More Fun Than Fun: What Can Coucals Teach Us About Parental Care?

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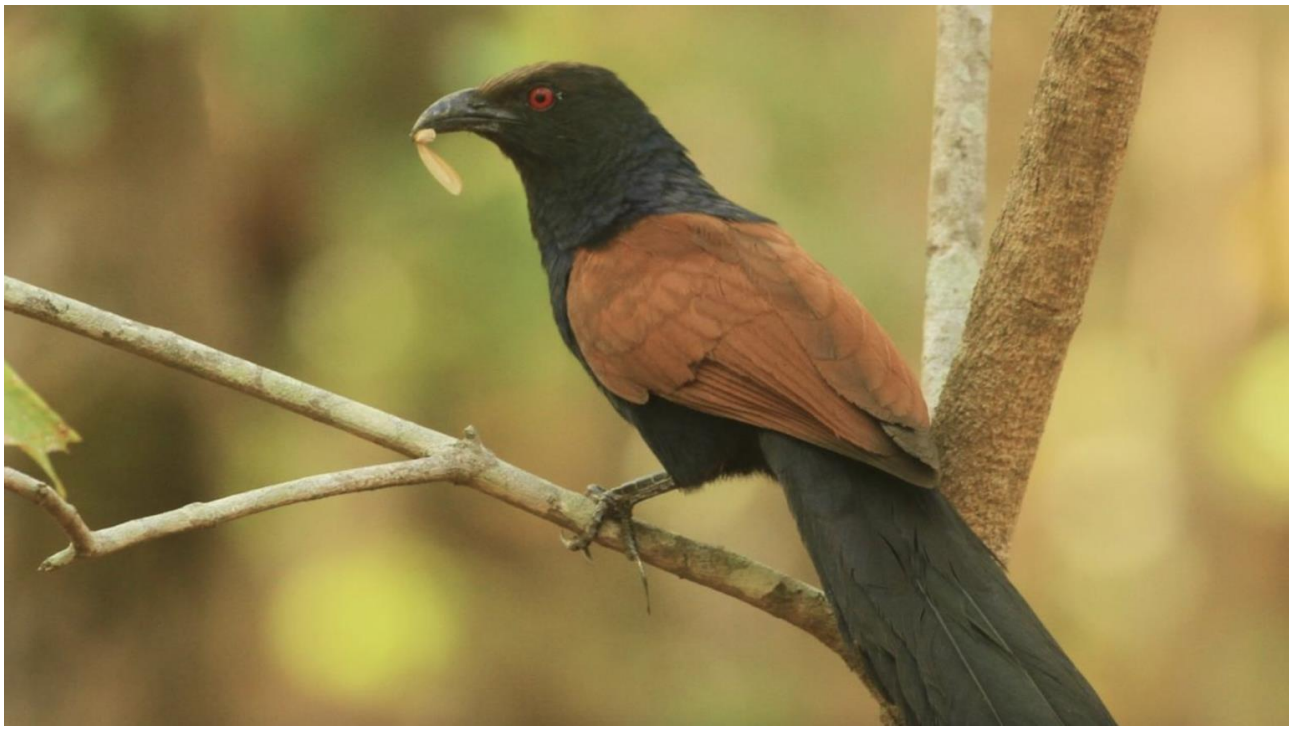


*The greater coucal (*Centropus sinensis*), also known as the crow-pheasant, is a common bird seen hopping on the ground or low branches in many parts of India. Photo: David V. Raju, CC BY-SA 4.0*

RAGHAVENDRA GADAGKAR

This article is part of the 'More Fun Than Fun' column by Prof Raghavendra Gadagkar. He will explore interesting research papers or books and, while placing them in context, make them accessible to a wide readership.

- *Coucals belong to the cuckoo family, but they build their own nests and rear their brood. Most coucal species breed in monogamous pairs care for the chicks together.*
- *The black coucal is an outlier in the coucal way of life. It is the most sexually dimorphic of all known coucals, with the females 70% larger than the males.*
- *Males also outnumber females by 2.5x in the breeding population, making females the limiting sex, with high variance in reproductive success.*
- *And among black coucals, the responsibility of incubating, feeding and protecting the chicks falls entirely to the males.*

The well-known evolutionary biologist and author of a popular undergraduate textbook on evolution, Douglas J. Futuyma, begins his new book *How Birds Evolve* (2021) thus:

> "This book is for birders and for all who enjoy nature and sometimes ask questions about what they see. Why are male birds more colorful in some species but not others? Why do some owls and other species come in different colors, independent of sex or age? Why is parental care of young the duty of females in some species, males in others, and both parents in still others? What are species, how do they arise, and why are there so many more in tropical regions than in the temperate zone? How and when did the astonishing variety of birds evolve?"

These are the kinds of questions that evolutionary biologists love to ask. But how do they go about answering them? Let us consider one of these questions and one possible strategy for answering it.

Who cares for offspring and why?

Why indeed "is parental care of young the duty of females in some species, males in others, and both parents in still others", not just among birds but in any group of animals? It turns out that the instances of no parental care, male-only care, female-only care and biparental care vary enormously between different groups of animals.

In mammals, the complete absence of parental and male-only parental care are never observed: 9% of the species show biparental care, and 91% of the species show female-only parental care. In birds, on the other hand, all species show some form of parental care: less than 1% of the species show male-only parental care, 90-95% of the species show biparental, and 5-10% of the species show female-only parental care.

These highly variable patterns are a goldmine for evolutionary biologists as they present a plethora of intriguing puzzles – it's like presenting Sherlock Holmes with a London full of unsolved crimes!

But where do we begin? Perhaps the most interesting puzzle concerns the small number of species that show male-only parental care – a reversal of the traditional pattern seen among the rest of the birds. In these species, females have stopped (in evolutionary time) caring for their chicks. Why?

Sex-role reversal

We need to study the evolution of sex-role reversal. But it is important to make sure that by sex-role reversal, we don't simply mean a reversal from the stereotypic sex roles that we see or imagine from a human perspective. It is necessary to define 'sex-role reversal' objectively by considering the dominant pattern of sex role in the taxonomic group under investigation and then identify deviations from this.

Thus, female parental care would be an instance of sex-role reversal in some groups where male care is the norm. Such a sex-role reversal from male care to female care has indeed been recorded in 6-8% of shorebirds.

Pheasant tailed jacana (Hydrophasianus chirurgus) is a resident breeder in much of India. The females are polyandrous and lay several clutches of eggs that are cared for by different males.
Photo: Dasari Vijay, CC BY-SA 4.0

The evolutionary biologist is thus challenged with many intriguing questions: Why should a transition occur from female care to male care or male care to female care? More generally, who should care for the offspring, males, females, both or none?

The logic of this line of reasoning is that individuals should behave so as to maximise their respective lifetime Darwinian fitness. In the case of parent-offspring relationships, there is much scope for complex dynamics as there are at least three parties involved: the father, the mother and the children.

When we throw in genetic relatedness and the idea of kin selection, it gets even more interesting. Parents and offspring are related to each other by half, and so are offspring to each other. Parents are usually unrelated to each other, but they have a joint investment in the offspring.

Female parental care

Evolutionary biologists have developed a reasonable body of theory and a pretty good understanding of why female parental care is by far the predominant pattern seen in animals. The basic idea is that, with some exceptions, males invest relatively little per offspring as sperm are cheap to produce.

In contrast, females invest much more in the form of larger and nutrient-rich eggs, not to mention pregnancy and lactation in mammals. This makes females the limiting resource for which males *compete*. As a result, most females get to mate, but mating success is highly variable in males; some get to mate with many females while many remain altogether unsuccessful.

It is thus evolutionarily more advantageous for the male rather than the female to desert and seek additional mating opportunities, especially when one parent is adequate to rear offspring.

Male parental care

On the other hand, male parental care, and especially *male-only* parental care, is urgently in need of explanation. Experts have often argued that the mystery of male-only parental care is somewhat mitigated by the fact that it has evolved in shorebirds, where the chicks need relatively less parental care. So perhaps the fathers can just about manage!

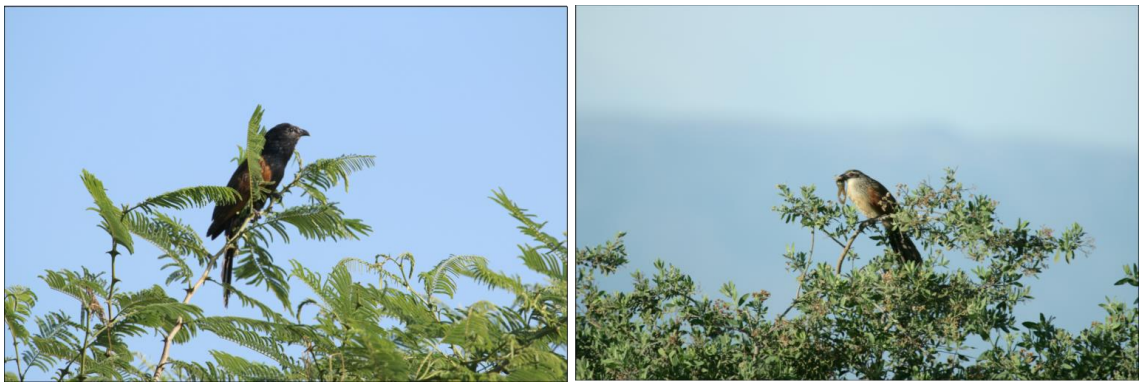
With regard to offspring development and the need for parental care, there are two kinds of birds: precocial and altricial.

In precocial birds, such as the domestic chicken, ducks, geese and shorebirds, the eggs are large and filled with more nutrition, so that the young are at an advanced stage of development at the time of hatching. Hence, the chicks can run around, forage for themselves and even flee from predators almost as soon as they hatch.

In altricial birds, such as herons, hawks, owls and passerines, on the other hand, the young are born pretty helpless, blind and naked, and are entirely at the mercy of parental care for warmth, food and protection.

Thus, the evolution of male-only parental care in precocial birds is less of a challenge. If males took all responsibility for rearing the chicks in an altricial species, however, that would be a real challenge – as much for the father birds as for the evolutionary biologist.

One such species – altricial, polyandrous and with male-only parental care – has indeed been discovered in the black coucal, *Centropus grillii*. And Wolfgang Goymann of the Max-Planck Institute for Ornithology in Seewiesen, Germany, has taken up the gauntlet and has been on the chase for over 20 years.



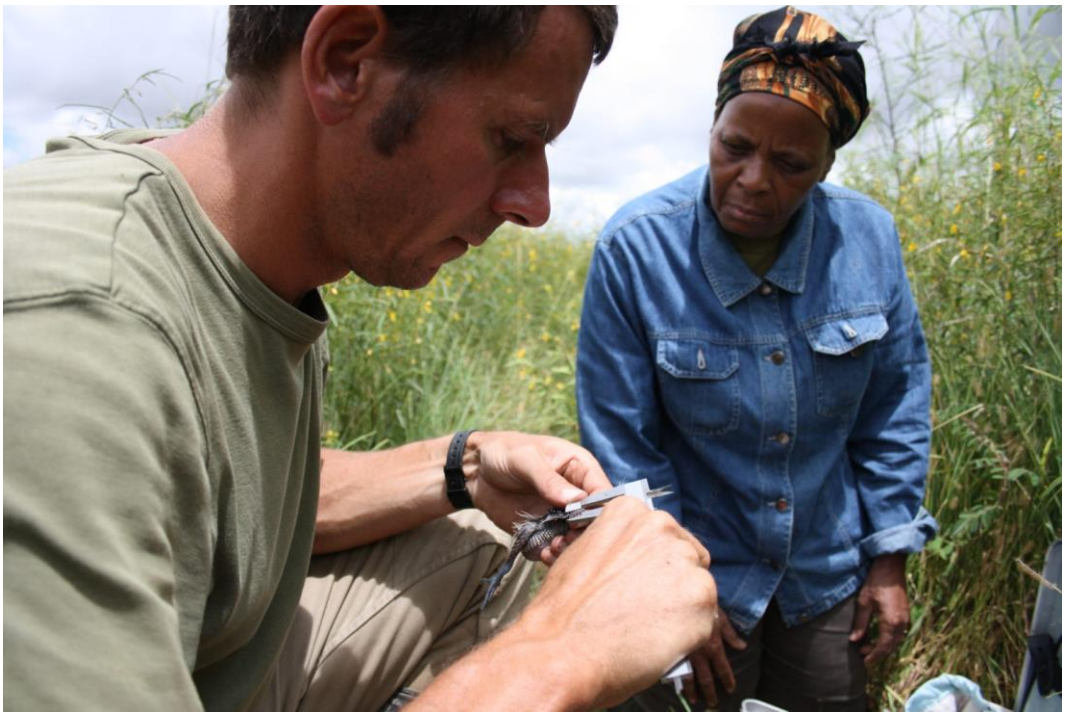
Left: A black coucal (Centropus grillii). Female on a song perch in Utengule, Mbeya region, Tanzania. © W. Goymann. Right: White-browed coucal (Centropus superciliosus) male with a frog about to feed his nestlings, Kapunga, Mbeya region, Tanzania. © W. Goymann

Goymann has discovered much new knowledge in the process, although the final answer remains elusive. Unlike Sherlock Holmes, who preferred to ignore the small fry and catch the big fish (read: Professor Moriarty), a scientist is happy to catch as many small fry as possible, and secretly wish that the big fish remains elusive and continues to yield an endless supply of the former.

For the scientist-detective, every wrong turn, every misguided chase up a blind alley means more knowledge to gain.

I am very interested in knowing how and why different scientists undertake their research projects, so I asked Goymann to let me in on his back story. Here's what he told me:

> "During my doctoral studies on the behavioural endocrinology of spotted hyenas, I thought a lot about what I want to do next in my scientific career. Because I was doing my mammalian work in an ornithological department, I read a lot about birds and hormones and stumbled across a study by Carl Vernon, who for the first time observed black coucals and suggested that they are the only altricial bird species with male-only parental care.
>
> After my thesis, I decided that I needed to do a pilot study to show that it is possible to work with them, otherwise, I would not be able to get funding for it. I told Wolfgang Wickler, at that time director of the Max Planck Institute for Behavioural Physiology, about my plans and asked him to fund a pilot study. He agreed to do so, and off I went with Dieter Schmidl, an expert in catching birds, and Andrea Wittenzellner, a technician and experienced field person.
>
> Deciding about the country where to study these birds was a different story. I had strong connections to Tanzania. Neil Baker, who knows every bird in Tanzania, first declared me crazy because black coucals only co-occur with buffalo, hippo and lion, not the best combination of animals, especially in high grasses in which you can barely see the next two metres. There were many difficulties, and we almost ended up in prison, but we finally succeeded."



Felister Urasa, a collaborator from the University of Dar es Salaam, with Wolfgang Goymann, who is measuring feather shafts and tarsus length of a nestling black coucal, at Kapunga, Mbeya Region, Tanzania. © W. Goymann

The Coucals

Coucals are common birds in many parts of Asia and Africa, usually seen hopping on the ground or low bushes, rather clumsily, as the legendary bird-man Salim Ali perceptively notes in *The Book of Indian Birds* (1979).

Coucals belong to the cuckoo family, but they are not parasitic: they build their own nests and rear their brood. Most of the 28-30 species of coucal breed in monogamous pairs showering biparental

care on the chicks. The females are generally slightly larger than the males, and the males usually contribute more than the females towards rearing the chicks.

However, the black coucal, *Centropus grillii*, is an outlier in the coucal way of life. It is the most sexually dimorphic of all known coucals, with the females 70% larger than the males. Males also outnumber females by 2.5-times in the breeding population, making females, rather than the males, the limiting sex with high variance in reproductive success.

And unlike most of the other coucals, the black coucal is polyandrous – the females defend territories by singing, mate with and maintain a harem of up to five males, and lay eggs in each male's nest, leaving the responsibility of incubating, feeding and protecting the chicks entirely to the males.

So immaculate is the role reversal that, just as males do in polygynous species, female black coucals not only sing to maintain their territories, but they also alter their songs when challenged, and pay special attention to those components of their rivals' songs that especially indicate competitive ability.

How could natural selection have favoured such a complete sex-role reversal? We must look at the problem from the points of view of both sexes, since both male and female black coucals deviate from their related species.

At first sight, there appears to be a simple solution to the problem. It has been known since the 1930s that the black coucal male has only one testis: its left testis is absent, a fact made even more intriguing because it is usually the left testis that is larger in birds. J. David Ligon of the University of New Mexico in Albuquerque proposed the reasonable hypothesis that the resulting reduction in testosterone and consequent 'feminisation' of the male may be causally related to the role reversal of the black coucal male.

It is well-known that the male hormone testosterone produced by the testes inhibits parental care, including nest-building and incubation. In species with biparental care, testosterone levels are high in males during the period of inter-male competition and territory establishment, but decline when the males begin to participate in parental care duties.

Because testosterone levels in males increase in response to territorial challenges by *other* males, the proposed function of testosterone has come to be known as the 'challenge hypothesis'.

Even if correct, Ligon's hypothesis offers only a proximate explanation for male sex-role reversal, leaving open the question of *why* it is evolutionarily advantageous for male coucals to behave like typical females.

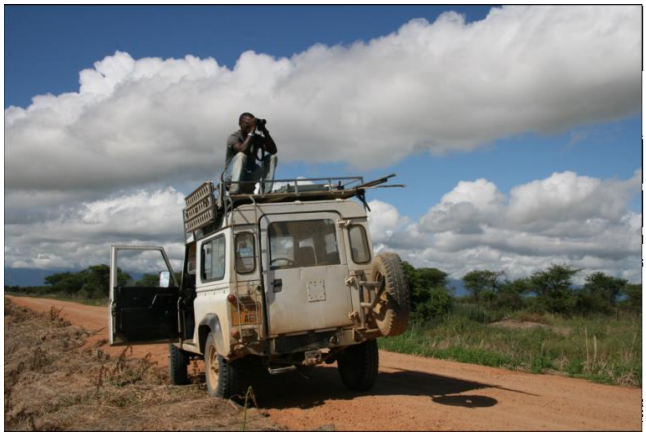
Nevertheless, it is a good start, and it is certainly an obvious hypothesis that cannot be left untested. Behavioural ecologists have also increasingly realised that proximate explanations often help find ultimate explanations and vice versa.

Proximate explanations

Goymann, therefore, set out to test Ligon's hypothesis in collaboration with John C. Wingfield of the University of Washington, the author of the challenge hypothesis. But Goymann and Wingfield did not find support for the idea that a missing testis could hold the key to sex-role reversal in the male coucal. They found that circulating testosterone levels in male coucals were not low – they were higher than in the females, as is the case with other monogamous birds.

If male coucals are like the males of monogamous birds in the matter of circulating testosterone levels, do they also increase their testosterone levels in response to threats by other males, as predicted by the challenge hypothesis?

The answer is 'yes'. Goymann and Wingfield showed this by challenging them with a dose of the gonadotropin-releasing hormone (GnRH), which simulates behavioural challenges by males. Males showed a significant increase in testosterone levels in response to GnRH challenge, but the females did not show any such change.




Left: Field assistant Musa Makomba on the mobile observation platform after radio-tracking coucals. © W. Goymann. Right: Field assistant Poyo Makomba and doctoral student Ignas Safari setting up a mist-net for catching coucals at Utengule, Mbeya region, Tanzania. © W. Goymann

The lack of response by the females is interesting because it means that as far as testosterone is concerned, females also behave like species without sex-role reversal. This further delinks black coucal sex roles from circulating testosterone levels.

How then do male black coucals manage to show female-typical behaviour despite being hormonally similar to males of monogamous birds? And how do female black coucals show male-typical behaviour despite being hormonally similar to females without sex-role reversal? The plot thickens.

It is hard to believe that sex roles in the black coucal have become entirely independent of testosterone. Could it instead be that males have become less sensitive to testosterone in their blood or that the females have become more sensitive? Levels of testosterone circulating in the blood are sensed by the appropriate receptors in the brain. Females could become more sensitive if they had more receptors.

One way to measure the concentration of the receptor proteins is to measure the rate of production of the messenger RNA (mRNA) molecules involved in their synthesis. Indeed, Voigt and Goymann found that females have higher levels of mRNA expression corresponding to testosterone receptors than males. This would make the females behave as if they had higher testosterone levels than they actually do.

Thus, although male-female differences in circulating testosterone levels are not what one might have expected in a sex-role reversed species, the differences in the concentration of receptors compensate for this apparent anomaly and restore the expected pattern.

With some understanding of the proximate factors, i.e. the physiological mechanisms involved in sex-role reversal, let us turn to the possible ultimate factors, i.e. factors that make natural selection *favour* sex-role reversal.

Ultimate (evolutionary) explanations

It is often hard to use direct experimentation to test evolutionary hypotheses. Therefore, we often use the comparative method – to contrast closely related species that are similar in most respects but differ in the features under investigation. In other words, we take advantage of nature's experiments.

Goymann and his colleagues have exploited the comparative method with much success. They have been conducting long-term field studies in the Usangu Plains in southwestern Tanzania, comparing the black coucal with sex-role reversal and the white-browed coucal (*Centropus superciliosus*) without sex-role reversal.

The black coucal and the white-browed coucal seem tailor-made for a comparative study. In addition to belonging to the same genus, they occupy the same habitat and have a similar diet of insects and frogs.

In striking contrast to the black coucal, the white-browed coucal is the least sexually dimorphic species: females are only 13% larger than the males. There are roughly equal numbers of males and

females in the breeding population, so neither is a limiting resource. The species shows biparental care. Consequently, both sexes have nearly the same variance in reproductive success.

Why are the two closely related species so starkly different in their reproductive and parenting behaviour? It turns out that even though they live in similar habitats, there are significant ecological differences between the black and white-browed coucals that might explain their contrasting behaviour. Not everything is clear, but the pieces of the puzzle are falling in place.

Biparental care is the ancestral condition for these birds so that both parents can care for their chicks. Thus, if conditions improve, making care by a single parent adequate, one of the parents may be selected to leave if it can get additional mating opportunities and add on to its fitness. Such a situation seems to exist for the black coucal but not for the white-browed coucal.

White-browed coucals are year-round residents in the area. They, therefore, establish their territories based on what is optimum for year-round survival. On the other hand, black coucals are migrants and arrive only during the breeding season and occupy areas that are exceptionally rich in food at this time of the year, even if they are poor at other times.

Shared habitat of the two coucal species with acacias, preferred as nesting habitat by white-browed coucals, and tall grasses, preferred by black coucals. Kapunga, Mbeya region, Tanzania.
© W. Goymann

But the question of which parent stays on to rear the chicks and which one leaves to seek additional mating opportunities remains. Because black coucal females are larger and fewer in number than males, they are more likely to find additional mating opportunities and lay additional clutches of eggs in the nests of different males.

Nearly all the asymmetries between males and females are reversed in the black coucal setting the stage for sex-role reversal. And as we have seen, the proximate hormonal mechanisms can be modified to go hand-in-hand with the new sex roles of males and females.

Goymann and his colleagues have convincingly argued that "a combination of high food abundance, high population density, high degree of nest loss and male bias in the adult sex ratio represent ecological conditions that facilitate role reversal and polyandry in coucals."

Many more fascinating results have come out of Goymann's research team. I will mention just three:
1. Both male and female black coucals are more stressed than the white-browed coucals in the breeding season – uniparental care takes a toll on both parents.
2. Males who so diligently care for their chicks are, however, not entirely faithful; they sometimes seek extra-pair copulations and are known to sire offspring being cared for by other males.
3. In a clever experiment, Goymann forced white-browed coucals to resort to uniparental care by removing one of the parents. Whether male or female, the remaining parent doubled the rate of feeding the chicks. Nevertheless, the chicks did not grow well under female-only care but did better

under male-only care, suggesting that if conditions change and white-browed coucals evolve single-parenting, it is likely to be a case of male-only rather than female-only care.

Thus, we see that coucals are poised to evolve male-only parental care: even in monogamous species, they show biparental care, males are smaller, contribute more to parental care, and are better than females at the job.

Even as the mystery of sex-role reversal in the black coucal continues to unfold under the careful scrutiny of Goymann and his collaborators, some things are already evident.

Both parents participate in parental care in the white-browed coucal not because two parents are somehow more necessary to rear chicks in that species, but because neither parent has adequate opportunities to mate with outside partners and sire additional chicks.

It is hard to say which features of the black coucal cause sex-role reversal and which are the effect. Under the proper environmental conditions, sexual selection, body size selection and adult sex-ratio selection can feed into each other to create reversed sex roles.

Sustained long-term ecological and physiological studies on carefully chosen species rooted in sound theory are needed to identify and explain such fascinating patterns in nature. But not enough is being done, especially in India.

Our own greater coucal, *Centropus sinensis,* commonly known as crow-pheasant, abundant in most parts of India, remains to be studied in any detail. Here is an excellent opportunity for an early career scientist to devote a lifetime of detective work and reap many intellectual rewards.

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