

Quick guide

Acorn woodpeckers

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What are acorn woodpeckers?

Acorn woodpeckers are medium-sized birds commonly found in oak woodlands and forests throughout the west coast of the United States, Mexico, Central America, and a few sites in Colombia. They are easily recognized by their distinctive clown-faced plumage (Figure 1) and *waka* greeting calls.

What's so interesting about them?

Acorn woodpeckers exhibit several unique behavioral adaptations. A hallmark behavior is their construction of 'storage trees' or 'granaries' in which they drill hundreds to thousands of small holes used for caching acorns each autumn (Figure 1). Acorn storage holes are typically in dead tissue, either snags, dead limbs, or thick bark, where the acorns are protected from decay and the elements. Although acorns serve as a critical winter food reserve, acorn woodpeckers are primarily insectivorous, hunting for insects

above the canopy or gleaning them from the bark of trees rather than by excavating in wood, as is typical of most other woodpeckers.

What else? Another notable trait is their cooperative breeding system. Cooperative breeding is a mix of social systems in which more than a pair of individuals cooperate to raise young at a nest. Around ~9% of birds, ~3% of mammals, and a few fishes breed cooperatively. As is the case for most cooperative breeders, acorn woodpeckers have 'helpers'. These are young from prior nests that delay dispersal and remain in their natal group, potentially for years, provisioning at subsequent nests rather than dispersing to breed on their own. Unlike some cooperative breeders, however, acorn woodpecker helpers are of both sexes. In addition, about half of acorn woodpecker groups are polygynandrous, meaning that multiple males share reproductive status ('cobreed') with multiple 'joint-nesting' females, all of which contribute to a communal clutch. Cobreeder males are usually brothers or a father and his sons while joint-nesting females are usually sisters or a mother and her daughters. Only a handful of species exhibit a similarly complex mating system.

What causes delayed dispersal and helping? The primary driver of delayed dispersal and group living by young acorn woodpeckers is the difficulty (or 'ecological constraint') of finding a suitable territory. This is because suitable territories require a granary in which to store acorns, tree cavities for nesting and roosting, and suitable habitat that produces a reliable supply of acorns each autumn. At a local scale, sites with a granary and suitable tree cavities are usually occupied by other social groups, making it difficult for young birds to find a territory. They thus make 'the best of a bad job' by delaying dispersal and remaining in their natal group as helpers until they can fill a reproductive vacancy in the population. At a broader scale, the species' distribution along the West Coast of the US is generally limited to areas with at least two oak species. This is likely due to the species' dependence on consistent acorn production. Acorn crops are highly variable and synchronized within, but not across, oak species. The presence of multiple species buffers against total acorn crop failure.

What's the role of kinship? Acorn woodpeckers mate strictly within groups and helpers do not breed within or outside their natal group.



Figure 1. Acorn woodpeckers.

An adult male acorn woodpecker (left), a small section of a granary filled with acorns (middle), and an adult female acorn woodpecker removing an egg laid by her sister from their joint nest (right).



As a result, the young provisioned by helpers are close relatives, often siblings. Groups with helpers raise more young than groups without helpers, and thus helpers gain kin-selected or indirect fitness benefits due to their provisioning of younger siblings. Such benefits do not, however, compensate for the direct fitness benefits they miss out on by not reproducing themselves. Kin selection plays an important role in acorn woodpecker societies but is insufficient to explain delayed dispersal and helping behavior.

How do acorn woodpeckers get to reproduce themselves? Birds achieve breeder status in two main ways: first, when the cobreeders of one sex all die. This creates a reproductive vacancy that is filled following a ‘power struggle’—a contest involving helpers from surrounding groups that may last for days and involve dozens of birds. Helpers from the same social group frequently team together in sibling coalitions to fight at power struggles, as larger coalitions are more likely to succeed. After winning a power struggle, most or all coalition members subsequently remain and cobreed together. This demonstrates that polygynandry is driven, in part, by reproductive competition. That helpers fight for the opportunity to disperse from their natal group also indicates that the fitness benefits of breeding, even when shared with relatives, are greater than those of remaining as a helper.

The second main way young become breeders is by ‘inheriting’ and attaining breeder status in their natal territory. This happens following the filling of a reproductive vacancy of the *opposite* sex by unrelated birds winning a power struggle. Male helpers inherit breeder status after the death and replacement of their mother (and her related cobreeders) by unrelated females, and *vice versa* for female helpers. Following the filling of a reproductive vacancy, inheritors cobreed with their parent and related cobreeders of the same sex, while helpers of the same sex as the reproductive vacancy generally leave or are driven out of the group. This system of inbreeding avoidance

renders incest rare, despite the close relatedness of group members.

Which of these two strategies is more successful? The potential to inherit the natal territory is one benefit of delayed dispersal. However, the fitness of inheritors is not greater than that of young that disperse and breed elsewhere in the population. This is partly because inheritors end up sharing reproduction with a larger coalition of same-sex relatives than dispersers. Although constraints are important drivers of polygynandry, joint-nesting females may achieve higher fitness than females breeding alone. The factors driving polygynandry are complex, involving both ecological constraints and benefits of group living.

What’s the community life of acorn woodpeckers like? All group members jointly provision at nests, harvest and store acorns, and defend the granary from intraspecific and interspecific intruders. Furthermore, the granary is a true communal resource. Any group member can remove and eat acorns stored by any other group member. Nonetheless, there is considerable competition within groups over reproduction. Among joint-nesting females, egg-laying is synchronized by a female removing eggs laid by her cobreeders until she is ready to lay her own eggs (Figure 1). Removed eggs are subsequently eaten by all group members, including the female that laid it. As a result of egg destruction, joint-nesting females share maternity equally within a nest.

Male–male competition consists of closely following the breeder female during her fertile period. Such ‘mate guarding’ only occurs when groups contain multiple cobreeder males, demonstrating that it is driven by within-group competition rather than the threat of extra-group mating. Despite (or maybe because of?) mate guarding, there is high reproductive skew, whereby one cobreeder male will often sire most or all young in a nest. The successful cobreeder male often switches from one nest to the next, however, evening out paternity over the long run among all

cobreeders. Whether this is due to female choice, sperm competition or some other mechanism is unknown, partly because copulations are concealed and rarely observed. Both egg destruction by joint-nesting females and mate guarding by cobreeder males involve close relatives. The eggs destroyed by females, for example, are potential nephews and nieces. Acorn woodpeckers offer a compelling example of how kinship, ecological constraints, and social interactions shape vertebrate social systems.

Where can I find out more?

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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