889.14	1.00
Plantations	6	1793.58	11.63	0.00	0.00	-890.78	1.00
Agroforests	6	1793.76	11.82	0.00	0.00	-890.87	1.00
Roads	6	1796.76	14.82	0.00	0.00	-892.37	1.00

3.6 Appendix B

Figure 3.1Total count of segments for each activity after matching 520 activity segments from each tagged bat with GPS locations reported around the same timestamp. The 520 activity segments were obtained from resulting datasets of each bat analyzed in AcceleRater web application and GPS locations were obtained from deployed tags. From the 2600 activity segments (520 segments from each tag), 495 segments were commuting, 1173 were foraging, and 932 were roosting.



Table 3.6 Total number of commuting, foraging, and roosting locations on specific cover type categories across all tagged bats in Tutuila, American Samoa. Cover type categories were treated as indicator variables: 1 if bat selected locations on specific cover type for any of the 3 activities,

ACTIVITY	COVER TYPECATEGORY	# OF LOCATIONS
СОММ	Agroforests	256
	Buildings	6
	Coastal forests	1
	Developed spaces	43
	Fresh water	0
	Lowland forests	33
	Ocean	0
	Plantations	9
	Roads	0
FORG	Agroforests	5
	Buildings	23
	Coastal forests	0
	Developed spaces	248
	Fresh water	0
	Lowland forests	106
	Ocean	1
	Plantations	27
	Roads	0
ROOST	Agroforests	4
	Buildings	13
	Coastal forests	2
	Developed spaces	65
	Fresh water	0
	Lowland forests	62
	Ocean	2
	Plantations	7
	Roads	1

0 if not.

3.7 References

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