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Instinctive and intentional food storage by animals and man

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It was assumed that during the neolithic period (e.g. $\approx 6000-3000$ B.C. in predynastic Egypt) man has observed and copied the inborn behaviour of food storage displayed by certain animals including some species of ants, beetles, birds and rodents. The subterraneous stores of dung ball-rolling Scarabaeinae and dung-collecting Coprinae as well as the tree granaries of acorn woodpeckers (*Melanerpes formicivorus*) are impressive examples of instinctive storage behaviour performed by the adult animals.

Ancient literary sources, e.g. the biblical books of Genesis and Proverbs referring to Jacob's son Joseph ($\approx 17^{th}$ -16th century B.C.) and king Solomon ($\approx 10^{th}$ century B.C.) as well as the Greek author Aisopos ($\approx 6^{th}$ century B.C.) advocated the philosophy of storage and thrift, in order to prevent human misery resulting from failing harvests and human idleness.

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1. Introduction

Man has occasionally declared himself as the inventor of food storage and elaborate granaries (e.g. in archaic Egypt, ≈3050-2613 B.C.) ensuring the continuous availability of food reserves and seed supplies in relatively dry and hot regions (Levinson & Levinson 1985). It seems, however, that *Homo sapiens* has merely copied the inborn behaviour patterns of various food-storing species of insects, birds and mammals.

2. Food storage by insects, birds and mammals

It is well known that considerable food stores are kept by certain insect species pertaining to the nestbuilding Apidae, Formicidae, Termitidae and Scarabaeidae. Underground seed storage by harvesting ant species including *Messor avenarius*, *Messor barbarus*, *Messor structor* and *Pheidole providens* as well as underground storage of mammalian excrements by the subsocial species of dung ball rollers (Scarabaeinae) and dung collectors (Coprinae) reveal the ardent care of these insects for their food reserves. Some species of *Messor* gather seeds for storage from both plants and ground, remove the seed husks and discard them outside the nest; eventually they bite off the radicle, in order to prevent seed germination. Moreover, those ants carry moist seeds out of their nest, expose them to the sun-rays and return the dried seeds to the granary of their nest (Moggridge 1873).

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Remarkably enough, food-storing vertebrates mainly occur among mammals and birds, while amphibian, fish and reptile species do not seem to maintain food reserves. Most of the food-storing mammals are seed-consuming rodents: hamsters, gerbils (Cricetidae), flying and ground squirrels (Sciuridae) keep their seed reserves in hiding-places, whereas bark- and leaf-feeding beavers (Castoridae) maintain underwater stores of tree branches. Foxes and wolves (Canidae) bury their food reserves (mainly vertebrate flesh and bird's eggs), while the predatory moles (Talpidae) store up numerous immobilized earthworms and insect larvae in their subterraneous magazines.

Several species of crows (*Corvus*), jays (*Garrulus*), magpies (*Pica*), nutcrackers (*Nucifraga*), tits and chickadees (*Parus*) as well as woodpeckers (Picidae) reveal a marked instinct (= inborn behaviour pattern occurring in response to certain external stimuli) of storing seeds and nuts; they usually hide these nutrient resources in bark crevices, under lichens, among needles of pine trees, or in the soil, in order to overcome periods of food scarcity.

2.1. Dung storage by the Sacred scarab beetle

A unique way of providing an insect species with food reserves has been adopted by the scarab beetle *Scarabaeus (Ateuchus) sacer* [Linné 1758] as well as some other Scarabaeinae and Coprinae (Lamellicornia, Coleoptera). The dung ball rollers (Scarabaeinae) employ their cephalic and tibial protrusions of the forelegs as digging and raking tools for gathering recently deposited ruminant excrements, shape the latter mainly by their mid- and hindlegs into compact dung balls (diam. \approx 4-5 cm) and roll them backwards to distant subterraneous and self-made nests (Fig. 1a, b). On the other hand, the dung collectors (Coprinae) stock masses of recently deposited ruminant excrements in underground burrows which they dig beneath dung heaps dropped by pasture animals.

The dung mass, comprising animal excrements, intestinal microorganisms and water, provides male and female scarab beetles (Scarabaeinae and Coprinae) with nutrients being essential for mating and reproduction. The females care for their offspring by converting the dung mass into compact pearlike structures serving as a shelter for the preimaginal stages and pharate adults as well as providing an ample food store to the growing larvae (Fabre 1897, 1899, Halffter & Matthews 1966, Halffter & Edmonds 1982).

The ancient Egyptians were attentive observers of animal life in the Nile valley and certainly noticed scarab beetles rolling their dung balls across the ground (Fig. 1a). The scholars of that time interpreted the above activity as an explanation of the sun's circuit from east to west. The sun-god Khepri was thus aptly manifest in the Sacred scarab beetle, and was believed to move the sun-disc in his journey from the Underworld across the sky. Moreover, the sun-god's name Khepri (= he who is coming into existence) had been first mentioned in the Pyramid texts of the fifth Dynasty (≈2465-2323 B.C.). The early Egyptians would have seen scarab beetles "emerging spontaneously" from dung balls (Fig. 1c) and imagined this chthonic beetle as a form of the creator-god Atum, who was self-produced without previous parental mating and postembryonic development (Levinson & Levinson 1996).

2.2. Nut storage by the acorn woodpecker

Melanerpes (Balanosphyra) formicivorus [Swainson, 1827] is a cooperatively breeding woodpecker and passionate acorn-storing bird occurring in several races which are resident in California, western Mexico, central America and northern Colombia (Fig. 2). Although this species is primarily feeding on insects (mainly Hymenoptera and Coleoptera), it has a pronounced predilection for acorns of several *Quercus* species such as *agrifolia, chrysolepis, douglasii, kelloggii* and *lobata* (Koenig & Mumme 1987). *Melanerpes formicivorus bairdi* [Ridgway, 1881] drills countless peck-holes into the bark layer of various trees including *Ficus, Pinus, Pseudotsuga, Quercus* and *Sequoia* storing there acorns and accasionally some other seeds and fruits, e.g. almonds, dates, eucalyptus, hazelnuts, maize, pecans and walnuts (Ritter 1929, 1938). The acorn woodpecker's instinct of storing is so dominant that the bird will peck holes also in timber structures including gables, cornices and telephone poles and fill them with inedible objects (e.g. pebbles of different size), whenever acorns are missing. Acorn woodpeckers usually feed on immature oak fruits as long as green acorns are available on the trees (mainly in late summer and early autumn), store mature acorns mainly in late autumn, while they feed on aged









Fig. 1a-c. Dung balls serving as food reserves for the scarab beetle *Scarabaeus (Ateucluus) sacer* [Linnaeus, 1758'] and their mythical significance in ancient Egypt. a. The two scarab beetles depicted in the background of the drawing are shaping their dung balls by adding more ruminant excrements, thus enlarging the balls and smoothing out their surface. The scarab beetle evident behind the larger dung ball (diam. \approx 4.4 cm) lowers the head and raises his abdomen while moving the dung ball in backward direction. An additional scarab beetle attempts to steal the larger dung ball from his conspecific. – Drawn by R. Oeffinger (1908). b. Following transportation of the dung ball to a distant underground nest, the scarab

beetle will ingest his compressed food reserves. Consumption of several dung balls is required to gain the capability of mating and reproduction in both sexes of *Scarabaeus sacer*. Subsequently, the fertile female lays a single egg into the neck-like projection of the brood-pear (not depicted), wherein the larva will grow, pupate and develop to an adult scarab beetle, subsequently penetrating the brood-pear and flying off. – Drawn by R. Oeffinger (1908). c. The early Egyptians imagined a scarab beetle, leaving the dung ball (called n w t) to be the sun-god at dawn (on the eastern horizon) and named him Khepri, i.e. literally: he who came into being. Solar resurrection was thus represented by Khepri as a scarab beetle emerging from his dung ball and unfolding his wings. As evident, the scarab beetle is pushing by his foreleg a small solar disc symbolizing the rising sun. Source: Wall painting in the Theban sarcophagus chamber of king Ramses VI (≈1151-1143 B.C.) as well as Book of the Earth, 3rd part, 11th scene (Hornung 1972, 1988).

(brownish) acorns of their tree granaries throughout winter (until the supply is exhausted).

Acorn woodpeckers insert their acorns into peck-holes of suitable size and push them well below bark level (Fig. 3b), first inserting the narrow tip of the fruit, while its broad base is facing the bird's bill. Acorns being deeply immersed to the holes of a tree granary are fairly well protected against pilferage by various species of birds and rodents (Ritter 1929, 1938). Some cooperative groups of *Melanerpes formicivorus bairdi* are capable of storing unusually large amounts of acorns within two or more years (Figs. 3a-c, Gunn 1972). Ritter (1929, 1938) reported that approximately 50000 acorns were found inserted in a large yellow pine and about 20000 acorns embedded in an old sycamore. Since the peck-holes of acorn woodpeckers rarely penetrate the cambial layer, it is improbable that tree granaries will have harmful implications on the host trees.

Acorns collected from tree granaries of *Melanerpes formicivorus bairdi* were found to comprise approximately 3.9-7.1 % protein, 5.6-26.5 % lipids, 12.6-17.4 % carbohydrates as well as 0.37-0.46 % of soluble tannins (based on dry weight of oak fruits). It follows that acorns represent an adequate source of nutrients, except for the soluble tannins which could bind to dietary proteins and thus reduce the

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Fig. 2. The acorn woodpecker *Melanerpes formicivorus formicivorus* [Swainson, 1827]. The male bird (length \approx 20-24 cm) is provided with a scarlet cap, whitish forehead and yellow throat, black orbitals, auriculars, nasal tufts and chin, whitish eyes, glossy greenish-black dorsum, glossy blackish forebreast, whitish/black-streaked hindbreast, a whitish ventrum as well as four toes on each leg. During flight, a white wing patch becomes bilaterally evident. The picturesque bird has a strong bill being adapted for puncturing the bark of forest trees (mainly oaks and pines) and storing therein acorns, other fruits and seeds (see also Fig. 3a, b). Male *Melanerpes formicivorus formicivorus* in dorsal (d), ventral (v) and lateral view (l). (Collection Dalmas 09.4142, Mexique Sciama, 1896 – ZSM).

digestibility of the latter by proteolytic enzymes (Koenig & Mumme 1987). On the other hand, the woodpecker's ability to tolerate dietary acorn tannins suggests the bird's adaptation to the latter, which may be related to a high pH level in the intestine and/or due to other means of tannin detoxification.



Fig. 3a-c. Tree granary established by cooperatively breeding *Melanerpes formicivorus bairdi* [Ridgway, 1881] in a Californian forest. **a.** Partial view of the trunk revealing numerous peck-holes which were drilled into the bark by the woodpecker's bill. The majority of the holes were filled with aged (brownish) acorns, while some of the pits were provided with seeds and nuts of different size (modified from Gunn 1972). **b.** Small region of the above tree granary (magnified ≈10 fold) showing smaller and larger acorns, driven into the holes until the acorn base is countersunk below bark level. The trees are scarcely harmed by the acorn woodpeckers, because their punctures in the bark fail to injure the cambium. **c.** Female *Melanerpes formicivorus bairdi* (\approx ½ of natural size) displays a transverse black band on her head which is lacking in the male. The flying acorn woodpecker (left corner) reveals the characteristic whitish rump and wing bands. The species feeds on insects mainly during spring and summer, while it stores acorns as well as other fruits and seeds in late autumn, consuming the latter mainly in winter.

3. Philosophy of food storage in antiquity

It is conceivable that "the philosophy of storing food in time, in order to provide sustenance for periods of lack" was derived from some striking events recorded in the books GENESIS and PROVERBS of the Bible. Jacob's son Joseph was superintendent of food supplies in ancient Egypt probably during the Hyksos' rule (\approx 1640-1530 B.C.) and took the following measures to prevent starvation of the population in a period of severe drought:

"They should collect all food produced in the good years that are coming and put the grain under Pharao's control as a store of food to be kept in the towns. This food will be a reserve for the country against the seven years of famine which will come on Egypt, and so the country will not be devastated by the famine." (Genesis **41**: 35-36).

"During the seven years of plenty when there were abundant harvests, Joseph gathered all the food produced in Egypt then and stored it in the towns, putting in each the food from the surrounding country. He stored the grain in huge quantities; it was like the sand of the sea, so much that he stopped measuring: it was beyond all measure." (Genesis **41**: 47-49).

"When the whole land was in the grip of famine, Joseph opened all the granaries and sold grain to the Egyptians, for the famine was severe." (Genesis **41**: 56).

The biblical Proverbs ascribed to king Solomon ($\approx 10^{th}$ century B.C.), comprise 31 chapters showing the way to righteousness and wisdom of mankind. Chapter 6 of the Proverbs condemns an easy-going, futile life and praises the dilligence and seed-storing habit of the harvesting ants:

"Go to the ant, you sluggard, observe her ways and gain wisdom. She has no prince, no governor or ruler; but in summer she gathers in her store of food and lays in her supplies at harvest. How long, you sluggard, will you lie abed? When will you rouse yourself from sleep?" (Proverbs 6: 6-9).

It is likely that king Solomon's exhortative proverb made a lasting impression on philosophers and writers of classical antiquity. The Greek author Aisopos (6th century B.C.) expressed the same idea in his parable concerning the ant and the cicada: "Store seeds for the future whenever you can and never mind entertaining the travellers." It is worth recalling that a modified version of Aisopos's parable is still in use at present: "Save up reserves in time and you will overcome periods of want." (Gerr 1997).

4. Epilogue

In his attempts to develop measures of large-scale food storage, man has repeatedly tried to copy and improve the foraging and storing behaviour of certain animals. In this respect, the food-preserving behaviour patterns of several insect, bird and mammalian species were certainly useful guidelines for the inexperienced farmers of the neolithic period ($\approx 6000-3000$ B.C.). Finally one ought to pay homage to the food-storing animals mentioned in this communication for the invaluable lesson they have taught mankind at the dawn of civilization.

Zusammenfassung

Homo sapiens bezeichnete sich gelegentlich als Erfinder der Lebensmittelspeicherung im Altertum (die beispielsweise im frühdynastischen Ägypten zwischen 3050 und 2613 v. Chr. begann), während er eigentlich nur das angeborene Verhalten der Nahrungsspeicherung bei manchen Tierarten nachahmte. Man kann annehmen, daß die primitiven Bauern des Neolithikums (beispielsweise im Niltal ≈ 6000-3000 v. Chr.) die Anlage relativ geräumiger und gut gehaltener Nahrungsspeicher mancher Ameisen-, Käfer-, Vogel- und Nagetierarten beobachtet und nachgebildet haben. Die unterirdisch angelegten Speicher der Dungkugel-rollenden Scarabaeinae (Abb. 1a-c) bzw. Dung-eintragenden Coprinae sowie die – in Baumstämmen angelegten – Speicher der Eichelspechte *Melanerpes formicivorus* [Swainson] (Abb. 2 sowie Abb. 3a-c) wurden als repräsentative Beispiele besprochen.

Die biblischen Bücher Genesis (41: 35-36, 47-49 sowie 56) bezüglich Joseph, Vorsteher der Nahrungsspeicher Ägyptens (\approx 17.-16. Jh. v. Chr.), und Sprüche (6: 6-9), die dem weisen König Salomo (\approx 10. Jh. v. Chr.) zugeschrieben wurden, sowie die belehrenden Fabeln des griechischen Dichters Aisopos (\approx 6. Jh. v. Chr.) befürworten eine Philosophie der Sparsamkeit und Nahrungsspeicherung, damit die katastrophalen Folgen von Dürre und Mißernten nicht in Hungersnot und Müßiggang ausarten können.

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