**Digital Feature Preview | John** 

## Putting Eggs in Many Baskets

Some wood duck hens lay eggs in nests that aren't theirs, while othe stay at home. The behavior isn't s cooperative or a con job. It's comp in the duck social "nestwork."

n April 17, 2016, a one-year-old female wood duck was taking her first steps toward motherhood by exploring nest sites. The tawny bird with white eye rings and iridescent blue wing patches was investigating several artificial nest boxes that our team had erected along a wooded stream near Davis, California. There was nothing unusual here, except that many of these nest boxes were already occupied by other females. That year, this female would go on to make 195 visits to 34 different nest boxes that were already in use, including 30 visits to her favorite box. It turns out that this duck, whom we call by her tag code E9BA0 (or E9 for short), wasn't just exploring her neighborhood. Our genetic studies show she was laying eggs in the nests of other wood duck hens. She laid a total of 12 eggs in four nest boxes, all in a row and just a few boxes down from where she had hatched the year before. What's more, E9 never incubated any of those eggs, relying instead on the nesting females in those boxes to do that.

E9's behavior wasn't entirely surprising. Wood ducks are known to be *conspecific brood parasites*, meaning that they lay eggs in the nests of other birds of their species. The word *parasite* doesn't normally invoke an image of a bird laying an egg in a nest. But this behavior is not so different from a worm in your gut. It potentially takes resources away from the mother who ends up caring for the egg. (That's one hypothesis, anyway.)

We thought initially when we began this work in 2014 that most wood duck hens would incubate their own eggs and



Courtesy of Bruce Lyon

would set up home in one site, whereas a few others might travel around a bit, perhaps laying some eggs parasitically. We completely underestimated the wily wood duck. According to our data, some females visit an incredible number of nest sites, visit many nests repeatedly over an entire breeding season, and frequently lay eggs in other females' nests.

Such was the case with E9, and her sneakiness paid off—10 of her 12 eggs were hatched by the host mothers. E9 returned the following year, and we wondered whether she might settle down, but she did not. Instead, she visited even more boxes (42), never incubated a nest, and again laid 10 eggs parasitically, of which 8 were hatched by the foster mothers.

Sneaking eggs into a neighbor's nest is unusually common in waterfowl. Almost a third of the 256 bird species known to practice conspecific brood parasitism belong to this single family of birds, the Anatidae. Wood ducks, also known as woodies or Carolina ducks, are well known for their parasitic propensity. As early as 1901, Walter B. Sampson reported on "An Exceptional Set of Eggs of the Wood Duck" in the San Joaquin Valley, California, perhaps the first documentation that more than one hen would lay in the same nest at the same time. Subsequent records abound in the ornithological literature, including observations of nests with more than 40 eggs.

As birds go, duck parents have it fairly easy. As soon as the offspring hatch, they are ready to fledge and can feed themselves (*see photo on right*). Female ducks provide a modicum of protection, warmth, and guidance—and that's about it. This relatively light workload makes it possible

for female waterfowl to raise a lot of babies. What has long been a mystery is why a female would risk the investment in her eggs to the care of another female.

As their name aptly implies, wood ducks such as E9 are cavity nesters: They require a tree hole in which to make a nest. Even in a healthy mature forest, cavities large enough to host a 600-gram female and an almost equal mass of eggs are likely at a premium. So, one challenge that hens may avoid through brood parasitism is the need to find an available nesting spot. Faced with the task of finding a vacant nest site, wood ducks may circumvent this limitation by using someone else's.

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Wood ducks' notoriety for laying eggs in one another's nests made them an ideal study animal for exploring questions about this behavior and its evolution. However, we couldn't get details such as those we collected about E9 until recently. Questions that long seemed unanswerable about where the birds go and which eggs end up where can now be addressed. With advances in radio-tracking tags, videography, and genetics, after more than 30 years studying brood parasitism in ducks, we've finally been able to get some answers. What we've found is a complex social network of wood ducks that we are still unraveling, one that defies single explanations for nest parasitism and instead shows that this behavior offers females flexibility to adjust their reproductive investments in the face of changing conditions.

Wood ducks can be aggressive or tolerant about nest sharing. In this video still, one wood duck hen lays an egg on the back of the nest owner, as the two nuzzle. Why these interactions are so variable is not yet known, but the authors and their collaborators are working on an answer. See the full video here: www.amsci.org/node/4891



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sy of Bruce Lyon

## **Why Ducks Parasitize Other Nests**

aying eggs in another female's nest once seemed so unusual and inexplicable that early authors dismissed it as an aberration and referred to it disparagingly as "egg dumping," as though females were simply ridding themselves of excess or unwanted eggs. It was not until 1980 that an influential paper by Yoram Yom-Tov of Hebrew University changed our thinking by considering the behavior from an evolutionary perspective. Yom-Tov and subsequent authors proposed several hypotheses to explain why females might lay eggs in the nest of a nearby neighbor.

Many females do establish a nest of their own, lay their eggs in that nest, and care for their offspring—this behavior is what we might think of as a typical nesting strategy for a bird (*Option A on the facing page*). However, other females are like E9 and lay some or all of their eggs as brood parasites. We wanted to know why this latter behavior might be advantageous enough to evolve in some ducks.

One possibility is that females are constrained from breeding on their own (*Option B*). Perhaps these females cannot compete successfully for a nest, or nest sites are in short supply, as is likely to be the case for a cavity-nesting wood duck. Alternatively, it might not "pay" (in reproductive terms) to nest on one's own, because of physiological stress, lack of experience, or poor body condition. Nonetheless, some reproduction is possible by laying a few eggs parasitically, without having to go all in.

Another possibility (*Option C*) is that females get the best of both worlds. If there is a limit to how many eggs a female can tend in her own nest, laying additional eggs in another hen's nest can increase total reproductive output without having to provide the care for those extra eggs and offspring. (The "gambler" variant of this hypothesis is that females put their eggs into many baskets to hedge their bets against losing all their eggs in a single nest to a predator—a catchy idea that unfortunately does not hold up under mathematical analysis.)

are freed from any parental care duties and instead invest the time and energy saved into making extra eggs or living longer.

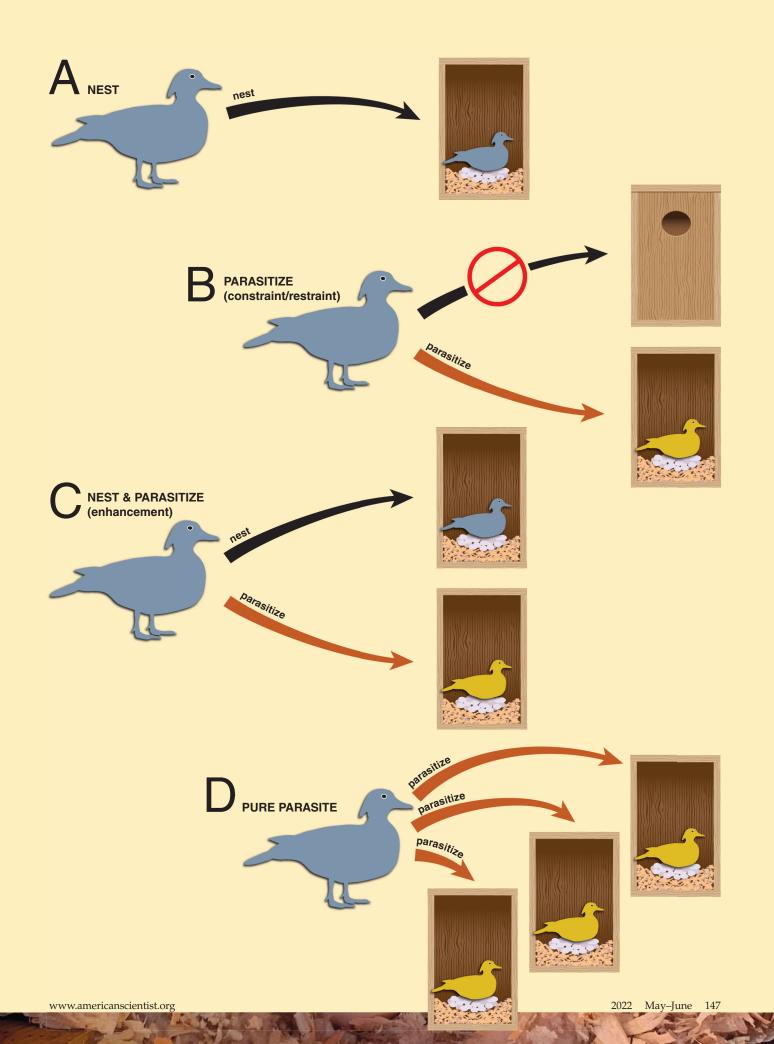
There is one other twist to this story. What seems to be parasitic behavior might actually be a form of cooperation. Cooperative behaviors that are costly on an individual level can evolve if they increase survival and reproduction of relatives that might not have reproduced otherwise (See "Why Some Animals Forgo Reproduction in Complex Societies," July-August 2014.) In many duck species, daughters return to their natal (birth) area to breed, where they can closely interact with their relatives. (In most other species of birds, the male returns to his natal area.) Malte Andersson of the University of Gothenburg in Sweden offered a novel idea to explain why conspecific brood parasitism is disproportionately common in waterfowl: Perhaps it is an interaction among kin, female family members sharing the costs of parental care and enhancing their own evolutionary success through the shared genes they help propagate. This perspective turns the concept of parasitism on its head. Rather than a competitive dynamic, perhaps brood parasitism among females within the same species is instead a form of cooperation between relatives—less a case of parasitism and more one of shared duckling daycare. But if ducks don't just parasitize the nests of their kin, there may be other reasons at play: Perhaps some cost to nesting can be avoided by a female that adopts brood parasitism, either partially or fully.

The challenge we faced was how to test these hypotheses. To study this behavior, we first needed to know which females are the parasites. To do that, we needed to identify the nests females were visiting and how many of those visits resulted in an egg laid.

Read the full online interactive feature

and learn what the authors figured out:





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