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TEMPORARILY TERRESTRIAL TROPICBIRDS: COURTSHIP AND TIME BUDGETS OF WHITE-TAILED TROPICBIRDS (*PHAETHON LEPTURUS*) ON MO'OREA, FRENCH POLYNESIA

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Abstract. Land breeding sites are important conservation priorities for the preservation of seabirds that cannot breed over the ocean. An example of a seabird that must breed on land is the white-tailed tropicbird (*Phaethon lepturus*). This bird is frequently seen on the island of Mo'orea in French Polynesia, but little is known about whether this species spends time there for the purpose of breeding. I hypothesized that these birds are breeding on Mo'orea and therefore conducted a study that included (1) observations of group interactions; (2) time budget construction; and (3) number surveys. My group interaction observations revealed courtship behavior previously described by the literature but I observed no definite evidence of cliff-face nesting. The time budget results showed that the tropicbirds spend a significant portion of their time flying over the land by themselves (73%), and at low elevation near vegetation (61%). The number survey revealed that the birds preferred to be on land at mid-day and favored one valley, 'Opunohu, over the 2 others I surveyed. Because of the amount of time the birds spend by themselves and the absence of definite nest site data, I am unable to conclude that white-tailed tropicbirds are breeding on Mo'orea at this time of year. However, their courtship behavior and extensive interaction with vegetation that may indicate potential nest sites in tree hollows lead me to conclude that Mo'orea could be a land breeding site for this species at other times of year.

Key words: seabird breeding; Phaethontidae; 'Opunohu valley

INTRODUCTION

The most important evolutionary issue for organisms is finding resources to sustain their lives and reproduce. The methods that have evolved in order to accomplish these tasks are numerous and quite varied. Some animals feed and live in environments where it is impossible to reproduce (Emlen 1973) so they travel to another area for reproduction. The advantage to this method is that there is less competition for food from conspecifics or similar species in non-breeding areas (Diamond 1978). The disadvantage is that, for breeding purposes, these animals must journey to an area for which they may not be as well adapted. An example of this can be seen in seabirds which spend most of their time feeding over the sea, but must find land

sites to breed (Diamond 1978). Such animals are ecologically important for study because their breeding sites are often low in number but high in importance to species success. As a result, loss of their breeding sites could have devastating repercussions for populations of endangered seabird species (Yorio et al. 1999).

One organism that is ideally suited to address this issue is the white-tailed tropicbird (*Phaethon lepturus*) (Phaethontidae). This seabird spends most of its feeding time solitary and pelagic (Lee and Walsh-McGehee 1998). Its diet consists of squid and fish that are found far from land (Pennycuick et al. 1990). It is also the most common of the three species of tropicbirds (Lee and Walsh-McGehee 1998), and therefore easy to locate for observational studies. Its distribution

includes both the Atlantic and Pacific Oceans, but declining populations of this species in the Atlantic Ocean have led Lee and Walsh-McGehee (2000) to regard these birds as a high conservation priority. Although this species is known to breed on several South Pacific archipelagos, only cursory information exists about its presence in the Society Islands in French Polynesia (Lee and Walsh-McGehee 1998). Thibault (1974) states that white-tailed tropicbirds breed year-round on the Society Islands, but gives no details about breeding or nesting behaviors. Mo'orea is an ideal study site for this species because the birds have frequently been seen flying over the island.

Breeding and nesting behaviors of the white-tailed tropicbirds have been studied previously in other locations. Diamond (1975) and Buckley and Buckley (1970) observed the courtship behaviors of white-tailed tropicbirds in the Indian Ocean and near Puerto Rico, respectively. These behaviors commonly consisted of aerial displays in groups of multiple birds. In contrast to red-tailed tropicbirds which always nest on the ground (Schreiber and Schreiber 2009), white-tailed tropicbirds nest in cliff faces, on the ground, or in tree hollows (Lee and Walsh-McGehee 1998). According to Diamond (1975) and Burger and Gochfeld (1991), the only requirement for white-tailed tropicbird nest sites is that there is enough vegetation around the burrow entrance to provide extensive shade. Invasive rats are known to have a profound impact on the breeding of all tropicbirds (Fleet 1972, Lee and Walsh-McGehee 2000), but due to their nest site versatility, white-tailed tropicbirds alone have the rat-proof option of nesting in cliff faces, if necessary.

Based on the current literature describing this species as pelagic and solitary unless breeding, and my preliminary observations of birds flying over land and interacting in groups, I hypothesized that white-tailed tropicbirds are breeding on Mo'orea. Specifically, I proposed that the birds were exhibiting behavior defined in the literature to

be related to courtship, and nesting in holes on cliff faces. However, due to difficulties in accessing these potential nest sites, I focused my observations on land-based behaviors, to determine if the birds are spending time on land for breeding purposes. I observed: (1) group interactions, to determine if stereotypical courtship behaviors are performed; (2) individuals, to construct a time budget and determine what percentage of time the birds spend interacting with each other; (3) number of birds in 3 valleys and in all daylight hours, to determine if there is a preferred time and location for group interactions. With more in-depth information about how these birds interact on land, it may be possible to determine whether they are breeding on Mo'orea.

METHODS

General

I observed the behavior of the white-tailed tropicbirds (*Phaethon lepturus*) on the island of Mo'orea, in the Society Islands of French Polynesia, from October 1 through November 10, 2009. The locations of my observations (Fig. 1) were: (1) Three Pines lookout (17°32.067'S, 149°49.323'W) (view of 'Opunohu

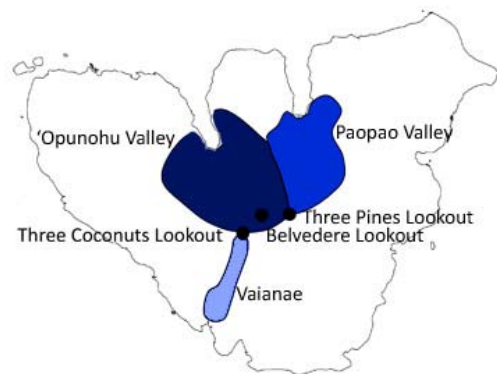


FIG 1. Map of study sites. From the Three Pines Lookout, Paopao and 'Opunohu valleys were visible. From the Three Coconuts Lookout, Vaianae and 'Opunohu were visible. From the Belvedere Lookout, only 'Opunohu Valley was visible.

and Paopao valleys); (2) Three Coconuts lookout (17°32.839'S, 149°50.516'W) (view of 'Opunohu and Vaianae); and, (3) Belvedere lookout (17°32.275'S, 149°49.85'W) (view of Opunohu valley only). Lookout (3) is located 10 minutes down Three Coconuts trail from the Belvedere, which made this site appropriate for dawn observations. I used a pair of Parks 10x42 binoculars to observe the birds, and dictated notes to my Nikon Coolpix 210 camera in sound record mode when it was necessary to follow an individual with binoculars without stopping to write notes. I replayed these recordings at a later time to transcribe the notes. I also noted weather conditions for each day (approximate temperature, cloud cover, wind severity, and rain).

Group interaction observation

For 10 minute intervals, I scanned the observation area looking specifically for birds that appeared to be interacting. I tallied the number of instances that I saw them perform the following stereotyped behaviors:

- *2 fly close*: 2 individuals fly close together, flapping wings more than usual, but do not touch

- *3 fly close*: 3 individuals fly close together, flapping wings more than usual, but do not touch. Tends to be associated with a 2 fly close tally, since one of the birds eventually branches off, leaving 2 behind

- *Dive*: 1 individual brings wings close to body and dives rapidly, usually in the presence of several other birds

- Also noted: how many other birds present during the dive

- *Tail drop*: 1 or both of the individuals involved in a 2 fly close drops its tail to a 45 degree angle. Always associated with a 2 fly close tally

- Also noted: whether top or bottom bird performed tail drop

- *Apparent mating*: 2 individuals fly close together and appear to touch cloaca

- *Multiple bird interaction*: any number of birds (from 2-6) birds circle together, making an apparent effort to keep close to the group, but without 2 fly close or 3 fly close behavior

- Also noted: how many birds in the group

Several of these behaviors (2 fly close, dive, and tail drop) have been previously described by in the literature by Diamond (1975) and Buckley and Buckley (1970).

Individual time budget

I randomly selected one individual to follow for a 10 minute interval or until it disappeared from view. Since I used binoculars constantly over the entire time interval, I dictated my observations to a Nikon Coolpix 210 camera in sound record mode. I later transcribed these notes using a time budget model, noting how long the Observed Individual (OI) spent doing each of the following activities:

- *Solitary flight*: Default behavior—whenever I have not noted a different behavior, it can be assumed that the OI is engaging in solitary, soaring flight

- *Multiple birds-no interaction*: Other birds can be seen in the binocular viewfinder with the OI, but they do not appear to be interacting (no excessive wing flapping, and the flight direction appears to be unchanged)

- *Multiple birds-with interaction*: Other birds can be seen in the binocular viewfinder with the OI, and appear to be interacting with it. Specifics of this interaction were noted (such as number of birds, actions that lead me to believe they are interacting)

- *Elevation*: rough estimation of low (50-400m), medium (400-800m), or high (800m+) elevation, based on how close the bird is to the vegetation and to the mountains

- *Exit method*: If the OI flies out of viewing range before the end of the 10 minute interval, I noted where and how it left (i.e., flies over mountain, disappears into fog or vegetation)

Number survey

At 10 minute increments throughout the observation period, I performed a slow, sweeping scan of the observation area with binoculars and counted the number of tropicbirds I saw. I ensured that there were at least 3 repetitions for 'Opunohu Valley for every 10 minute increment between 06:00 and 18:00 (approximately dawn to dusk), and at least 5 repetitions for each of the three valleys.

Statistical analysis

General— I used JMP 8.0 statistical analysis software for all data analysis. I evaluated the normality of all data sets using the Shapiro-Wilk W test. Although I found none of my data to be normal, I still used parametric tests for analysis, since they can often be used for non-parametric data (Box, 1953).

Group interactions— I used a Spearman's ρ test to determine if there was a correlation between the 2 fly close and dive behaviors. I also compared the sum of literature-defined courtship behaviors (2 fly close, dive, and tail drop) to each date using a one-way ANOVA to determine if different day conditions affected how much courtship behavior occurred.

Individual time budgets— I used two-tailed Wilcoxon sign-rank tests to compare the different components of the two time budgets (solo flight vs. flying with multiple birds or low vs. mid vs. high elevations). To determine if these time budgets changed significantly from day to day, I used a one-way ANOVA comparing date to time spent solo, and a two-way ANOVA comparing date and elevation to time spent at each elevation.

Number survey—I compared date and time of day to the number of birds I saw in 'Opunohu valley using two ANCOVAs, one for the morning hours and one for the afternoon hours. I also considered the date and time of day variables separately. For the time of day effect, I used a one-way ANOVA,

grouping time of day into twelve categories, one for each hour. I then used a Tukey-Kramer HSD post-hoc test to see which times of day had a significant effect on the bird count. To determine if date had an effect on the number of birds in 'Opunohu valley, I used a one-way ANOVA. I then used 4 one-way ANOVAs to compare each of the weather conditions I recorded (temperature, cloud cover, wind, and rain) to the 'Opunohu valley bird count. I also ran two one-way ANOVAs to comparing the counts of 'Opunohu valley to Paopao valley, and 'Opunohu valley to Vaianae. To avoid confounding variables with these tests, I included only the counts I conducted at times when I counted the birds in both valleys.

RESULTS

Group interaction observation

I observed the white-tailed tropicbirds interacting in all of the ways described in *Methods* except for mating. The correlation between the dive and 2 fly close behavior (Fig. 2) was significant (Spearman's ρ , $P < 0.0001$), with a Spearman's correlation coefficient of 0.338. The comparison of the sum of literature-defined courtship behaviors (2 fly close, dive, and tail drop) and each observation day was not significant (ANOVA, $F = 1.80$, $df = 15$, $P = 0.056$) Fig. 3 shows the numeric details of some behaviors I observed (number of dive observers, top/bottom tail drop, number of group interaction members).

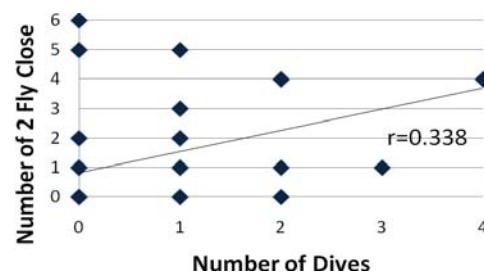


FIG. 2. Number of dives observed during one observation session compared to the number of 2 fly closes observed during the same session.

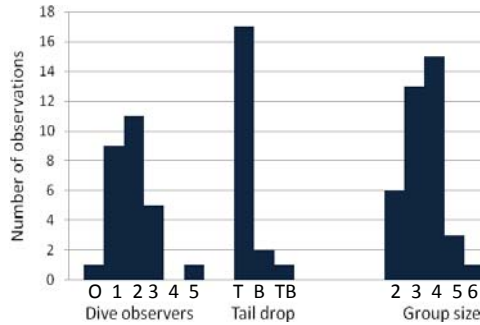


FIG. 3. The number of observations for more detailed information regarding the dive (number of birds observing the diver), tail drop (whether the top (T), bottom (B), or both (TB) birds in a 2 fly close performed the tail drop), and multiple bird interactions (how many birds were interacting in a group without performing any of the other behaviors described)

Individual time budget

For every individual observation that I recorded (n=60), I calculated the percent of time the bird spent flying by itself, with other birds but not interacting, and with other birds while interacting. I then averaged the percents for all of the observation sessions (Fig. 4). The percent of time the birds spent solo was significantly greater than the percent of time spent with other birds (Wilcoxon sign-rank, t-ratio=-6.56, df=59, P<0.0001). Using the same method of averaging percents, I constructed a time budget for elevation (Fig. 5). All three elevation categories were significantly different from each other (Table 1). (Wilcoxon sign-rank, low-mid: t-ratio=-3.90, df=57, P=0.0004, low-high: t-ratio=-3.99, df=57, P<0.0001, mid-high: t-ratio=-2.68, df=57, P=0.0077).

The date did not have a significant effect on the ratio of time the tropicbirds spent solo or in the company of birds (ANOVA, F=0.937, df=13, P=0.5240). There was also no date effect for the ratio of time spent at each elevation (Table 1).

I observed a total of 55 exit methods at the end of my observations. There were five

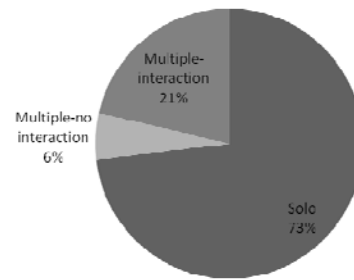


FIG. 4. Average percent time the white-tailed tropicbirds spent by themselves (solo) or in the presence of other birds (multiple, with or without interaction).

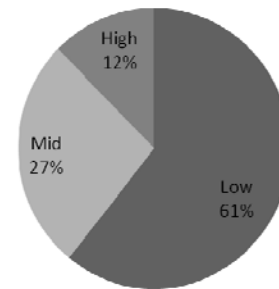


FIG. 5. Average percent time the white-tailed tropicbirds spent at low, mid, or high elevations.

TABLE 1. Results of the two-way ANOVA comparing elevation level and date to the ratio of time the birds spent at each elevation.

Effect	F	df	P
Elevation	27.06	2	<0.0001*
Date	0.07	13	1.0000
Elevation*Date	0.94	16	0.5581

categories: (1) disappearance into vegetation, (2) disappearance into clouds, (3) out of my range of view, (4) mixup with other birds, and (5) other (due to logistical difficulties unrelated to behavior). Fig. 6 shows how often each of these exit methods occurred.

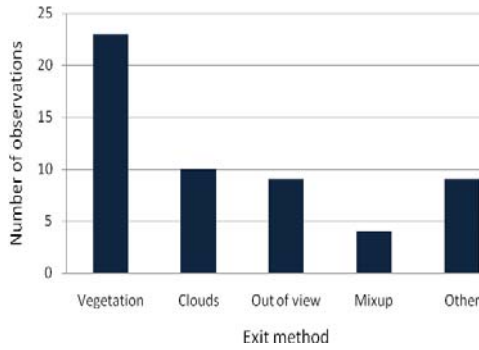


FIG 6. Number of the five categories of exit methods observed at the end of individual observations.

Number survey

Because the two ANCOVAs for both morning and afternoon hours showed significant interaction between time and date, I considered each variable separately (Both morning and afternoon $F=9.85$, $df=15$, $P<0.0001$)

The average number of birds for each ten-minute interval of daylight is shown in Figure 7. There were significant differences between the 12 hours (ANOVA, $F=11.94$, $df=11$, $P<0.0001$). The results of the Tukey-Kramer HSD post-hoc test, showing which hours are significantly different from each other, are shown in Fig 7.

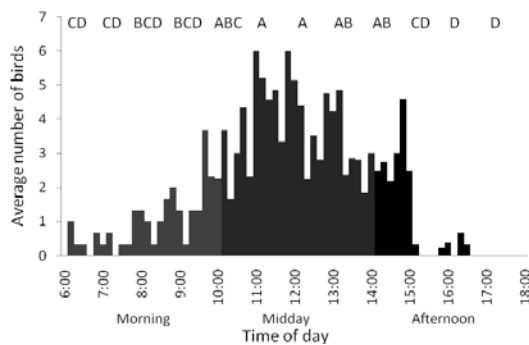


FIG. 7. Average number of white-tailed tropicbirds in Opunohu Valley for each ten-minute interval. The letters ABCD are the results of the Tukey-Kramer HSD test; hours that have no letters in common are significantly different from each other. Morning, midday, and afternoon times are indicated by differential shading.

The date also had a significant effect on the number of birds in 'Opunohu valley (ANOVA, $F=8.82$, $df=19$, $P<0.0001$) Temperature and wind severity did not have a significant effect on the bird count (Temperature: ANOVA, $F=1.78$, $df=2$, $P=0.1705$; Wind: ANOVA, $F=2.35$, $df=2$, $P=0.0976$), but cloud cover and rain did have a significant effect (Cloud cover: ANOVA, $F=3.79$, $df=2$, $P=0.0236$, Rain: ANOVA, $F=6.82$, $df=2$, $P=0.0013$).

'Opunohu valley had significantly more birds than both Paopao valley (ANOVA, $F=3.88$, $df=1$, $P<0.0001$) and Vaianae (ANOVA, $F=3.91$, $df=1$, $P<0.0001$).

DISCUSSION

Group interaction observation

The courtship behaviors I observed, though often occurring in complex patterns, sometimes were performed in sequences within a short time period. For example, I found that the dive and 2 fly close behaviors were significantly correlated with each other. More specifically, I observed that dives were often followed by a 2 fly close with one of the dive observers, with the diver usually on top. Tail drop behaviors always occurred during a 2 fly close (I never observed a solo bird dropping its tail). However, it was difficult to accurately determine how many 2 fly close behaviors were accompanied by a tail drop, since in many cases the 2 fly close occurred too far away or at a poor angle to observe a tail drop. Sequential courtship behaviors would also occur when large groups of birds (6-10 individuals) would perform these behaviors in approximately the same location. Therefore, there would be multiple dives and 2 fly close behaviors by different individuals in one short time period.

Although some courtship patterns emerged, other behaviors were more complex. Interactions occurring in larger groups (more than 4 birds) often led to the most complex courtship display patterns, with some

individuals diving two or three times in a row, sometimes with accompanying 2 fly closes but sometimes ignored by the other birds in the group. The exact sequences that occurred at these times were highly variable and often never repeated. In addition, the details of some courtship behaviors were variable (Fig. 3). For example, Buckley and Buckley (1970) described the tail drop always being performed by the top bird in a 2 fly close, but I observed the bottom bird and in one case both birds also performing the behavior. There also does not seem to be one number of dive observers or group size that stands out as the most common. Therefore, although there are a few stereotyped sequences of behaviors involved in white-tailed tropicbird courtship, the process appears to be very complex, especially when large groups are involved.

There were similarities and differences between the courtship behavior of the white-tailed tropicbirds that I observed on Mo'orea and that of the tropicbirds elsewhere previously described by Diamond (1975) and Buckley and Buckley (1970). Diamond (1975), observing white-tailed tropicbirds at the Aldabra Atoll in the Indian Ocean, observed dives in the presence of a group of birds that varied in number, which is similar to what I observed. However, Diamond (1975) noted that tail-dropping behavior was not apparent, and also observed pairs of birds sometimes flying to a nest site immediately after courtship displays, which I never observed. Buckley & Buckley (1970) observed and described the tail drop and 2 fly close behaviors in great detail for white-tailed tropicbirds at Puerto Rican cliffs. They also noted the variable number of birds in courtship groups and never observed the birds landing, which is consistent with my observations. However, the tropicbirds performed many of their aerial courtship displays over water near the cliffs, while I only observed courtship behavior over land. Diamond (1970) proposed that some birds performing courtship displays were not even breeding. This hypothesis is valid to consider

applying to the tropicbirds on Mo'orea, since I never saw conclusive evidence of nesting.

Individual time budget

The most surprising result from my study was the finding that birds spend a significant portion of their time over land flying by themselves (73%). There could have been a slight bias, since individuals by themselves were often easier to select for observation. However, the significance value is so strong that this was probably not a confounding factor. This result does not support my hypothesis that the white-tailed tropicbirds are on land to breed, since they are spending a majority of their time by themselves, rather than with other potential mates. It does support Diamond's (1975) suggestion that these birds are participating in courtship activities, but not breeding. However, it appears that coming onto land would be energetically costly, since these birds are expending energy to travel to land and also missing feeding opportunities over the ocean. A future investigation is warranted into what evolutionary payoff other than breeding success would exist for tropicbirds coming onto land.

The results of the elevation time budget and exit method portion of my study could have implications for nest site selection in this species. I found that the tropicbirds spent significantly more time at low elevation than at either mid or high elevation. Also, the most common exit method at the end of the observations was for the bird to disappear into the vegetation (41.8%). These results indicate that there could be an association between the white-tailed tropicbirds and the vegetation that they flew close to at low elevation and disappeared into at the end of observation periods. Lee and Walsh-McGehee (1998) found that white-tailed tropicbirds nest in a variety of habitats (including tree hollows) as long as there is sufficient vegetative cover, which the trees in 'Opunohu valley would provide. I did observe a few birds hovering near one point

on a cliff face, which could indicate cliff-face nesting. Therefore, future studies could focus on where exactly the birds disappear into the vegetative canopy and a more extensive survey of potential cliff face nest sites to determine if these birds are nesting in tree hollows, cliffs, or both.

Number survey

The time of day and date effects on the number of birds in 'Opunohu valley shed some light on where white-tailed tropicbirds spend their time when not on Mo'orea. The mid-day hours had significantly more birds than the morning or afternoon time periods. One possibility is that they are spending the night over the open ocean, feeding in the morning or afternoon, and coming into 'Opunohu valley to participate in courtship activities during midday. Duffy and Hoch (1995) proposed that red-billed tropicbirds that showed a similar mid-day courtship display peak were at sea during the night. However, Pennycuick et al. (1990) found that white-tailed tropicbirds rearing a chick spent several days foraging pelagically before returning to feed the chick. Although I never observed any birds on Mo'orea visiting a chick, it is possible that it still takes several days for non-parenting birds to find a suitable feeding site. Therefore, if feeding is the only reason the birds leave the courtship site, their reappearance on land might be more determined by how quickly they are able to return than their ability to target a specific time of day. This hypothesis, however, is not supported by my finding that the birds apparently take cloud cover and rain into account before appearing on land, since these weather conditions had a significant effect on the number of birds in 'Opunohu valley. A future study where the courting tropicbirds are radio-tracked would shed light on how often individuals return to Mo'orea, where they spend their time when not on land, and therefore why there is a mid-day peak of courtship activity.

The result that 'Opunohu valley is significantly more populated than either Paopao valley or Vaianae illustrates the site preferences of courting white-tailed tropicbirds. PaoPao valley is visibly more developed agriculturally and residentially than 'Opunohu valley. Considering that the birds spend a significant portion of their time at low elevation over vegetation, they could prefer the location that has more undisturbed vegetation. Although Vaianae appears to have approximately the same level of development as 'Opunohu valley, the area is much smaller. I observed the birds often covering large areas of land in distances in short periods of time, and they could therefore prefer a valley where there is more room to display. Another hypothesis relates to Diamond (1978)'s discussion of information as a resource. It is possible that the habit of performing courtship displays at 'Opunohu valley was established arbitrarily, and now the birds continue to conduct courtship behavior there because it has already been established, and information has been transmitted, that it is the best place to convene. A future study that surveys the entire island of Mo'orea and compares the characteristics of all courtship locations would contribute further to the knowledge of courtship location preferences for white-tailed tropicbirds.

Conclusions

My observations of the land-based behaviors of white-tailed tropicbirds both support and oppose my hypothesis that they are breeding on Mo'orea. Courtship behavior is definitely occurring within the group interactions of birds, which supports my breeding hypothesis. However, the time budget studies yielded conflicting results with regard to my hypothesis. The finding that the birds spend most of their time by themselves contradicts the breeding hypothesis, although the elevation time budget showing that they spend a significant portion of time at low elevation flying around and into vegetation

suggests the presence of tropicbird nest sites in tree hollows. The number count portion of my study supports my hypothesis that there is a preferred time and location to perform courtship behavior. Although I observed courtship behavior and possible nest sites, the significant amount of time they spend by themselves combined with the lack of definite nest site data leads me to be unable to state conclusively that white-tropicbirds are breeding on Mo'orea at this time of year. However, the evidence in support of my breeding hypothesis suggests that they could be breeding there at other times of the year, and therefore my study has contributed to the knowledge of temporarily terrestrial tropicbirds.

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