6 ℓ of water a day: of that, 5.5 ℓ are reabsorbed in the kidney, 0.3 ℓ are reabsorbed by the ceca, 0.1 ℓ by the colon and cloaca, and 0.1 ℓ is excreted.

Under periods of unusual water stress when even the above solutions may not be adequate to ensure water balance, birds have other safety valves to which they can resort. Just as heat stressed birds allow their body temperatures to exceed a lethal level while keeping the head cool, water-stressed birds may be able to withstand periods where they tolerate higher osmotic concentrations of the plasma than normal. The Savannah Sparrow, for example, can tolerate serum concentrations as high as 610 milliosmoles per liter (normal values for birds are 300–350 mOsm/ℓ) (Skadhauge 1981). Reduction of cutaneous evaporative loss during dehydration and high ambient temperatures has been documented but the mechanism by which this is achieved is not well understood. Behavioral adjustments such as reduced activity and avoidance of high ambient temperatures help reduce respiratory evaporative water loss. For example, the respiratory water loss of a Budgerigar (*Melopsittacus undulatus*) during moderate activity is 150 mg per hour, while at rest it is only 44 mg per hour (Phillips et al. 1985).

Using a combination of these physiological, behavioral, and anatomical adjustments to water restriction, birds have successfully colonized xeric environments. Several species, such as the Black-throated Sparrow (*Amphispiza bilineata*) of the North American desert, have even become totally independent of free water.

FOOD STORAGE

While many mammals take advantage of seasonal resource variation by storing food for later use, this behavior has, until recently, been known for only a few exceptional species of birds. Recent studies, however, have shown that some form of food storage occurs more commonly in bird species, and new examples of species that store food are discovered each year. The classic cases of food storage occur in the Corvidae (the crows, jays, magpies, and nutcrackers) and the Picidae (woodpeckers); recent work has uncovered rather complex food-storage behaviors in the titmice (Paridae) and nuthatches (Sittidae).

Food storage is an attempt by a bird to save resources that are periodically superabundant for use when natural availability of that resource is limited. The time scales involved range from the storage of a daily excess for the next day to storage systems lasting years. Many bird foods do not lend themselves to storage for long periods; fruits and insects decay within short periods of time, as does the prey of carnivores. Only a few carnivore species have been observed storing prey for a day or two. Noteworthy among these are the shrikes (Laniidae), also known as butcher-birds for their habit of impaling extra prey on thorns or barbed-wire. In contrast, seeds have basically evolved to be dormant for some period of time, in many cases a year or more. This presents many options for a foraging bird. On a seasonal basis, seeds may be stored in the fall for use in the winter when they would either be in short supply or inaccessible due to snow cover. Gray Jays (*Perisoreus canadensis*) stick seeds to tree trunks with saliva, supposedly to keep them accessible following snowfall. Acorn Woodpeckers (*Melanerpes formicivorus*) store acorns and other seeds in small holes they have specially excavated for this purpose (Fig. 9-10). These "larders" or granaries are then used to feed the birds through the cold winter months and may also be used to feed the nestlings produced the following summer. Less sophisticated storage techniques employ natural cavities or crannies and crevices in branches and bark, while some species even store seeds in the ground.

Figure 9-10 Portion of a larder or granary tree built and used by Acorn Woodpeckers (*Melanerpes formicivorous*) for storing acorns and other hard seeds. (Photograph courtesy of Peter Stacey.)

Other species that store seeds may be responding to even longer term variation in food supply. Some oaks and pines produce seeds every two years or so, but usually they then produce massive crops. Pinyon Jays (*Gymnorhinus cyanocephalus*), nutcrackers (*Nucifraga* spp.), and other food-storing species are able to store large numbers of these food items. It has been suggested by some that this interaction is mutualistic, one in which both species benefit. The birds serve the trees as specially adapted seed dispersers that actually bury seeds in favorable habitats and fail to recover them all, while the trees provide the birds easy access to high-quality food sources. The occurrence of periods of high resource availability (mast years) ensures that there will be more seed than the seed eaters can eat, so that much of the seed will be stored (buried) and not later recovered. The alternative strategy of production of equal amounts of seeds each year would likely result in larger bird populations that would recover a high proportion of stored seeds. This would not result in the seed dispersion favorable to the tree. In the latter case, the bird would be considered a seed predator, as it would be destroying all the seeds. Only if more seeds are dispersed than recovered does the relationship constitute mutualism.

One of the best studied of these interactions between a seed-eating bird and a seed-producing tree is that between the Clark's Nutcracker (*Nucifraga columbiana*) and the Pinyon Pine (*Pinus edulis*) (Table 9-2). In this case, many characteristics of both bird and tree suggest a mutualistic relationship. The pine

TABLE 9-2

Characteristics of bird and pine that favor a mutualistic system such as that of the Clark's Nutcracker and Pinyon Pine, compared to birds and trees with more typical seed predator systems

	Eat seed for immediate energy	*Cache seed for later use*
Bird		
1. Size	Small	Large
2. Energy state	Negative to neutral	Positive
3. Relative longevity	Short	Long
4. Residence status	Migratory-transient	Permanent
5. Ability to find hidden food	Poor	Good
Environment		
1. Predictability	High	Low
2. Harshness	Mild	Severe
Seed		
1. Amount	Rare	Abundant
2. Ease of obtaining	Difficult	Easy
3. Ease of concealing	Difficult	Easy
4. Size	Small	Large
5. Permanence of uncached food	High	Low
6. Permanence of cached food	Perishable	Stable

Source: From Balda 1980.

produces seeds that are large but not winged (thus they cannot be easily wind-dispersed), have rather thin seed coats, and are displayed in upright cones without sharp scales (in contrast to most pines where the seeds are protected within scaly cones that hang downward to aid in wind dispersal). Pinyon Pine seeds are relatively large, which attracts the birds, and fertile seeds are readily distinguished from infertile seeds (which increases the seed disperser's efficiency). While wind dispersed pine seeds are usually all released at once to reduce the effects of seed predators, Pinyon Pine release their seeds over several months, which ensures maximum dispersal. As stated above, though, these periods of seed production occur only every few years; in the Pinyon Pine it appears that bumper crops appear every six years, with somewhat smaller crops in intervening years.

What does the Pinyon Pine get in return? It has been estimated that a typical Clark's Nutcracker will cache (store) 22,000–33,000 Pinyon Pine seeds during the production of a seed crop. Yet, each nutcracker needs to recover only about 850 of these to survive through a typical winter. Quite obviously, the pine is getting a vast number of seeds dispersed and planted by the nutcrackers.

For doing all this work, the nutcracker has access to a very nutritious food that many species cannot harvest. As long as it can remember where it has hidden the seeds, it has easy access to food for a long period of time. This food is nutritious enough that it allows the nutcrackers to breed early in the spring, before other foods are available. It also is nutritious enough that it comprises a substantial proportion of the diet fed to the young, an unusual trait among seed-eating species. Pinyon Jays actually will breed in the autumn during seed crop years, apparently cueing in on the presence of green seed cones.

For food storage to be a successful strategy, the bird must be able to remember where it has put the food. Recent studies have examined the ability of birds to remember where they have stored food items. Early workers thought that birds did not recall particular storage sites but that food storage involved placing food items in locations where they would be found through normal foraging later on. Storage, therefore, did not involve any great capacity for memory of locations. Recent studies, however, show that birds have a highly developed capacity to remember exact locations where they have stored food items. Laboratory experiments by Russell Balda and his students (Kamil and Balda 1985) with jays and nutcrackers show that they can remember a large number of exact locations for many months. In his experiments, jays and nutcrackers stored seeds in a special grid of sand-filled cups within a laboratory room, then were kept away from that room for a lengthy period. When birds were released to find this food, they did amazingly well, even after several months. Graduate students presented with the same situation did much more poorly than the birds! In studies of wild chickadees, observers watched individuals store food items, then moved them. In many cases, a bird did not find a food item moved just a few inches, presumably because it had such an exact recall of where the seed was stored. These studies have suggested that a chickadee may be able to recall up to 300 exact locations where it has stored seeds.

We have already suggested that patchily abundant food supplies often favor group foraging. Such is often the case with seed-bearing trees, and food storage may enhance this tendency towards sociality. This is particularly true when the food is stored in a special location like the granary trees of Acorn Woodpeckers. Several of the jay species associated with mast crops have unusual group-breeding social systems, which is due at least partly to this interaction with their food supply. Pinyon Jays are able to feed their young Pinyon Pine seeds. Groups store seeds, then recover them later to feed themselves or young. Young birds may face a decision early in life that favors staying with the group so that it has a chance to share group-stored food and thus survive, even if that means not breeding for several years.

The most unusual social system found among food-storing species is that of the Acorn Woodpecker. The granary trees mentioned above (Fig. 9-10) are often guarded and provisioned by a group of up to 15 birds. These birds all help to ensure that food is saved when it is available, then all are able to use it during food shortages. When the breeding season comes, though, only a few birds breed at a single nest. As we shall discuss in somewhat more detail in Chapter 13, this may be a monogamous pair, or a group with two of one sex and one of the other. Other birds in the group help with the breeding but do not breed themselves. This unusual social system seems to revolve around the constraints put upon this species by its system of food storage and the fact that the holes used to store food take a long time to make.

Many examples of birds that store food have been discovered in recent years, and more will likely appear. The form of storage will vary with the foods available and the characteristics of the birds involved. Long-term mutualisms, like that of the Pinyon Pine and nutcracker, require birds that live long enough to respond to the long-term food cycling. Jays and nutcrackers are large and sufficiently long-lived to be able to adapt to multiyear cycles. Smaller species like chickadees often do not live long enough to adapt to such long cycles; for these species, we may find that seed storage is purely an adaptation of a seed predator taking advantage of a seasonally abundant resource. Plant-animal mutualisms of the sort discussed above should be rare, as should be the occurrence of group-breeding social systems revolving around food storage.

Even though food storage is rare, it exemplifies the range of adaptations birds have evolved to survive in harsh and seasonal environments. Next, we shall look at those species that apparently cannot adjust to a single location through the whole year and have evolved migratory behavior.