



WHEN CHICKENS GO WILD

The feral chickens of Kauai provide a unique opportunity to study what happens when domesticated animals escape and evolve.

BY EWEN CALLAWAY

“Don’t look at them directly,” Rie Henriksen whispers, “otherwise they get suspicious.” The neuroscientist is referring to a dozen or so chickens loitering just a few metres away in the car park of a scenic observation point for Opaekaa Falls on the island of Kauai, Hawaii.

The chickens have every reason to distrust Henriksen and her colleague, evolutionary geneticist Dominic Wright, who have travelled to the island from Linköping University in Sweden armed with traps, drones, thermal cameras and a mobile molecular-biology lab to study the birds.

As the two try to act casual by their rented car, a jet-black hen with splashes of iridescent green feathers pecks its way along a trail of bird feed up

to a device called a goal trap. Wright tugs at a string looped around his big toe and a spring-loaded net snaps over the bird. After a moment of stunned silence, the hen erupts into squawking fury.

Opaekaa Falls, like much of Kauai, is teeming with feral chickens — free-ranging fowl related both to the domestic breeds that lay eggs or produce meat for supermarket shelves and to a more ancestral lineage imported to Hawaii hundreds of years ago.

These modern hybrids inhabit almost every corner of the island, from rugged chasms to KFC car parks. They have clucked their way into local lore and culture and are both beloved and reviled by Kauai’s human occupants. Biologists, however, see in the feral animals an improbable experiment

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A wild rooster in Kauai, Hawaii. in evolution: what happens when chickens go wild?

The process of domestication has moulded animals and their genomes to thrive in human environments. Traits that ensure survival in the wild often give way to qualities that benefit humans, such as docility and fast growth. Feralization looks, on its surface, like domestication in reverse. But closer inspection suggests that the chickens of Kauai are evolving into something quite different from their wild predecessors, gaining some traits that reflect that past, but maintaining others that had been selected by humans. In this way, they are similar to other populations of animals, including dogs, pigs and sheep, that have broken free of captivity and flourished.

By looking at feral animals, some evolutionary biologists hope to determine how domestic animals and their genes change in response to natural pressures. The research could also help to inform tricky conservation questions about how such animals affect native species, and ultimately whether and how to control them.

The natural history of the Kauai fowl makes them an important test case. “People have a really complicated relationship with the chickens,” says Eben Gering, an evolutionary ecologist at Michigan State University’s Kellogg Biological Station in Hickory Corners, who is in Kauai with Henriksen and Wright. “Some people absolutely want them gone. Some consider them an integral part of the local culture.”

FOUL-WEATHER FOWL

The Polynesian mariners who first settled the Hawaiian Islands about 1,000 years ago brought what they needed to start civilization anew. Staple plants such as taro, sweet potato and coconut palm made the trans-Pacific voyage, as did domestic dogs, pigs and, naturally, their prized chickens.

The Polynesian poultry probably bore little resemblance to the birds that provide much of the world’s protein today. Archaeological and genetic evidence suggests that they were more like red junglefowl (*Gallus gallus*) — small, furtive birds that still roam the forests of south-east Asia and are ancestral to all domestic chickens.

By the time that Captain James Cook landed in Waimea in southern Kauai in 1778, the Polynesian chickens had already, in essence, become feral. They wandered freely between Native Hawaiian villages and the neighbouring forest. Later, European and US settlers imported predators such as mongooses, which devastated birds of all kinds. Polynesian chickens were all but wiped out everywhere but Kauai and neighbouring Niihau, where the predators were never introduced.

On Kauai, chickens flourished. Although the birds’ numbers have not been tracked precisely, many residents contend that the population surged after hurricanes in 1982 and 1992 blew modern chickens from people’s back yards into the forests, where they encountered the descendants of the Polynesian chickens.

Gering says it is possible that interbreeding between the two populations allowed the birds’ numbers to swell. And during his first trip to the island in 2013, he and Wright noticed¹ that many of the feral chickens they encountered had flecks of the white feathers common in modern domestic breeds, in addition to the darker plumage usually seen in wild populations. Many had yellow legs (red-junglefowl legs are grey). And some of the roosters’ crows sounded conspicuously like the drawn out cock-a-doodle-doo of their barnyard brethren, rather than the truncated calls of red junglefowl.

DNA from 23 chickens revealed just how far domestic-chicken genes had infiltrated¹. The birds’ nuclear genomes seemed to be a mixture of genes from red-junglefowl-like Polynesian chickens and domestic chickens, whereas their maternally inherited mitochondrial markers traced back to European and Pacific domestic poultry. Gering and Wright think that a single hybrid population of feral chickens now roams Kauai, bearing a mixture of traits from modern and ancient birds.

In unpublished work, the two have scoured the birds’ genomes for stretches of DNA with very little variation across the population. This

homogeneity suggests that a gene has surged through the population in the recent past, probably because it offers some benefit. If feralization were domestication played backwards, then these ‘selective sweeps’ might appear around the DNA sequences that distinguish domestic chickens from red junglefowl. Instead, the researchers have found that most of the swiftest-evolving genes in the Kauai chickens are distinct from those suspected involved in modern domestication.

In some cases, genes from the Polynesian chickens are helping the hybrid feral chickens to adapt to Kauai’s habitats. For example, modern domestic fowl have been bred not to sit on, or brood, their eggs (making the eggs easier to collect). But in the wild, this trait puts unhatched chicks at risk. Wright and Gering found that feral chickens possess red-junglefowl gene variants that are linked to brooding.

But some genes of domestication do seem to be handy outside the coop. A variant linked to increased growth rates and reproduction in domestic chickens, for example, persists in the Kauai population, even though the average adult feral chicken is half the weight of a month-old bird bred for meat.

CHICKEN AND EGG

“You won’t see a bird as healthy-looking as that,” Wright says of the hen that he and Henriksen had captured at Opaekaa Falls. “Her plumage is perfect.” In the basement of a rented house on Kauai, the researchers have set up a makeshift laboratory where they photograph the bird, draw its blood and then kill it and prepare it for dissection. Wright starts with the hen’s Brazil-nut-sized brain.

Their unpublished research has shown that the brains of domestic chickens are smaller than those of junglefowl, relative to their body size, and organized differently. The team hopes to identify the genes responsible for these changes and others, such as the diminished visual-processing systems of domestic birds. Life in the wild has also altered the reproductive systems of the feral chickens. Domestic breeds lay eggs almost daily, but breeding seasonally could allow feral chickens to reapportion the minerals devoted to eggs (which come from spongy

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tissue in the centre of their bones) to making their skeletons more robust. The researchers sample the hen’s femur and also find that its ovaries are empty of egg follicles, which could be a sign of seasonal breeding.

Feralization has garnered much less attention from scientists than domestication (which gets a nod in chapter one of Charles Darwin’s 1859 *On the Origin of Species*). But swapping of domestic and wild genes has been happening all over the world for thousands of years. A feral-sheep population that has lived on the island of St Kilda in the Scottish Outer Hebrides for as long as 4,000 years acquired beneficial alleles that determine coat colour from a modern domestic sheep breed some 150 years ago². A 2009 study in *Science*³ found that some wolves in Yellowstone National Park, Wyoming, carry a domestic-dog version of a gene linked to dark coats that shows hallmarks of positive selection, possibly helping wolves from the Arctic to adapt to forested environments. “People would have thought that genes to live in a farm and house aren’t going to be any good in the wild, but that’s not necessarily true,” says Jonathan Losos, an evolutionary ecologist at Harvard University in Cambridge, Massachusetts.

And like Kauai’s feral chickens, other feral animals such as dingoes in Australia and urban pigeons practically everywhere have not evolved back to the state of their wild ancestors — even if certain traits may trend in that direction.

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To hear more about the chickens of Kauai, visit: go.nature.com/gnh7dj

FREE BIRD

The feral chickens of Kauai, Hawaii, are descendants of birds brought to the island by Polynesian settlers hundreds of years ago, which later mated with more modern domestic breeds. The chickens offer lessons in the genetics of feralization and on which traits tend to revert to a wild-like state.

COMB

Three of the fastest-evolving genes in the Kauai chicken are linked to comb size, a sexually selected trait that is not generally under pressure in domesticated breeds.

REPRODUCTION

Domestic egg-laying chickens do not sit on (or brood) their eggs, a trait selected by humans to make egg-collection simpler. Feral chickens favour gene variants associated with brooding, and the hens seem to lay eggs less frequently than domesticated birds — possibly seasonally.

FEATHERS

The plumage of the Kauai chickens is the most obvious sign of their mixed ancestry. White feathers, sported by many modern domestic breeds, compete with colours common to the red junglefowl (*Gallus gallus*) from which all chickens descend.

SIZE

A gene variant linked to fast growth in domestic breeds persists in the Kauai chickens, yet a full-grown feral chicken is about half the size of a month-old domestic bird bred for meat.



Feral chicken

Domestic chicken

LEGS

Domestic chickens have yellow legs, whereas those of the red junglefowl are grey, owing to variations in a gene called *BCDQ2*. Both yellow- and grey-legged chickens roam Kauai.

WILD TO FERAL

Feralization is not domestication in reverse, even though it can look a bit like it. But feral and domesticated animals are known to breed with wild populations.



WILD → DOMESTICATED → FERAL



NO LOOKING BACK

Domesticated animals have gone feral all over the world. Interbreeding with wild animals can pose interesting questions for geneticists and headaches for conservationists. Human influences on these animals and on the environments they inhabit are probably intertwined, and almost definitely irreversible.



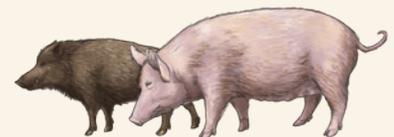
CANINE CONUNDRUM

Genes of domestication can carry advantages. Domestic-dog genes are helping North American wolves to adapt to a world with less tundra. In Yellowstone National Park, Wyoming, some grey wolves carry a dog gene variant linked to darker coats that may be beneficial in forests.



EQUINE EQUIVALENCE

The lines between wild, domestic and feral are fuzzy. Przewalski's horse on the Mongolian steppe has been touted as the last population of truly wild horses. But genome sequencing suggests that the group's ancestors routinely interbred with domestic horses.



SWINE SENSIBILITY

For some traits, domestication seems to be unidirectional. Feral pigs in Sardinia have regained the brain-size proportions and density of neurons involved in olfaction that are found in their wild relatives. But they nevertheless lack a molecule important for wild boars' exquisite sense of smell.

Like chickens, other domesticated animals tend to have smaller brains than their wild cousins, relative to body size (see 'Free bird'). And brain regions involved in processing things such as sight, sound and smell are among the most diminished, perhaps because humans bred animals to be docile and less wary of their surroundings. Feral pigs in Sardinia seem to have regained large brains and high densities of neurons involved in olfaction, but not the abilities that come with them: their neurons do not express a protein that has been linked to the exquisite sense of smell in closely related wild boars⁴. Likewise, feral dogs, cats and pigs often lack the savvy of their wild brethren and still depend on human niches for their survival, notes Melinda Zeder, an archaeologist at the Smithsonian Institution's National Museum of Natural History in Washington DC. Packs of feral dogs, for instance, do not form the complex hierarchies that make wolves such fearsome predators. "There's no leadership the way you get in a wolf pack. It's just a bunch of shitty friends," says Greger Larson, an evolutionary geneticist at the University of Oxford, UK, who is part of a team examining the mixed ancestry of Kauai's feral pigs.

Wright and Henriksen take less than an hour to dissect the captured hen and preserve samples of its brain, bone, liver and other tissue for gene-expression studies. They will use the RNA molecules expressed in different tissues to come up with a list of genes that might influence traits that distinguish the feral chickens from domestic birds and red junglefowl. They are eager to add to their study sample, and they jump at an offer to visit a nearby farm to collect more chickens.

PECKING ORDER

"They are a scourge. They are vermin. They cost us thousands and thousands of dollars every year," says the farm's owner (who asked not to be named). The birds scratch at tree saplings on his orchard, exposing the roots and killing fruit trees before they can mature. He patrols his property in a beaten-up luxury sedan with a high-powered air rifle and a hired hand who gets US\$5 per kill. Every few months, he invites hunters with night-vision goggles to visit and pick off the birds as they roost.

Few Kauaians share his malice towards feral chickens. Many locals give them a 'no-big-deal' shrug when asked. And the island's many tourists tend to view the birds with curiosity followed by mild annoyance after a couple of 3 a.m. wake-up calls. Feral-chicken merchandise — postcards, kitchen chopping boards, T-shirts — are ubiquitous. A popular children's television show hosted by a character called Russell the Rooster has been on air for nearly two decades.

As descendants of the birds imported by the Polynesians, Kauai's feral chickens occupy a zoological purgatory somewhere between native plants and animals and the dreaded invasive species that plague island habitats such as Hawaii. "It's much more complicated than just a feralized chicken," says Gering. "Even though junglefowl were not here before the Polynesians colonized the island, they have been a part of this ecosystem for much longer than the domestic chickens."

The chickens enjoy semi-official protection as 'wild chickens' in nature preserves. But if the same birds wander into developed areas or private property, they are considered 'free-flying domestic chickens' with no sanctuary. "Locals are free to take them (if they come onto your property) and put them in the pot," says a State of Hawaii website. (Gering and Wright, with a freezer full of the animals, consider making 'feral coq au vin'.)

Kauai may have no shortage of feral chickens now, but if mongooses arrive on the island or political winds change, they could be at risk. Hawaii's most populous island, Oahu, has mounted a controversial culling campaign against its feral chickens (whose ancestry is uncertain). But Gering thinks that the Kauai chickens' long tenure and unique cultural position makes some form of conservation worth considering. "Before deciding how important it is conserve them, manage them or cull them, it would be good to at least know about their impact," he says. Researchers want to know about everything from the animals and plants that the birds eat to how they alter landscapes — information that Gering hopes to gather on future trips to the island.

Kauai's chickens are hardly the only creatures to occupy a nebulous space between native and alien. When Przewalski's horses, which live on the Mongolian steppe, were first described in the late nineteenth century, they were believed to be the planet's last wild, undomesticated horses. But a 2015 genome study⁵ found that the 2,100 or so remaining horses carry substantial amounts of domestic-horse DNA. They also show significant signs of inbreeding, owing to a captive-breeding programme begun in the 1940s.

"WHAT FERAL ANIMALS MAKE US DO IS CONSIDER THIS ALL-TOO-EASY DICHOTOMY BETWEEN WILD AND DOMESTIC."

Some conservationists view domestic genes as pollutants that are tarnishing the genomes of wild animals such as wolves, coyotes and even the red junglefowl native to southeast Asia. Some even contend that there are no 'pure' red junglefowl left.

"What feral animals make us do is reconsider this all-too-obvious, all-too-easy and all-too-wrong dichotomy between wild and domestic," says Larson.

And the ability of supposedly wild animals to thrive in a world increasingly altered by human activity may be due in part to the domestic genes that they now carry. What better way to adapt to human-moulded environments than to borrow traits from human-moulded creatures?

HOME TO ROOST

"Cock-a-doodle-doo," announces a rooster masked by dense forest in Kokee State Park, an achingly beautiful nature reserve on Kauai's western coast, on a sunny autumn morning. A faint but unmistakable "cock-a-doodle-doo" volleys back, from maybe a kilometre away.

Although the birds are a fixture even in this rich and remote landscape, most of the chickens in the reserve stick near the car parks and picnic areas, where human hand-outs are easy to come by. The park's birds are among the most brazen and comfortable around humans in all of Kauai, and it's hard to enjoy a meal in Kokee's central meadow without attracting the attention of a flock or two. But "give them a chase and they'll disappear down a 300-metre ravine that's so thick with vegetation it's impossible to follow," says Gering. "That's not something I think about barnyard chickens as being able to do."

A park website discourages visitors from feeding the chickens, in the hope of reducing their numbers and their dependence on humans. This interest in 'rewilding' the feral chickens is probably motivated by the desire to reduce their numbers through methods other than culling. It may well be a matter of time before feral animals fully shed their yokes and evolve into creatures less dependent on humans — but perhaps it will never happen. "The environmental niches that feralized animals are exploiting are very different and bear a human stamp that wasn't there when their ancestors developed," says Zeder. "Why should anyone expect a feralized animal to go out and become the noble savage animal again?"

Wright, however, thinks there is a possibility that if the chickens in Kokee are left alone for long enough, they may well become not a facsimile of their red-junglefowl ancestors, but some other kind of creature just as deserving of being called wild. Whatever wild means. ■

Ewen Callaway writes for Nature from London.

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