

FOOD CACHING IN THE TROPICAL FRUGIVORE, MACGREGOR'S BOWERBIRD (*AMBLYORNIS MACGREGORIAE*)

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ABSTRACT.—Males of MacGregor's Bowerbird (*Amblyornis macgregoriae*) cache fruit. In a study population in eastern Papua New Guinea we found 437 cache sites at 39 bowers. Adult males stored an average total of 17.6 fruits (range 0–82) at 13.6 sites (range 0–55), significantly more than immature males. All sites were located in vegetation above ground within 13 m horizontal and 9 m vertical distance from the males' bowers. For 3 males studied intensively, the rate of replacement of caches averaged 0.13 replacements·site⁻¹·day⁻¹, with no significant differences among males. Caching occurred only during the seasonal periods of bower attendance and breeding activity. Females did not store fruit and did not take fruit stored by males. We suggest that by extending the time males can remain at their bowers, caching may increase interaction time with females and decrease rates of bower marauding by rival males. There was no evidence that cached fruits served as bower decorations. Received 7 May 1984, accepted 4 October 1984.

FOOD storing refers to the deposition of food items in a particular location for later consumption. It has been observed in a number of bird and mammal species (Roberts 1979, Vander Wall and Balda 1981, Smith and Reichman 1984). In birds, food storage occurs as either a long-term strategy, to yield food during times of scarcity, or on a short-term basis for temporary retention or accumulation of items that cannot be eaten at one time.

Long-term food storage occurs predominately in nonmigratory species and in habitats with seasonal fluctuations in resource abundance (Roberts 1979, Smith and Reichman 1984). The food stored is generally durable and particulate, such as seeds. Birds for which long-term food storage is an important contribution to reproductive success and winter survival include woodpeckers (Koenig 1978), corvids (Tomback 1977, Bossema 1979, Vander Wall and Balda 1981), and parids (Ulfstrand 1976, Sherry et al. 1982). Short-term food storage is known primarily in shrikes (*Lanius* spp., Craig 1974) and birds of prey (Newton 1979, Walter 1979) and in some cracticids, parids, and corvids (Pizze 1980, Smith and Reichman 1984).

Long-term food storing apparently is more common in temperate than in tropical avifaunas (Smith and Reichman 1984). This may reflect both the greater importance of seasonal

changes in food abundance in temperate habitats and the cooler temperatures that allow for storage of perishable items over a longer period of time (Roberts 1979, Vander Wall and Balda 1981). Nonetheless, tropical jays (Turček and Kelso 1968) and woodpeckers (Skutch 1969) store food, as do their temperate counterparts, particularly in montane areas.

In this paper we describe food-storing behavior in MacGregor's Bowerbird (*Amblyornis macgregoriae*), a frugivorous species found in montane rain forest in New Guinea. This behavior is separate from fruit gathering by males for bower decoration. We present data on occurrence, type, location, and replacement rates of stored food items and discuss caching in relation to the species' social organization and bower-building behavior. Food storing has not been described previously in any bowerbird or, to our knowledge, any tropical frugivorous passerine.

METHODS

Our observations were made on the southwestern slope of Mt. Missim, Kuper Range, Morobe Province, Papua New Guinea (7°16'S, 146°47'E). The study area comprised 750 ha of primary, midmontane rain forest between 1,450 and 2,200 m altitude and included three drainages and the ridge lines separating them. Annual rainfall averaged about 2,000 mm, and daily temperatures varied from 9° to 25°C. More detailed descriptions of this area are presented in Pruett-Jones and Pruett-Jones (1982) and Pratt (1983).

Observations on MacGregor's Bowerbird were made during 21 months of fieldwork between August 1980 and December 1983. We first discovered caching in

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this species in September 1982. Most data presented here were gathered during the 6-week period from 17 October to 4 December 1983.

Caching behavior of 3 adult males that maintained adjacent bowers on a single ridge was studied in detail. We visited these 3 bowers 4 times over the course of 1 week and mapped and marked the cache sites before the start of regular sampling. We define a cache site as a specific location where one or more fruits, of one or more species, were stored. If a structure (e.g. a small tree) had fruits cached in several locations, each location was considered a separate site. Changes in the number and species of fruits at each cache site were recorded from 3 to 22 November. Sites were checked twice daily, between 1100 and 1300 and between 1600 and 1800. To facilitate an accurate measure of replacement, all cached fruits within reach of the observer (up to 3–4 m vertical height) were marked with small spots of nontoxic paint, and those fruits out of reach were noted for color or variety.

A cache replacement was defined as a decrease followed by an increase in the number of fruits at the site, or vice versa, irrespective of the number of fruits involved (i.e. a replacement occurred when the male removed some or all of the fruit at a cache site and then replaced it, or added fruit and then removed it). Fruit change refers to the absolute number of removals of marked fruits and replacements of unmarked fruits at each site. Some new caches were discovered near the study bowers after initiation of sampling. In our analysis of replacement rates, we include only those sites that were monitored for at least 8 days (about the maximum length of time over which a replacement might occur). Based on direct observations of males eating cached fruits (see Results), we assumed that only the resident male was responsible for the disappearance or replacement of fruits at cache sites at a given bower.

To see whether males would detect and use offered fruits, two experimental sites were established at each of the three study bowers; one site was within 1 m and the other from 5 to 10 m from the bower. Fruits of the same species the male stored were placed at these sites and their subsequent recovery monitored during normal cache checks for 7 days following first placement. Each day, new fruits were placed at empty sites.

On 29 November we removed all fruits cached at the 3 bowers. Once a day for the following 5 days we recorded reestablishment of cache sites, initiation of new sites, and rates of fruit change for these males.

Between 23 November and 1 December, the entire population of active bowers on the study area was checked for cache sites. At each bower we recorded the number of sites found in 30 observer-min of search time and, for each site, the horizontal and vertical distance from the bower. All cached fruits were collected, and identified if possible.

As part of other studies (Pruett-Jones unpubl. data), we monitored activity at bowers weekly or biweekly throughout 1982 and 1983. These records provided data on the relative seasonal occurrence of fruit caching and its relation to bower maintenance and breeding.

RESULTS

General biology and caching behavior.—On average, 47 (range = 43–54) male MacGregor's Bowerbirds were active on our study site each season from 1980 and 1982. Adult males construct a maypole bower (twigs piled up around a slender sapling) that is decorated with fruit, fungus, charcoal, and insect frass. Immature males build rudimentary structures that may be abandoned after a few weeks of use.

Bowers were regularly and linearly spaced along ridge-line habitat, with a mean inter-bower distance during the 1980 and 1981 seasons of 182.8 m ($n = 98$, range = 60–423, $SD = 72.9$). The local placement of bower sites appears to be determined primarily by habitat characteristics of the ridge line (Pruett-Jones and Pruett-Jones 1982). Observations of marked males in 1980 indicated that they spent an average of 54% (range = 20–75%) of daylight hours within a 20-m radius of the bower, and this core area was aggressively defended.

A. macgregoriae was primarily frugivorous; 95% of its diet consisted of medium to large drupes and, to a lesser degree, arillate fruits. Arthropods made up the remainder of the diet. The birds foraged singly or in small groups, with females and immature birds overlapping extensively in use of space and fruiting trees with males. Males did not defend food resources. Analysis of fecal samples showed at least 130 species of fruit utilized by *A. macgregoriae* on our study area; individual males ate fruit from about 30 species of trees, shrubs, and vines (Pruett-Jones and Pruett-Jones unpubl. data).

Dynamics of fruit caching.—Fruit caching was observed only in males and only during the breeding season. Males maintained their bowers for about 9 months/yr (May–February); however, breeding was restricted to September–February. From May to August activity was irregular while males rebuilt their bowers. During this early phase males did not store fruit. Caching was observed only during the period when males were in regular attendance

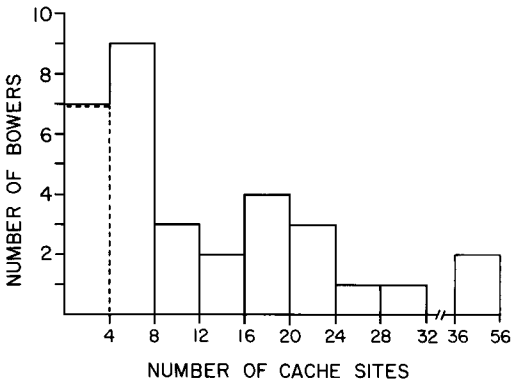


Fig. 1. Frequency distribution of number of cache sites at 32 complete bowers of adult males (solid line) and 7 rudimentary bowers of immature males (dashed line).

of their bowers and the majority of intersexual interactions occurred. Late in the season, caches were maintained until residents abandoned their bowers. Males remained in the vicinity of their bower site throughout the year, despite the marked seasonality of bower attendance and abandonment. Females did not store food, nor did they take the food cached by males.

During 140 h of behavioral observations in 1982, we saw 20 instances of caching and recovering of fruits by 5 males. Fruit was the only food item cached, and it was gathered after a foraging bout, i.e. it did not appear that males went to fruiting trees specifically to gather the fruit. Fruit was wedged in or placed at a cache site, and when retrieved it was either partially or totally consumed or it was moved to a nearby site. We observed fruits to be recovered from a site and replaced simultaneously, after a few hours, after several days, or not at all. It was our impression that there was considerable variability in the actual storage and recovery of individual fruits; however, because our sampling was limited to twice a day, we were not able to quantify these patterns completely.

To examine the relationship between relative activity levels of males at bowers and the degree of caching behavior, we scored bower completeness (from 1 to 5) and compared this with the number of cache sites at each bower. A score of 5 represented a complete bower with a full maypole and numerous decorations of different kinds, and a score of 1 indicated an incomplete bower structure, lacking a border and base to the maypole and without decora-

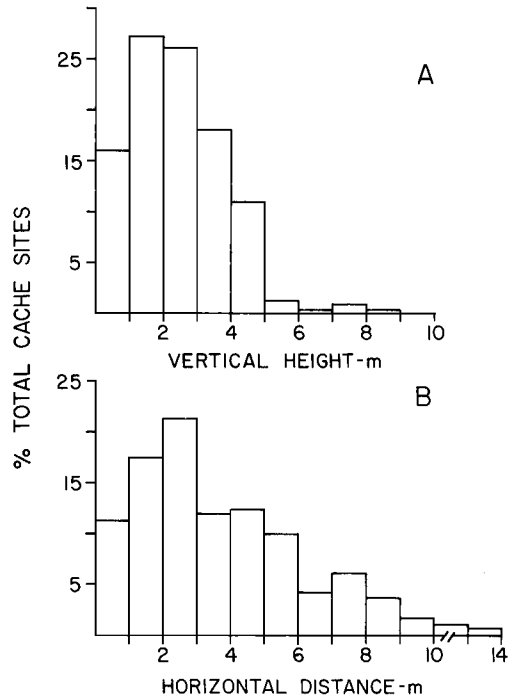


Fig. 2. Distribution of vertical height and horizontal distance measurements of 421 cache sites at 31 bowers. Vertical height is the distance from the cache site to the ground. Horizontal distance is the distance from the edge of the bower to the cache site.

tions. There was a significant and positive correlation between the rank of and the number of cache sites at a male's bower (Spearman rank correlation, $r = 0.721$, $P = 0.0001$ for all males; $r = 0.516$, $P = 0.0025$ for adult males). Males that had the most complete bowers, resulting from greater activity at the site, were also the males maintaining the most cache sites.

Caching behavior: population.—We examined 39 bowers, 32 of adult males and 7 of immature males, for cache sites. A total of 437 was found. One (14.2%) immature and 30 (93.8%) adult males had caches. Adult males had a mean of 13.6 (range = 0–55, SD = 12.0) cache sites at their bowers, and the single immature male had 3 (mean for all immature males was 0.4, range = 0–3, SD = 1.1). The differences between immature and adult males were significant ($t = 6.083$, $P < 0.005$). The frequency distribution of cache sites for all males is shown in Fig. 1. Some cache sites probably were missed at each bower during the census because of the relatively short time spent searching.



Fig. 3. Example of a cache site in a fork of a tree. The fruit is *Timonius* spp. (Rubiaceae).

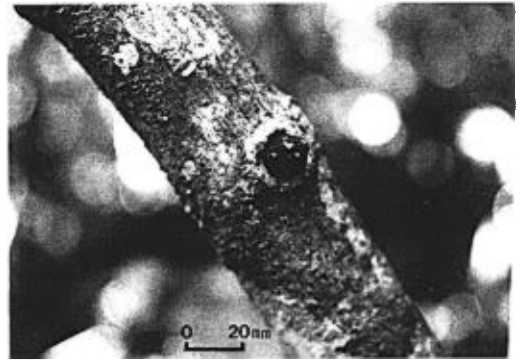


Fig. 4. Example of a cache site in a cavity of a small tree. The fruit is an unidentified drupe.

so that drying could occur, nor were they hidden from view.

The spatial dispersion of 37 cache sites at one of the study bowers is shown in Fig. 5. Scatterhoarding (Morris 1962) best categorizes the placement and spacing of stored fruit. Many cache sites, each with one or a few food items, were located within the small core area of each male's home range.

Generally, males cached fresh, ripe fruit, although green, unripe fruit occasionally was stored and recovered (presumably eaten) before ripening. Rotten fruits were not cached, but fruits sometimes rotted at the cache site before being eaten. Such fruits were left at the site untouched.

The total number of fruits cached and the number of fruits at each site varied among males. The 31 males with at least 1 cache site stored a mean total of 18.3 fruits (range = 1-82, SD = 16.8) and an average of 1.3 fruits (range = 1-13, SD = 0.5) at each site. Adult males had a mean total of 17.6 fruits (range = 0-82, SD = 17.0). Most cache sites chosen by the occupant males could hold only 1 fruit; at 83.6% (352) of the sites, only 1 fruit was found.

The number of species of fruit cached by males ranged from 1 to 14 and was significantly and positively related to the number of cache sites utilized (Pearson correlation, $r = 0.95$, $P < 0.001$). A total of 40 species of fruit was collected from cache sites during the population census. The species of fruit stored showed the range of size and morphology of fruits normally represented in the species' diet.

Caching behavior: study bowers.—We monitored a total of 113 sites at 3 study bowers (21

Sites were located 0-12.5 m horizontal distance from the bower (mean = 4.0, SD = 1.3, $n = 421$ sites at 31 bowers) and 0.2-9.0 m vertical height from the ground (mean = 2.6, SD = 0.8; Fig. 2). Our ability to see sites above 6 m was limited, so our sample may be biased towards those near the ground.

The types of sites used for caching varied among males. The following were encountered: fork of tree trunk and branch (Fig. 3), point of contact between epiphytic vine and tree, horizontal branch or large vine, top of tree stump, fallen log, crown of tree fern, and small cavity in tree trunk or branch (Fig. 4). We did not consider fruits on the ground as cached, and marked fruits that had fallen to the ground were not recovered by males. Sites were not modified by males, and not all sites permitted secure retention of fruit. Dislodging of fruit by wind or movement of the site did occur.

As the canopy averaged about 30 m high on the study area, cache sites were located in the understory of the forest, well shaded except for diffuse light. Sites were not exposed to the sun

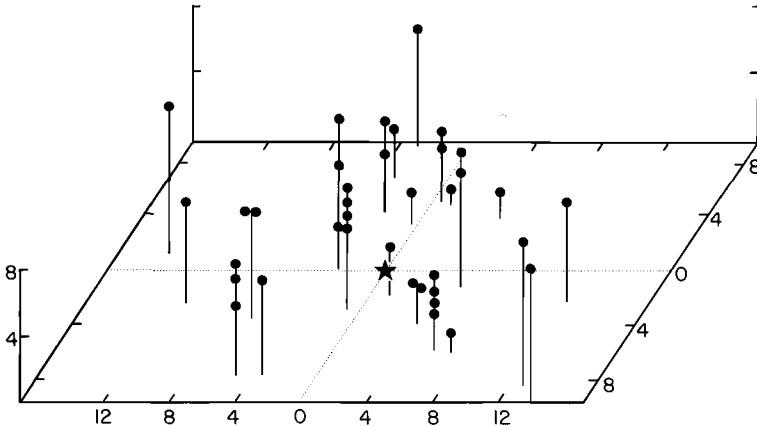


Fig. 5. Spatial distribution of cache sites at bower C. The star indicates the position of the bower; solid circles represent cache sites. Most of these sites were in small trees. The scale (m) is indicated.

at bower A, 37 at bower B, and 55 at bower C). Ninety-one of these sites were included in an analysis of replacement (Table 1). Each male made fruit changes at each cache site an average of 0.34 times/day. A cache replacement occurred on average once every 6–7 days, with a mean of 0.13 replacements·site⁻¹·day⁻¹. The differences among males in rates of site replacement were not significant (ANOVA, $F = 0.06$, $P = 0.9375$) and did not vary with the number of cache sites (Table 1). Thus, on average, males used each of their cache sites at approximately the same rate, regardless of the number of sites.

Extreme differences in rates of replacement existed among sites. During the 19 days of sampling, the total number of replacements observed at individual sites varied from 0 to 14 (mean = 2.5, SD = 2.6, $n = 70$ sites). One or zero fruit changes occurred at 14 (20%) of these sites.

Neither rate of cache replacement nor fruit change was correlated with proximity of the site to the male's bower. The rate of fruit change at cache sites was greater during the morning hours than in the afternoon. Comparing changes from the previous night's sample to the noon sample on a given day with changes from the noon to afternoon sample, cache sites at bowers B and C had an average daily rate of fruit change of 0.24 during the morning and 0.12 during the afternoon over the 19 days of sampling (differences were significant; $t = 4.125$, $P < 0.001$).

At bowers B and C, five instances of fruits being shifted from one cache site to another

were recorded. Fruit shifts occurred only over short distances (<2 m) with no consistent trend as to the species of fruit shifted, directionality of shift, etc.

Of the experimental sites set up at each study bower, only those sites placed within 1 m of the bower were used. As many fruits as were offered at the sites (1–4) were removed and presumably eaten, and in 3 instances were moved to the males' natural cache sites.

We removed all cached fruit from 104 sites at the 3 study bowers. At 47 (45%) of these sites, the fruits were eventually replaced. Males replaced the fruit within an average of 2.5 days for those sites where fruits were cached again. Time to replacement was not correlated with horizontal distance of cache site to bower, with the rate of cache replacement, or with fruit change at those sites prior to the experiment. Mean rates of cache replacement and of fruit changes at replaced sites were 0.04 and 0.37/day. The rate for site replacement was significantly lower than the preremoval rate (see above, $t = 4.85$, $P < 0.001$). Only 3 new cache sites were established by males as a result of the removal experiment.

DISCUSSION

One explanation for the occurrence of fruits placed near the males' bowers is that they serve a decorative function and possibly play a role in intersexual interactions. Males of all bower-building ptilonorhynchids adorn their bowers with a wide variety of objects, including fruit

TABLE 1. Comparison of use of fruit caches at three study bowers.

Bower	Number of sites sampled ^a	Rate of site replacement/day ^b		Rate of fruit change/day ^b		Number of fruit taken/day ^c
		Mean	SD	Mean	SD	
A	15	0.148	0.128	0.336	0.304	2.52
B	30	0.128	0.105	0.306	0.316	4.59
C	46	0.136	0.152	0.376	0.440	8.64
Overall	91	0.135	0.133	0.346	0.381	5.25

^a Includes only those sites at each bower for which we had 15 samples. Sites at bower A were sampled over 8 days and at bowers B and C, 19 days.

^b Rates were calculated for each site and averaged over all sites at each bower.

^c Values represent means for each male. Values were calculated by taking the number of removals of fruit at all sites and dividing by the number of days sampled.

for most species (Gilliard 1969, Cooper and Forshaw 1977, Diamond 1982a). There are, however, notable differences in the nature of fruits used as decorations and fruits stored for food by *A. macgregoriae* (Table 2). Fruits used for decorations generally are selected on the basis of color and size, usually are not species eaten by the bowerbird, and may be used by males in courtship display. Additionally, decorative fruits are arranged on the bower itself or within 1–2 m of the structure, in clear view of visiting females. In contrast, cached fruits were only of species known to be important in the diet of *A. macgregoriae*, were scattered inconspicuously in the vegetation, and usually were more than 2 m from the bower. We contend that fruit gathered and stored in the context described in this paper has no function other than as a food source for the male.

Although females do not eat or appear to respond to the presence of the stored fruit, we cannot rule out the possibility that they may use the number of cache sites as an assessment of a male's general foraging ability in their choice of mates. We have not quantified relative mating success of males in our population, a necessary prerequisite for addressing this question.

MacGregor's Bowerbirds scatter-hoard fruit within the exclusive display space around their bowers where individuals spend the majority of their time. Males indirectly protect their cache sites from conspecifics by placing them within the area they aggressively defend. However, no attempts to take stored food were documented for rival males or visiting females. Scatter-hoarding often suggests competitive pressure from interspecific fruit thieves (Smith and Reichman 1984). Males may reduce loss

of fruit to nocturnal marsupials, bats, and rodents by dispersing caches in unrich patches, making it less economical for these competitors to steal from a cache than to forage for fruit elsewhere. The distribution of cache sites for *A. macgregoriae* also may be attributed to the limitation of suitable sites that can retain larger numbers of fruit or to the likelihood that large piles of fresh fruit may succumb more rapidly to molds and bacteria. The absence of ground- or below-ground-level cache sites also points to the need to protect stored fruit from decomposers, where, in tropical environments, rotting is accelerated (Roberts 1979).

Caching behavior was more common in adults than immature males. This is consistent with the differences between adult and immature males in bower-building skills, maintenance, and attendance. Immature males infrequently build bowers and attend those they do build on an irregular basis. Caching behavior probably develops along with bower-building behavior.

The observed patterns of use of cache sites and the dynamics of caching behavior lead us to conclude that fruit caching in this species is an adaptation within the general context of their social organization and foraging ecology, rather than a primary determinant of spacing and behavior. We suggest that males store food to extend their time at the bower. Cached fruit may provide sufficient energy to allow males to remain at their bowers longer than otherwise possible and consequently may cut down the length and/or number of foraging trips.

Bowers are essential to males in mating interactions with females; males apparently cannot gain matings without an intact, complete bower. Additionally, bowers are subject to rap-

TABLE 2. Comparison of characteristics of fruit cached for consumption by male *A. macgregoriae* and fruits used as decorations by bowerbirds generally.

Variable	Fruits cached	Fruits as decorations	Source ^a
Nature of fruit	Fresh, food species	Primarily nonfood species, sometimes dried	1
Proximity to bower	1-14 m from bower	On or within 1 m of bower	1
Placement of fruit	In vegetation only, singly or in small piles up to 13	On ground, in piles of 10-100 fruits, or panicles hung in vegetation	1, 3
Preference for color	None	Strong	1, 2
Occurrence of stealing	None	Frequent	1, 4
Consumption by male	Regular	Not known	1
Use in courtship display	None	May be held in bill by male	1

^a Sources for information on fruits as decorations. 1 = Gilliard 1969, Cooper and Forshaw 1977, and Diamond 1982a; 2 = Schodde 1976 and Diamond 1982b; 3 = Pruett-Jones and Pruett-Jones 1982; 4 = Borgia 1985.

id and often frequent destruction by marauding males (Pruett-Jones and Pruett-Jones 1982). Any behavior that would allow males to spend more time at their bowers (i.e. to be present for females and to protect the bower against intruders) could potentially increase the reproductive success of the male. Considering the low rates of female visitation in this species (Pruett-Jones and Pruett-Jones 1982), it is possible that the primary determinant of mating is related to the amount of time a male can spend in attendance at his bower. Assuming that bower attendance is constrained by foraging needs, there are relatively few ways a male could extend his attendance time. He might 1) make shorter foraging trips or forage only within sight of the bower, 2) place his bower near quality foraging areas, or 3) cache fruit. We do not know the extent to which males attempt the first two options, but given the temporally and spatially unpredictable fruit resources that exist on Mt. Missim (Beehler 1983, Pratt 1983), fruit caching may be the only option open to a male. We do not know exactly when males eat the stored fruit in relation to their foraging trips or the times females or other males visit their bowers. However, our findings show that bower attendance by males and rates of visitation are greatest during the morning hours, corresponding to the period of greatest use of cached fruit.

Other species in which food storing has been studied appear to depend more directly on the stored food for winter survival or for the provisioning of young (Smith and Reichman 1984). This is not the case in MacGregor's Bowerbird. Males do not cache fruit during the

nonbreeding season, and females do not cache fruit or take the fruit cached by males to feed young. Determining whether the use of cached fruit increases long-term survival of males requires further study. We have not yet assessed the males' daily energy requirements or what fraction of it is met by utilization of cached fruit. At bower C, with the greatest number of cache sites, the male took an average of 8.6 fruits/day. While small, this number might potentially reduce stress to the male. Additionally, the male is taking advantage of this number of fruits daily for up to 6 months, a cumulative effect that might increase survival. If the number of stored fruits eaten by the male would otherwise be normally consumed during foraging trips, then the male's total daily consumption would be the same, and survival probably would be unaffected. If, on the other hand, fruits eaten from cache sites are above some base level eaten by an average male, then survival is likely to be influenced.

It is not known whether other species of bowerbirds cache food. Caching has not been observed in the most thoroughly studied species, the Satin Bowerbird (*Ptilonorhynchus violaceus*), which feeds on a mixed diet of fruit and insects (Donaghey 1981). We suspect that other rain forest bower-building ptilonorhynchids will be shown to store fruit. J. Diamond (pers. comm.) reported food-gathering behavior in the forest species, *A. inoratus*, that may be indicative of caching. Grassland species (*Chlamydera* spp.) may be an exception because of the structure of their habitat and varied diets. Fruit caching by bowerbirds is an area worthy of additional study.

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