J. Field Ornithol., 56(3):236–245

NEST MATERIAL PREFERENCES OF GREAT FRIGATEBIRDS

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Analyses of various passerine nests (Kilgore and Knudsen 1977, Collias and Victoria 1978, Jacobs et al. 1978, Thomas 1983) and laboratory studies (Sargent 1965) have shown some nesting material preferences. No such studies have been done on marine species, and none has compared selected nesting material to material availability in the environment.

We compared the nesting material in nests of Great Frigatebirds (*Fregata minor*) on Eastern Island, Midway Atoll, Pacific Ocean, to that available in the environment. We experimentally tested whether Great Frigatebirds prefer certain types of sticks or merely take sticks in proportion to their availability.

METHODS

We conducted our study during May and early June 1983, in the frigatebird colony located on the windward, south central side of Eastern Island, Midway Atoll which contained 76 nests built in the crowns of *Scaevola* bushes about 2 m above the ground. Inter-nest distances in the same clump were highly variable (approximate range 1 to 10 m). At the beginning of the study, most nesting frigatebirds were incubating (n = 59), but 5 pairs brooded chicks; 2 pairs had just formed and had not produced eggs; and 10 males were still displaying. By the end of the study, most nests still contained eggs (n = 36), but 22 nests contained chicks, and no males were displaying. Thirteen nests had been abandoned.

We examined 6 recently abandoned nests. Five of the 6 nests were examined immediately after abandonment prior to any nest destruction by other frigatebirds. The sixth nest was examined several hours after abandonment but appeared intact. We measured the length of each stick in each nest to the nearest millimeter and quantified the size and number of branches of all sticks by assigning a value of 1.0 to a branch if the branch was about the same diameter as the main stem of the stick. We assigned a value of .5 to a branch if the branch diameter was less than the stem diameter. The sum of all values of branches of a stick is the Branching Index (BI) of the stick. We log transformed all stick lengths and branching values. Since the BI of a stick containing no branches would be zero and would not allow us to log transform branching data, we added one to all BI's prior to log transformation. Thus, the BI of a stick without branches equalled 1.0. If BI = 2.0, the stick contained either one large branch or two small branches. We used ANOVA to test whether differences in length or branching existed between nests.

We surveyed the ground around the nesting area for sites that contained sticks. Open areas that were smaller in any direction than about 2 m (the wing span of frigatebirds) were not considered because frigatebirds probably could not easily land or hover and hence retrieve sticks from them. We sampled sticks on 5 main paths and 4 fields in the nesting area. We deliberately selected, as one of the four fields, a site with many large sticks that appeared appropriate for frigatebird nests.

We used a m^2 quadrat to sample ground sticks and adopted a sampling regime to determine whether the proximity of the sample to the edge of the path or field affected stick distribution. Sticks were sampled every 10 paces, or approximately 6.6 m, along each path: the first sample on the right side of the path, the second sample in the path center, and the third sample on the left side of the path. This sequence of sampling was repeated along the length of the path and a similar staggered sampling regime was used for fields: we took samples along both sides, along the field's midline, and half way between the midline and either side of the field. At each sample location, we measured and assigned a branching index to all sticks that were at least 10 cm long and totally or partially within the m^2 quadrat. Stick lengths and branching were log transformed and analyzed by ANOVA to test whether differences existed among quadrats within a given area. Differences among quadrats were found only in the area we deliberately selected because of the high density of large sticks. Excluding this area, quadrats were pooled within areas and ANOVA then tested whether differences existed among areas.

To test preferences in sticks, we asked two questions: (1) Is stick position with respect to the ground important to frigatebirds? And (2) does stick type and/or position with respect to the ground affect frigatebird stick selection? To answer the first question, we collected straight sticks of various lengths and divided them into 2 groups equal in number and average lengths. We painted the tips and middle of the sticks by group for later identification. To control for paint color, the two stick groups differed only in the sequence of red and blue bands of paint. We placed all sticks from one group singly on the tops of *Scaevola* bushes near the nesting colony. Sticks from the other group were placed singly on the ground at the edge of a field in front of the same bushes. In the first of two trials, we used 32 sticks in each group and left them unattended after placement. Two days later, we searched the area thoroughly and collected and counted all remaining sticks. We surveyed frigatebird nests and the ground around the nesting area daily for painted sticks. Our cautious nest surveys had only a minimal effect on nesting birds at the possible expense of failing to sight painted sticks that may have been incorporated into nests. In the second trial, we used 20 sticks per group and observed all activity near the bush and ground containing our sticks for one hour following initial placement.

To answer the second question, in each of 12 trials, we constructed two nests each with 20 branched sticks and placed one in a *Scaevola* bush and the other on the ground in front of the bush. We constructed a

TABLE 1. Dimensions of sticks on the ground in paths and fields and in frigatebird nests. The mean density, length, and branching index ± 1 standard deviation are presented.

Site	Area (m^2)	n (quadrats)	n (sticks)	Density (sticks/m^2)	Length (cm)	Branching index
Path 1	473	15	135	9.0 ± 8.5	21.6 ± 11.7	1.08 ± 1.24
Path 2	466	9	70	7.8 ± 5.7	18.6 ± 9.8	1.04 ± 1.19
Path 3	299	15	118	7.9 ± 7.8	20.4 ± 14.2	1.11 ± 1.30
Path 4	1090	15	144	9.6 ± 6.5	21.1 ± 18.4	1.09 ± 1.28
Path 5	301	15	148	9.9 ± 12.7	18.8 ± 11.5	1.07 ± 1.25
Field 1	1026	15	234	15.6 ± 13.8	19.1 ± 12.5	1.08 ± 1.24
Field 2	334	10	95	9.5 ± 11.5	21.3 ± 10.1	1.06 ± 1.23
Field 3	452	14	209	14.9 ± 12.8	18.2 ± 8.3	1.07 ± 1.30
Field 4	78	5	271	54.2 ± 43.0	21.5 ± 14.2	1.07 ± 1.21
Nest 1			30		41.8 ± 13.0	1.98 ± 1.72
Nest 2			30		44.9 ± 21.7	2.20 ± 2.06
Nest 3			47		42.5 ± 14.5	1.99 ± 1.88
Nest 4			35		45.9 ± 15.3	1.64 ± 1.53
Nest 5			48		36.8 ± 16.1	1.86 ± 1.70
Nest 6			46		39.3 ± 15.4	1.90 ± 1.50
All sites (ground)	4510	113	1424		20.0 ± 12.0	1.08 ± 1.25
All nests			236		41.4 ± 16.1	1.90 ± 1.80

third nest of 20 sticks containing no branches and placed it on the bush within 2 m of the branched stick nest. To control for possible differences in our selected nest locations, we reversed the position of the two nests in the bush in each experiment. All nests were constructed from sticks obtained from abandoned frigatebird nests to diminish the possibility of using sticks that were inappropriate for frigatebirds. We observed these nests from about 75 m away for 1 h and recorded the number of landings on each nest, the cumulative time birds spent on each nest, the number of attempts by birds to remove sticks from each nest, and the number of sticks actually removed and carried from each nest. At the end of the hour we disassembled all nests and counted the number of sticks remaining.

The above experiment confounds stick type and apparent nest size. Although all nests contained 20 sticks, branched sticks are more massive than sticks without branches. Thus, the branched stick nests appeared more massive than the straight stick nests. To control for the effect of the apparent nest size in our third experiment, we constructed a small nest with 20 branched sticks and a large nest with 30 sticks containing no branches. We placed both nests in a *Scaevola* bush within 2 m of each other. About 18 h later, we disassembled the nests and counted the number of remaining sticks in each.

RESULTS

Frigatebird nests averaged 39.3 ± 8.6 sticks (n = 6 nests). Stick density in all paths was 8.5 ± 8.3 sticks/m^2 (n = 69 quadrats), and no significant

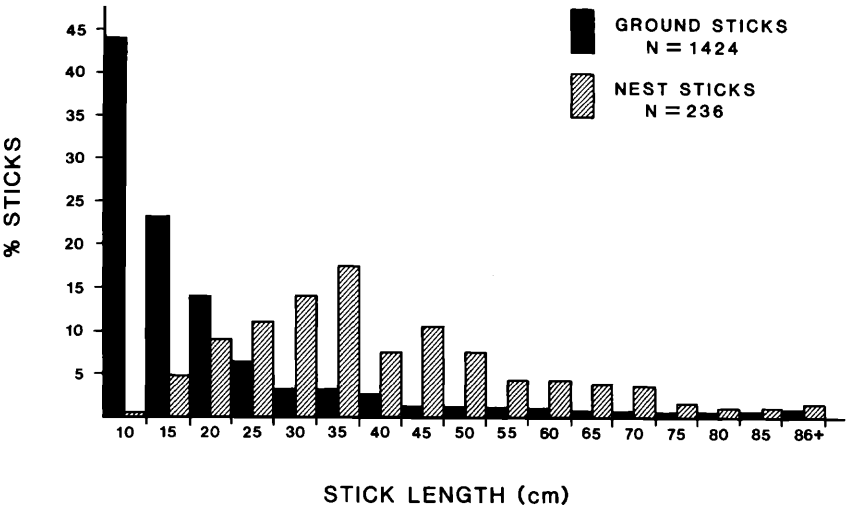

FIGURE 1. Ground and nest stick lengths. The solid bars represent ground sticks, and the hatched bars represent nest sticks. Sticks are lumped into 5-cm size classes for illustrative purposes only.

difference existed among the 5 paths ($F_{3,64} = .17$, $P > .05$, Table 1). While there was no significant difference in stick density in 3 of the 4 fields ($F_{2,34} = 1.94$, $P > .05$), the density in these fields was significantly greater than in paths ($F_{1,104} = 8.76$, $P < .005$). The average density in fields was 13.8 ± 12.8 sticks/m² (n = 39 quadrats). The average stick density was greater in the fourth field, 54.2 ± 43.0 sticks/m² (n = 5 quadrats).

Average stick length in nests was 41.4 ± 16.1 cm (n = 236), whereas the average length of ground sticks was only 20.0 ± 12.0 cm (n = 1424, Table 1) and significantly shorter than nest sticks ($F_{1,1658} = 628.1$, $P < .001$, see Fig. 1). The difference between the length of ground and nest sticks would be even greater had we included in our ground samples the numerous sticks that were less than 10 cm long.

Significantly more branched sticks were found in nests than on the ground ($\chi^2 = 586.1$, df = 1, $P < .001$). Only 9.9% of all ground sticks (n = 1410) were branched, whereas 77.5% of nest sticks (n = 236) were branched. The average branching index of ground sticks was 1.08 ± 1.25 (n = 1410). As expected, large ground sticks were more likely to contain branches than shorter sticks ($r = .152$, df = 1417, $P < .01$). While significant, the correlation between length and branching is weak. Ground sticks had significantly fewer branches than nest sticks ($F_{1,1644} = 1070.9$, $P < .001$, see Fig. 2). The average branching index of nest sticks was 1.90 ± 1.80 (n = 236). There is no significant correlation between length and branching of nest sticks ($r = .067$, df = 234, $P > .05$). The average ground stick had no branches. The average nest stick had at least one major branch or 2 minor branches.

In our first experiment, we recovered 28 of the 32 sticks containing no branches that had been placed singly on bushes. Some sticks had fallen to the ground, perhaps indicating unsuccessful attempts by birds to remove them from bush tops. One of 4 missing bush sticks was recovered directly beneath a frigatebird nest about 40 m from initial stick placement. We recovered all ground sticks, usually exactly where initially placed. After we placed 20 sticks without branches on a bush, within an hour 2 frigatebirds flew down, hovered over the bush, and each picked up a stick and flew off with it. No sticks were taken from the ground.

During 12 replicates of the artificial nest experiment, frigatebirds responded during 8. In these 8 experiments, frigatebird responses began 21.5 ± 17.9 min after the nests were placed and continued for 24.1 ± 18.2 min. Often by the end of the observation period one of the nests had been destroyed and sticks were scattered about the bush and surrounding ground.

Frigatebirds restricted their activity primarily to bush nests (Table 2). Only one bird landed on the ground nest, and only one bird attempted to remove sticks from the ground nest. On bushes, the total time frigatebirds spent on the straight stick nest was not different from the total time spent with branched sticks. The total number of landings on branched stick nests, however, was about 60% greater than on those nests constructed of sticks without branches. Hence, activity around the branched stick nest was greater than the activity associated with the unbranched stick nest. The number of sticks taken from branched stick nests was twice the number taken from nests containing sticks without branches, and the total number of attempts to remove sticks from branched nests was also about twice that from straight stick nests. Consequently, the effectiveness or the ease of stick removal was not much different. Given the small sample sizes, however, the above results were not significantly different as determined by chi-square tests.

These results are somewhat misleading. About 30% of the time, when a bird flew into the area, one nest was already occupied. Thus the incoming bird had a choice of either selecting the unoccupied nest or displacing the bird from the occupied nest. We observed only one displacement. Generally, the incoming bird selected the unoccupied nest or flew off. If one considers only those attempts when all nests were unoccupied, birds selected the branched stick nest 3 times more often than they selected the nests of sticks without branches (Table 2), and the difference is significant ($\chi^2 = 7$, df = 1, $.005 < P < .01$).

These behavioral data correspond with an analysis of nest contents. The percent of attempts (75%) by frigatebirds at branched stick nests was not significantly different from the percent of branched sticks (77.5%) found in their nests ($\chi^2 = .12$, df = 1, $P > .05$), but was significantly different from the percent of branched sticks (9.9%) found on the ground ($\chi^2 = 118.6$, df = 1, $P < .001$).

In our experiment using different-sized nests, we recovered 29 of the

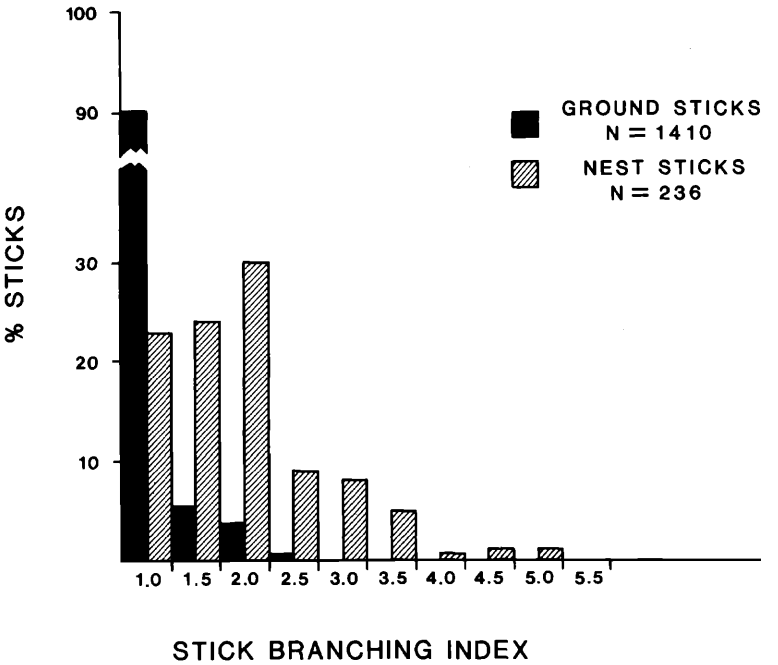

FIGURE 2. Degree of branching of ground and nest sticks. The solid bars represent ground sticks and the hatched bars represent nest sticks. The Branching Index (BI) combines the number of branches with branch size. If BI = 1.0, the stick has no branches. If BI = 1.5, the stick has one small branch. If BI = 2.0, the stick has one large branch or two small branches. See text for explanation.

30 original sticks from the large, unbranched stick nest, but only 7 of 20 branched sticks that comprised the smaller nest. While branched nests were destroyed in half of the experiments in which frigatebirds participated, nests of sticks without branches were never destroyed, probably because fewer birds approached straight stick nests. Even if activities between nest types were similar, branched stick nests would be more prone to destruction than straight stick nests because in removing a branched stick from a nest, the branches tend to catch other sticks and disrupt them.

DISCUSSION

On Midway, frigatebird nests were constructed almost exclusively of *Verbesina* sticks. Large fields of *Verbesina* surrounded the frigatebird colony, so potential nesting material was abundant. *Scaevola* and *Casuarina* sticks were also abundant but not commonly found in frigatebird nests. No frigatebird nest contained sticks that were obviously collected from living plants, although *Verbesina* tassles from living plants were frequently used to line the stick nests. All sticks were woody, bleached,

TABLE 2. Responses of Great Frigatebirds to 3 artificial nests placed near colony. The numbers in the table are the total number of observations of the specified activity in 8 replicates of the experiment.

Activity	Straight-stick nest in bush	Branched-stick nest in bush	Branched-stick nest on ground	Total
Number of landings	9	15	1	25
Total time birds on nest (min)	23	20	0.5	43.5
Average time on nest/landing (min)	2.6	1.5	0.5	
Number of sticks taken	4	8	0	12
Number of attempts to remove sticks	14	26	1	41
Removal effectivness (no. taken/no. attempts)	0.29	0.31	0	
Number of attempts when all nests were unoccupied	7	21	1	29
Number of destroyed nests	0	4	0	4

and obviously dead. Consequently, the year's current crop of *Verbesina* was probably not used except as nest lining.

Since a frigatebird nest is composed of about 40 sticks on Midway Atoll and since the density of sticks was about 8 sticks/m^2 on paths and about 14 sticks/m^2 in fields, a pair of frigatebirds could theoretically obtain a sufficient number of sticks from about 5 m^2 of path or 2–3 m^2 of field. In 1983, only 76 frigatebird nests existed on Midway. Since the island is over 8000 m^2, the amount of nesting material per se is obviously not limiting to this population. However, most ground sticks were not suitable nesting material. They were too short and contained too few branches. Less than 18% of ground sticks fall within one standard deviation of the mean length of nest sticks. The average ground stick branching index was about 1.0, whereas that of nest sticks was nearly 2.0. Less than 10% of ground sticks were branched at all.

Because we sampled ground sticks after most frigatebirds selected their nest materials, we underestimated the average length and branching index of ground sticks that were available to frigatebirds. If we corrected our ground stick samples to include the nest sticks that we would have found on the ground prior to frigatebird selection, the average ground stick length would increase by less than 3%, and the average branching index would increase by less than 2%. These minor differences due to when sticks were sampled cannot account for the major differences we found between nest and ground sticks.

Our stick experiments suggest that the location of the sticks is important. No sticks were ever taken from the ground in our experiments. All the removed sticks came from the bushes regardless of whether the sticks were placed in their respective sites singly or clumped together in nest fashion. Despite frigatebirds' preference for sticks on bushes, there are very few accessible dead sticks on or in bushes on Midway.

However, frigatebirds can and do hover directly above ground sticks in large open areas and pick them up without landing (Nelson 1975, pers. obs.), and this appears to be the major way frigatebirds gather nesting material.

In our experiments, frigatebirds selected, when a choice was possible, sticks from the branched stick nest 3 times as often as they selected sticks without branches. Although the percent of branched sticks selected in these experiments was the same as the percent of branched sticks found in nests, there is another possible explanation of our experimental results. Because artificial nests of 20 branched sticks were more massive than those of 20 straight sticks, the preference might have been for the seemingly larger nest rather than for the branched sticks themselves. However, if nest size was important, the larger straight stick nest with 30 sticks should have been destroyed in our last experiment. Instead we found that the smaller branched stick nest with 20 sticks was destroyed, indicating a clear preference for branched sticks.

Our results provide strong evidence that frigatebirds preferentially select long, branched sticks as nesting material despite their low availability on the ground. Branched sticks might be preferred because they are easier to anchor in the *Scaevola* branches and in the nest itself than are sticks without branches. Longer rather than shorter sticks may be necessary to make a nest large enough to accommodate a frigatebird.

Like Marsh Wrens (*Cistothorus platensis*; Picman and Picman 1980), Great Cormorants (*Phalacrocorax carbo*; Urban 1979), and Broad-tailed Hummingbirds (*Selasphorus platycerus*; Calder 1972), frigatebirds destroyed abandoned or unattended conspecific nests. High mortality of frigatebird eggs and nestlings has been attributed, in part, to this behavior (Nelson 1975). Nest robbing might occur because the greatest concentration of preferred sticks, particularly late in the nesting season, is found in other frigatebird nests, not on the ground.

That nests provide the greatest concentration of nesting material is particularly important because frigatebirds are known to breed somewhat asynchronously (Stonehouse and Stonehouse 1963, Diamond 1973, Nelson 1975). Our own observations that 10 males were displaying in the colony of 76 pairs and another 2 were just forming pairs while 5 pairs were already brooding chicks indicates nesting asynchrony in the Midway colony. Late nesters might expedite nest construction by robbing other nests of sticks and thus minimizing the search time necessary to find suitable sticks. In most other seabirds, the late nesters are young birds (Coulson and White 1958, Fisher 1969, Mills 1973, Blus and Keahey 1978, Ryder 1980, Massey and Atwood 1981). In our stick experiments, all participants were males (with the possible exception of one young bird whose sex was not determined), and most of the participants had at least some white breast feathers indicating that they had not obtained mature adult male plumage.

These experiments suggest that frigate birds are actively selecting specific material for nest building from what is available in the envi-

ronment. Our data begin to clarify nest construction characteristics for this species but do not clarify factors regulating the frigatebird population on Midway. Further data are needed on factors such as the role of bushes as nesting substrate, food supply, and climatological factors.

SUMMARY

Great Frigatebirds build stick nests in bushes on remote oceanic islands, preferentially selecting nest material from what is available. Nests consist primarily of long, branched sticks despite the low availability of such sticks in the environment. In choice experiments on Midway Atoll, Great Frigatebirds selected branched rather than straight sticks 75% of the time, and they preferred to pick up nest material from bushes rather than from the ground. The proportion of branched sticks in frigatebird nests was not significantly different from the proportion of branched sticks selected in choice experiments.

ACKNOWLEDGMENTS

We thank Dr. Robert Shallenberger of the Fish and Wildlife Service, Honolulu, CMD James Harris, and CMD William Parthum, for facilitating the stay on Midway. We greatly appreciate Russell and Beverly Shea for providing logistical support and companionship in the field. We thank Drs. M. McVey, J. F. Downhower, and E. H. Burtt, Jr. for their constructively critical comments on earlier drafts of this manuscript. We thank The Ohio State University and Florida Atlantic University for providing partial funding for this work.

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Received 8 Jan. 1985; accepted 17 June 1985.