THE AUK

A QUARTERLY JOURNAL OF

ORNITHOLOGY

VOL. 82 APRIL, 1965 No. 2

THE ROLE OF SALIVA IN FOOD STORAGE BY THE GRAY JAY

DOUGLAS D. DOW

A PAIR of greatly enlarged mandibular salivary glands has been described in jays of the genus *Perisoreus* (Bock, 1961). Bock postulated that the glands function in coating the tongue with mucus, thus transforming it into a "lime-stick" for probing and extracting seeds from cones or insects from bark crevices. This, he suggested, is the basic adaptation enabling the birds to subsist in the rigorous winters prevailing in the northern coniferous forests, from which most other breeding birds migrate. However, Bock pointed out the lack of observations on the feeding behavior of members of this genus and stressed the fact that his idea of tongue-probing still had to be verified by direct observations.

The purpose of the present study was to examine the feeding behavior of the Gray Jay (*P. canadensis*) and thus attempt to determine the role of saliva.

METHODS

Six Gray Jays, intermediate in characteristics between *P. c. griseus* and *P. c. bicolor*, were netted in the Cascade Mountains of southern British Columbia in the late summer of 1963. During the following winter, I made observations of these birds in an outdoor aviary on the campus of the University of British Columbia in Vancouver. The aviary, $6 \times 8 \times 6$ feet, was located in a sheltered position; the ground was covered with coniferous forest duff, and small deciduous and coniferous trees providing perches and shelter were present at all times. Three small wooden shelves were placed on the walls of the aviary to receive stored food. The staple food consisted of a commercial dog food moistened with water. Birds were regularly given meat and a variety of other foods.

Observations were supplemented with still and motion picture photography. I examined the hyoid apparatus to determine the presence of any structural adaptations for tongue-probing. Two Steller's Jays (*Cyanocitta stelleri*) were introduced into the aviary for several weeks in March and April for the purpose of comparing certain aspects of feeding behavior. More detailed discussions of methodology are included later as necessary.

Tongue-probing as a Possible Method of Obtaining Food

The ability of the captive birds to obtain food by tongue-probing was tested in a controlled artificial situation. A wooden block, 30 × 30 × 4 cm, drilled with a grid of 100 vertical holes each 25/64 inches in diameter, was designed to determine depths from which food could be obtained. The diameter was that at which the closed bill could be inserted to its base. The depth of each hole could be adjusted by means of a wooden plug inserted from the lower end and fastened in position. Cheese was selected as bait because it could easily be pressed into standardized pellets, and the birds had shown a previous preference for it. A single pellet was placed in the bottom of each of the 100 holes, and jays were filmed at 32 frames per second as they attempted to remove pellets from different depths. The birds were deprived of all other food when the apparatus was introduced into the aviary.

No evidence was obtained that the jays could remove food pellets at a distance greater than that at which they could be grasped in the bill. Films showed the pellets being just barely nipped between the ends of the mandibles. The tongue, however, was found to be highly manipulative in moving food from the mandible tips into the mouth.

The only active use of the tongue in normal feeding was observed when birds, deprived of food, foraged about the ground. Then the tongue could be observed darting in and out, exceedingly rapidly, through scarcely separated mandibles. Additionally, when the bird lifted its bill into a horizontal plane, the tongue continued to flicker in and out two or three times before the head was again lowered. This action was filmed at 64 frames per second but the film did not show any particles being picked up by the tongue. When finely crumbled food (commercial soft-billed bird food) was scattered on the ground, the same behavior was observed. It seems likely that such food was being taken into the mouth by the tongue.

Conifers as a Possible Source of Food

A test was designed to compare the responses of the birds to cones and other objects that they might take as potential foods. Various objects were placed on a shelf in the aviary; prior to this time, only food had been placed there, and thus I assumed that the birds would investigate the objects as potential foods. These objects were: branches of Douglas fir (*Pseudotsuga menziesii*) with needles and attached cones, alpine fir (*Abies lasiocarpa*) branches and cones, a log with deep furrowed bark (Douglas fir), a rotted log, and several glass vials. These were presented randomly and each object was presented twice, for 30 minutes immediately following a four-hour period of food deprivation. The glass vials were used as a control to reveal the general curiosity to something that had no food value.

TABLE 1

RESPONSES OF GRAY JAYS TO VARIOUS POTENTIAL "FOOD" OBJECTS

	Control	*Alpine fir cones*	*Douglas fir cones*	*Log with bark*	*Rotted log*
Number of seconds of investigation in 60 minutes	286	240	224	700	1162
$P <$*	–	0.20	0.20	0.001	0.001
Number of pecks in 60 minutes	28	10	24	784	216
$P <$*	–	0.20	0.80	0.001	0.001

* P values are based on Chi-square tests between particular objects and control.

The durations of the visits by each bird to each object were recorded. Visits were counted only if a bird appeared to be investigating the object (i.e., pecking or examining with cocked head). The responses of five birds in the two trials, with respect to number of pecks at each object and time spent investigating it, were used as an index to the birds' interest in the objects as food (Table 1).

Responses to bark-covered and rotted logs were much alike. Birds grasped portions in their bills and wrenched them off with a twist of the head. These parts were nibbled for a short time, then dropped. Pecks at the conifer branches were mostly directed at the cones.

The values obtained were tested for statistical significance by means of Chi-square. As can be seen from Table 1, the responses to Douglas fir and alpine fir cones were not significantly different from those to the control, whereas the responses to bark-covered and rotted logs were significantly greater than those to the control. With none of these four objects was actual feeding observed, but a greater amount of gleaning and searching was obvious with the logs. If the index is a valid measure of interest in an object for its potential as a food, or in connection with food, then it is apparent that logs are more attractive than branches with cones, the latter perhaps not being recognized as food-associated objects. It is possible, however, that a cursory investigation of the cones was sufficient for them to be ignored as possible sources of food, whereas the greater surface area of the logs induced a longer period of examination.

The birds were presented later with some partly open cones of lodgepole pine (*Pinus contorta*) containing visible seeds. After having been deprived of food for several hours, they pecked at the cones but made no attempt to extract the seeds.

STRUCTURE OF THE HYOID APPARATUS

Since no evidence of tongue-probing was noted, the hyoid structure and salivary glands were examined in three frozen specimens obtained about

the same time as the aviary birds were caught. The salivary glands were clearly apparent in the position described by Bock (1961). The exposed portion of the glands ranged in length from 15.2 to 19.8 mm, in width from 5.3 to 7.6 mm, and in depth were slightly greater than 3 mm. The mean weight of four glands removed from two birds was 0.16 g. The glands from a female which died on 27 January were smaller than those described above, being 13.3, 3.4, and 1.7 mm respectively.

Bock (1961: 360) states that "The tongue of these birds is a normal corvid tongue . . . which is completely suitable for tongue-probing." The tongue of the Gray Jay is relatively unspecialized. Those of all specimens examined were frayed at the tip. In two birds the dorsal surface was flat, while in others it was strongly concave due to upturning of the edges. No minute spines or papillae were found on the anterior surface of the tongue; two large lateral papillae extended posteriorly from the back of the tongue, and several smaller papillae were found medial to them. The flickers (*Colaptes*), which are the best known example of birds which feed with a saliva-coated tongue, have the whole dorsal tract plentifully supplied with minute spines to hold mucus (Gardner, 1926: 9). Lucas (1897: 1005) indicated the correlation between protrusibility of the tongue and the relative length of the epibranchials. If this correlation is valid, then the tongue of the Gray Jay can be protruded only very little since the epibranchials are relatively short and no longer than the ceratobranchials. The maximal distance which the tongue was protruded as measured on film was about 3 mm beyond the tip of the mandible.

Therefore, if the Gray Jay does feed by tongue-probing, the major adaptation must be a copious supply of adhesive saliva. The tongue appears to lack morphological adaptations for such a habit, and the distance it can be protruded is very small.

Food Manipulation and Bolus Formation

The high degree of manipulative ability of the Gray Jay's tongue has been mentioned previously. A common part of the feeding behavior of these birds was the oral manipulation of food. Food of any consistency was manipulated: bread, cheese, fruit, meat, dried or moistened dog food, oatmeal, mealworms, suet, etc. Oral manipulation consisted of opening the bill and turning the food over and over with the tongue. Frequently, food was rolled out to the mandible tips then quickly withdrawn (Figure 1, A). Saliva flow must be copious at this time, since oral manipulation resulted in the formation of a pellet or bolus of food thickly covered with saliva (Figure 1, B). When a bolus was composed of crumbled food it was shaped to the contours of the buccal cavity. It was larger and more ellip-

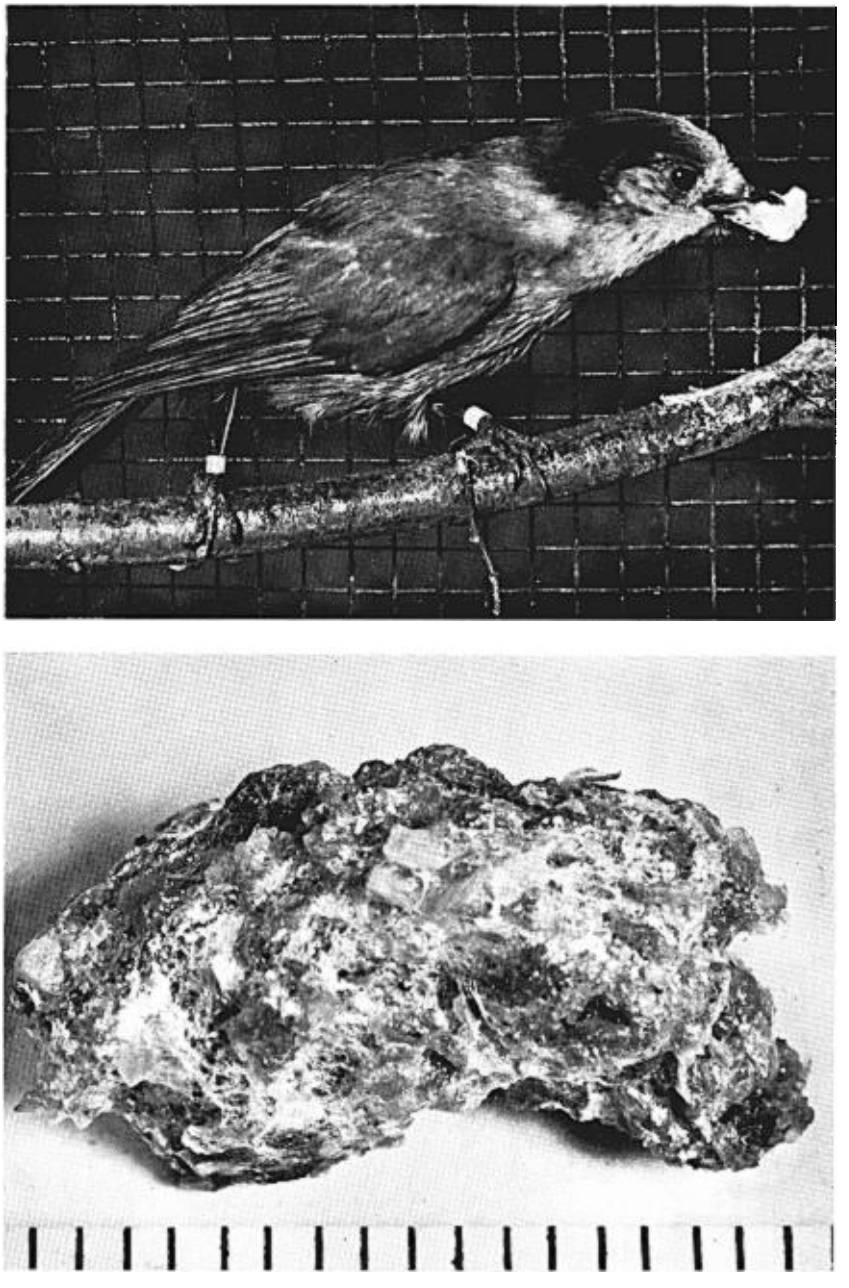

Figure 1. A (upper). Gray Jay manipulating food to form a bolus permeated and covered with saliva. Note the active use of the tongue. B (lower). A typical bolus formed from dry dog food (scale in millimeters).

Figure 2. Boli formed from foods of various consistencies (e.g., suet, cheese, oatmeal, and dog food). The four, darker boli directly below the coin are composed of mouse flesh.

soid when formed from more solid food, such as suet (Figure 2). Occasionally, a bolus was eaten immediately, but more often it was stored. Sometimes a bolus was deposited on the perch where it was grasped with one foot. While held in this position, it was torn apart with the bill, and after each portion had been taken into the mouth, the aggregate was manipulated for some time. This procedure was often repeated a second or third time; the result of such action was the production of a bolus of food, not only coated with saliva but completely permeated by it.

Not only was food actively manipulated; often it was also carried in the throat. In a bird carrying a large amount of food, an obvious distension of the gular region was noticeable, with the feathers of that region tending to stand erect. It is possible for a bird to hold a bolus in the throat while ingesting other food. On a number of occasions, when the birds had been feeding on cheese, mealworms were placed in the aviary. It was common for a bird to bolt down several mealworms and immediately afterwards deposit a bolus of cheese. I do not think that these boli were ever regurgitated from the stomach. (Pellets formed of indigestible matter were regurgitated, as discussed later.)

TABLE 2

ACTIONS OF BIRDS RELATED TO BOLUS FORMATION DURING 30-MINUTE PERIODS

Actions	*Individuals*				
	1	*2*	*3*	*4*	*5*
Number of boli manipulated	36	26	14	14	15
Mean and range of time spent holding or manipulating bolus (in seconds)*	28 (10–41)	46 (15–72)	33 (20–41)	96 (44–390)	50 (38–59)
Percentage of time birds held or manipulated food	56	66	26	75	42

* Times were measured from the moment the bird picked up either fresh food or a bolus (not necessarily its own) until the bolus was deposited.

The length of time that food was held or manipulated in the mouth, as recorded in 85 observations, varied from 10 to 390 seconds (average, 45.3). Table 2 shows the amount of time that each of the five birds was seen holding or manipulating food in periods of 30 minutes of continuous observation of each bird. Cheese was placed in the aviary at the beginning of the 30-minute period; the birds were not deprived of food prior to this time. It was common for a single bolus to be manipulated and deposited many times by one or more birds. In 85 instances of bolus manipulation, only 33 mouthfuls of fresh food were taken; the remaining 52 observations involved boli which had been "remouthed." Frequently, a bolus formed by one bird and deposited on a branch or dropped to the ground was picked up by the same or another bird, manipulated and redeposited. When a bird was observed picking up two boli or mouthfuls of food without having deposited one in the intervening period, I assumed that the first had been eaten, and the manipulation time was measured to the last time the food had been seen.

Although captive Steller's Jays manipulated food, the frequency of occurrence and amount of time spent was considerably less than that for the Gray Jays. Steller's Jays were never observed forming boli. Bock (1961) did not find enlarged salivary glands in the Steller's Jay or in any jay outside the genus *Perisoreus*.

FOOD STORAGE

The storing of food is a widespread habit among the Corvidae (Amadon, 1944). The Gray Jay is no exception. Places utilized for the storage of food in the aviary varied widely; branches, forks of trees, shelves on the walls, and all crevices were used. Most stores were located above the ground, but some birds were seen burying food. In addition to crevices in the aviary structure, the right angle formed by the wall and roof was used

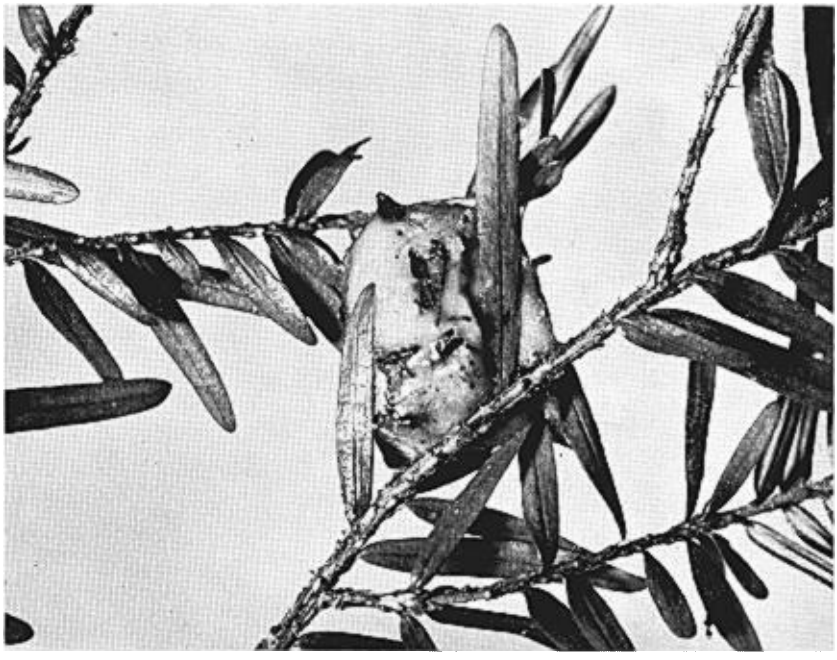

Figure 3. A typical bolus formed from suet, coated with saliva, and stored among the needles of a hemlock. Wild jays store similar boli among needles of spruce, fir, and pine.

often. Food was sometimes attached to vertical wooden supports where it was held only by the adhesiveness of the saliva or food and saliva. On 30 November, jays attached three boli to the flat surface of a vertical wooden post which had been placed in the aviary. I removed this post with the boli attached and placed it outside the aviary in a situation of comparable exposure. The boli were still firmly attached on 12 March, more than three months later.

Usually boli were stored singly, but sometimes a bird formed a small cache and drove other birds away from it. A very common place of storage was among the needles of conifers which were available in the aviary at all times (Figure 3).

No other behavior involving the use of saliva was observed; therefore, I think that the main function of the saliva of the Gray Jay is for the formation of food boli and their subsequent storage.

The general positions of food stored by five birds in 150 minutes (one 30 minute period of observation of each bird) are presented in Table 3. Of all boli formed during this time, 79 per cent were stored. Of the stored

TABLE 3

DISPOSITION OF BOLI*

	Attached to					*Buried in ground*	*Eaten*
	Conifer needles	*Tree crotches*	*Tree branches*	*Storage shelves*	*Aviary walls*		
Number of boli	25	12	6	7	9	8	18
Percentage of boli	29.4	14.1	7.1	8.2	10.6	9.4	21.2

* Based on 85 boli and 150 minutes of observation.

food, 11 per cent was buried, 37 per cent was placed among conifer needles, and the remainder was stored in other locations above the ground.

Four of the Gray Jays were observed burying food. Burying was not confined to any particular type of food, and a bolus was usually, but not always, formed before the food was buried. Most often, buried food was covered with a hemlock cone or, occasionally, with a dead leaf. As a rule, only one object was used in covering; the bird obtained this object by turning and picking it up without moving away from the store. Occasionally, a leaf would be picked up, then dropped, and then another picked up and used. Sometimes three leaves would be picked up and only the last one used. However, when a cone was picked up, it was invariably used. I never observed a bird covering food stored above the ground.

The entire sequence of food burial was highly stereotyped and consisted of the following distinct stages. (1) The bird flew to the ground with a bolus of food in its mouth or throat, or it picked up food while on the ground. Usually, the food was manipulated as the bird hopped about the ground looking for a place to bury it. (2) The bird stopped and, with the bolus in its mouth or throat and the bill closed, formed a hole by inserting the bill to its full length in the ground. (3) The food was pushed into the hole with the tongue. The bill was not extracted from the moment the bird began to dig until the food had been deposited in the cavity. (4) The stored food was covered with a cone or leaf. The sequence from the start of digging until the covering of the store lasted from four to seven seconds. In digging, when the closed bill was probed to its base in the ground litter, the neck usually was stretched forward so that the bill entered the ground at an angle of about 45 degrees. It was uncommon for a jay to insert the bill vertically, and only rarely did one probe at an angle directed toward the feet. The cavity was formed by shuffling the head, i.e., a rapid, alternating movement along the long axis of the bill. The covering material, usually a cone, was held in the open bill, and the covering action involved the same shuffling motion. Sometimes the cone was given a final light peck, but it was never hammered into place. The Gray Jays were never

seen to hammer food or other objects; in fact, captive jays were unable to open sunflower seeds. When food was stored in clumps of conifer needles, similar shuffling motions were observed. It seems, therefore, that basic motor patterns are used in the deposition of food, regardless of whether it is placed among needles or buried in the ground.

Food buried or otherwise stored in the aviary was utilized later. Boli stored above the ground were quickly removed when the birds were deprived of fresh food. After four or five hours of deprivation, birds were most frequently seen foraging on the ground, often five or six together. There was some indication that they associated hemlock cones with food. A bird would hop along the ground frequently stopping to cock its head, pick up a hemlock cone, throw it to one side with a shake, and probe with its bill into the depression in which the cone had lain. This was repeated, and sometimes a store was located. Thus, the general impression was one of a random search beneath hemlock cones which sometimes resulted in the location of food. Most of the probing about the ground was done with the neck slightly extended, and was accompanied by shuffling movements similar to but slower than those used in burying food.

On 3 February I searched the ground adjacent to the wall of the aviary six hours after the removal of all food. I located 16 boli, 10 of which were under cones. I removed these and later saw the birds uncovering more. Sometimes I saw a bird manipulating a bolus consisting of a type of food which had been introduced into the aviary some four or five days before.

Pellet Regurgitation

Gray Jays in the aviary regularly regurgitated pellets of indigestible material. These were frequently found lying about on the ground and apparently were not picked up by other jays (in marked contrast to their response to boli of food). Pellets were regurgitated and held in the bill, then either dropped to the ground or deposited on a branch. These pellets were moist when fresh but quite unlike saliva-covered boli in their composition and shape. Formed mainly of small pieces of chaff-like vegetable fibers from the dog food, they tended towards a spindle shape and ranged in length from 11 to 19 mm and in width from 7 to 9 mm. Also found in them were feathers, wood chips, and the chitinous parts of beetles (*Tenebrio*). Each pellet examined contained from one to three needles of hemlock or Douglas fir.

The first indication that jays ingest conifer needles was a bolus, found on the ground, containing a hemlock needle in its saliva covering. The alimentary tract of a female which died on 27 January contained 10 needles of western hemlock; the stomach contained only a single hemlock needle

and a small bract from a hemlock cone. Some of the needles near the posterior end of the large intestine gave little indication of being much more digested than those at more anterior locations. I think that needles and other objects such as small twigs and perhaps even bracts of cones are ingested inadvertently by these birds when they recover boli of stored food. After the saliva dries and hardens around needles, it would seem unlikely that a bolus could be recovered and eaten without the birds also ingesting some of them (see Figure 3).

Discussion

No evidence was obtained that would suggest that Gray Jays can feed by tongue probing. Jays may pick up small particles of food with the tongue but certainly appear unable to pick up anything as large as a conifer seed. In view of these findings and in the absence of morphological specialization of the hyoid apparatus for such a habit, little importance can be attached to the use of saliva for this purpose. Instead, the primary function of the saliva appears to be to enable members of the species to hoard food efficiently.

In the literature I can find only one reference to the saliva of the Gray Jay. Bendire (1895: 392–393) quotes L. M. Turner as follows: "I obtained a specimen which had the dried bracts of a spruce cone in its beak. This mass was quite large and covered with a viscid saliva. Inspection proved that this substance contained no larvae which could have tempted the bird to swallow the mass through inability to tear it apart."

The oral manipulation of food by these birds was recorded by Simpson (1925), but he did not describe the formation of boli. Warren (1899: 17) states that food fed to young Gray Jays was always in a soft, partially digested state. This probably was due to manipulation and mechanical mixing with saliva rather than to digestion.

The fact that wild Gray Jays form a bolus of food and coat it with saliva was reported to me by Mr. Valerius Geist, of the University of British Columbia, even before I had questioned him on this particular aspect of their behavior. Geist has made considerable observations of the behavior of Gray Jays in northern British Columbia. He states that food regularly is placed in crotches of trees, in crevices of bark, or pushed among needles of alpine fir or Engelmann spruce (*Picea engelmannii*).

In the late summer of 1964 I had an opportunity to observe a pair of Gray Jays for several days as they stored food obtained at my campsite in Algonquin Park, Ontario. Both birds manipulated food and formed saliva-covered boli in a manner similar to that which I have described for captive birds. Boli were stuck to various parts of trees; none was buried. Places of storage ranged from 3 to 15 meters above the ground. Boli were stored

under bark scales and in needle clusters of white pine (*Pinus strobus*), and among needles and against the vertical trunk under horizontal branches of white spruce (*Picea glauca*). Another common place of storage was in the crevices of a lichen (*Physcia*) growing on the upper side of forks in white pine branches. Much of the food was stored within sight of the campsite. Sometimes food was carried away by the jays as they flew over the tree tops and out of sight. I do not know if the food was stored in these cases. On several occasions, I observed jays recovering stored food; however, the length of time that the food had remained in storage could not be determined.

The adaptive value to Gray Jays of using saliva in the formation of food boli and of the adhesion of these boli to various parts of trees is fairly obvious. While the Blue Jay (*Cyanocitta cristata*), Steller's Jay, and European Jay (*Garrulus glandarius*) have been recorded placing food in crotches and about the branches of trees, this would seem to be much less effective, since it must be assumed that food, if left in these positions, would soon be knocked or blown down by rain or wind. The boli of the Gray Jay, on the other hand, are quite securely fixed in position and require forceful extraction after having been there for some time. Both J. L. Brown and J. W. Hardy (pers. comm.), who have made the only extensive studies of the behavior of New World jays, have told me that, although manipulation of food occurs, the formation of boli appears to be entirely absent in the jays which they have studied (*Cyanocitta* and *Aphelocoma*). From my own observations, the manipulative ability of the Gray Jay is much more highly developed than that of the Steller's Jay. Brown (pers. comm.) states that he has never observed a trace of moisture on anything his jays have stored, and he has never seen a food pellet coated with saliva in any species of jay. This is quite in contradistinction to the Gray Jay; a fresh food bolus of this species leaves strands of saliva on the fingers if handled, and the wet glistening saliva usually can be seen on the object from as much as a meter or two away.

The natural food of the Gray Jay has received little investigation. In summer these birds take insects and their eggs as well as a few nestling birds and the seeds and fruit of various plants (Bent, 1946: 8, 31; Jewett *et al.*, 1953: 457). In winter, such foods are undoubtedly scarce. Jays also feed on carrion and pilfer meat or other food which is left exposed about human habitations. Their storage of such food has been mentioned frequently but is poorly documented, the most detailed description being given by Brewster (1937). Geist (pers. comm.) has observed jays feeding on carcasses of big game; it seems likely that wolf kills form a substantial part of their winter diet. Harper (1953) records Gray Jays feeding on a carcass of caribou, and suggests that they may follow wolf packs. They are known

to follow man and immediately partake of his game kills (Baird, 1870: 308; Rand, 1954: 24). R. J. Rutter (pers. comm.), Park Naturalist, says jays utilize deer killed by wolves in Algonquin Park, Ontario, but he does not know from how far they will come to a kill. Is it possible that altitudinal movements and sporadic migrations such as those described by Skinner (1921) and Eifrig (1905) are reflections of movements or population changes of big game mammals?

The method of food storage which I have described is probably mainly adapted to the hoarding of meat taken from carcasses which become available for short periods throughout the winter. Thus, the discovery of a carcass may provide sufficient food to sustain a pair of birds for several days or perhaps weeks. It may be that the storage of food is a critical factor in permitting very early nesting and rearing of young.

I have observed aviary birds forming boli of meat torn from mice or from large bones of fowl. Geist (pers. comm.) has observed meat from carcasses being stored in nearby trees. Thus, a newly found carcass could quickly be torn apart by several birds and food dispersed in nearby trees. Interspecific competition for such dispersed food is probably small; the Boreal Chickadee (*Parus hudsonicus*) would be the most likely competitor among the resident avian species occupying the same range as the Gray Jay.

No work has been done on the social behavior of the Gray Jay. It is territorial during the breeding season and available evidence suggests that it is territorial during the winter, forming aggregations only in areas of continuous food supply (Harper, 1953; Rutter, pers. comm.). According to Mr. A. Blomgren (pers. comm.) of Sweden, the closely related Siberian Jay (*Perisoreus infaustus*) defends a winter territory which is larger than that held during the breeding season.

The general foraging and gleaning behavior of the Gray Jay is probably conducive to the locating of stored food. Birds spend much time going carefully over the branches or clinging to the bark; many authors describe their habits and appearance as having much in common with those of titmice as they search for food. I think that they tend to store food in the same types of places as those in which food is found originally, and are thus successful in locating hoarded food through random searching; the bark, branches, and needles of conifers probably are sources of insect food mainly in summer, but also to some degree in winter.

If hoarding of food is primarily a winter habit, it is possible that the salivary glands may undergo seasonal changes in size or rate of secretion. It is not known whether the saliva contains any elements which might preserve stored food; likely, temperatures in winter are sufficiently low so that this is not a problem.

The fact that captive Gray Jays stored food among conifer needles with the same stereotyped movements that they used in digging, and the fact that the bill was seldom used for hammering are probably related to the small bill, which in turn may reflect the absence of such foods as acorns from the habitat of the species. Most of the New World jays and those of the Old World genus *Garrulus* possess large sturdy bills. All of these birds do much digging and store food by burying it in the ground; their behavior includes the hammering of objects. The Gray Jay's behavior is notably devoid of hammering, and wild Gray Jays have not been recorded burying food. The Gray Jay's habit of storing food above the ground by sticking it to various parts of trees nicely explains how the species can hoard food which can be utilized despite the relatively small bill of these birds.

It seems unlikely to me that the burying of food in the aviary was solely in response to natural cavities provided by the bare ground or resulted only through the adaptable nature of the species. Rather, I think that, in the captive Gray Jays, the stereotyped covering behavior represents the vestigial motor pattern of an action now of little value since food is stored above the ground in a habitat deeply covered with snow much of the year. A stereotyped form of digging behavior and, more important, a covering action is found in similar behavior of other jays such as the European Jay, Blue Jay, Steller's Jay, Scrub Jay (*Aphelocoma coerulescens*), and Mexican Jay (*A. ultramarina*) and is probably indicative of their phylogenetic relationship. The digging and covering pattern of the Gray Jay differs from that of *Aphelocoma* and *Cyanocitta*, which dig and cover with lateral jerks of the bill (Brown, 1963: 141–142). It is closest to the pattern described for the European Jay by Goodwin (1951: 619). The burial of food by wild Gray Jays has never been recorded.

According to Amadon (1944) the jays originated in the Old World and were rather extensively displaced there by the more successful crows and magpies. It seems likely to me that the habit of storing food existed long ago, in the ancestors of present-day old and new world forms. Some of these, which have become successsful in regions of mild winters, have developed the habit of burying food. In *Perisoreus*, on the other hand, the habit of storing food above the ground with the aid of a copious secretion of saliva, selected for by the agency of deep snow cover, may have been the major adaptation enabling the genus to occupy the boreal forests during winter.

ACKNOWLEDGMENTS

I am grateful to Dr. John F. Eisenberg for suggestions and advice throughout this study. Thanks are due to members of the Department of Zoology at the University of British Columbia and others who contributed in many ways. The following people provided me with useful information: J. L. Brown, J. W. Hardy, R. J. Rutter, and

A. Blomgren. I would particularly like to thank Mr. V. Geist for information on the behavior of wild Gray Jays in northern British Columbia. Finally, I thank J. F. Eisenberg and W. J. Bock for reading an earlier draft of this paper.

Summary

The feeding behavior of the Gray Jay was investigated, using captive birds in an aviary. Particular attention was paid to tongue probing as a method of food-getting, to the habit of food storing, and to the function of saliva.

Jays were unable to obtain food from an appropriately designed artificial apparatus by probing with their tongues. Minute food particles may be taken from the substrate into the mouth via the tongue. Some evidence was obtained which suggested that Gray Jays failed to recognize pine and fir cones as potential sources of food.

The greatly enlarged salivary glands described by Bock (1961) were observed. The hyoid apparatus appears to lack structural adaptations for tongue probing.

The tongue was used importantly in oral manipulation of food. This resulted in the formation of boli, permeated with saliva. These boli were then stored, mainly above the ground, and the saliva covering served to fasten them to conifer needles and other parts of trees. Some boli were buried in the ground.

Pellets of indigestible food were regurgitated and conifer needles were found in the alimentary tract of one bird examined. These probably were inadvertently swallowed when boli were being recovered.

The adaptive value of the formation, and adhesion to trees, of food boli seems to be related to the habitat and environment of the species. The habit of storing food above the ground and the copious saliva secretion from the enlarged glands may have been the major adaptations enabling the species to occupy the boreal regions during winter.

Literature Cited

Amadon, D. 1944. The genera of Corvidae and their relationships. Amer. Mus. Novit., no. 1251: 1–21.

Baird, S. F. 1870. Geological survey of California. Ornithology. Vol. 1. Cambridge, Cambridge University Press. 592 pp.

Bendire, C. 1895. Life histories of North American birds. U. S. Natl. Mus., Special Bull. 3, x + 518 pp.

Bent, A. C. 1946. Life histories of North American jays, crows, and titmice. U. S. Natl. Mus., Bull. no. 191: 1–495.

Bock, W. J. 1961. Salivary glands in the Gray Jays (*Perisoreus*). Auk, **78**: 355–365.

Brewster, W. 1937. The birds of the Lake Umbagog region of Maine. Part 3. Bull. Mus. Comp. Zool. Harv., 66: 403–521.

BROWN, J. L. 1963. Social organization and behavior of the Mexican Jay. Condor, **65**: 126–153.

EIFRIG, C. W. G. 1905. An unusual abundance of the Canada Jay (*Perisoreus canadensis*). Auk, **22**: 313.

GARDNER, L. L. 1926. The adaptive modifications and the taxonomic value of the tongue in birds. Proc. U. S. Natl. Mus., **67**: 1–49.

GOODWIN, D. 1951. Some aspects of the behaviour of the jay *Garrulus glandarius*. *Ibis*, **93**: 414–442; 602–625.

HARPER, F. 1953. Birds of the Nueltin Lake expedition, Keewatin, 1947. Amer. Midl. Nat., **49**: 1–116.

JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, AND J. W. ALDRICH. 1953. Birds of Washington state. Seattle, Univ. of Washington Press. 767 pp.

LUCAS, F. A. 1897. The tongues of birds. Rept. U. S. Natl. Mus. [for 1894–1895]: 1003–1020.

RAND, A. L. 1954. Social feeding behavior of birds. Fieldiana: Zoology, **36**: 1–71.

SIMPSON, G. B. 1925. Oregon jays. Canadian Field Nat., **39**: 29–30.

SKINNER, M. P. 1921. Notes on the Rocky Mountain jay in the Yellowstone National Park. Condor, **23**: 147–151.

WARREN, O. B. 1899. A chapter in the life of the Canada Jay. Auk, **16**: 12–19.

Department of Zoology, University of British Columbia, Vancouver 8, British Columbia, Canada. Present address: Department of Zoology, University of Western Ontario, London, Ontario, Canada.