

Hoopoes modulate their alliance with beneficial bacteria along the nesting phase

Alliances with microorganisms are crucial for animal life and survival. Beneficial associations between animals and bacteria and other microbes are quite diverse. Perhaps, the most widely extended and known association between animals and microorganisms is that of bacteria of the digestive tract of animals allowing food processing and producing essential vitamins and minerals for animal life. However, examples of bacteria that protect animals from pathogenic infection have also been described in several taxa from worms to mammals, including mollusks, insects, amphibians and birds. Most of these animals are born without symbiotic bacteria, so these beneficial alliances need to be established as soon as possible, during the first days of life.

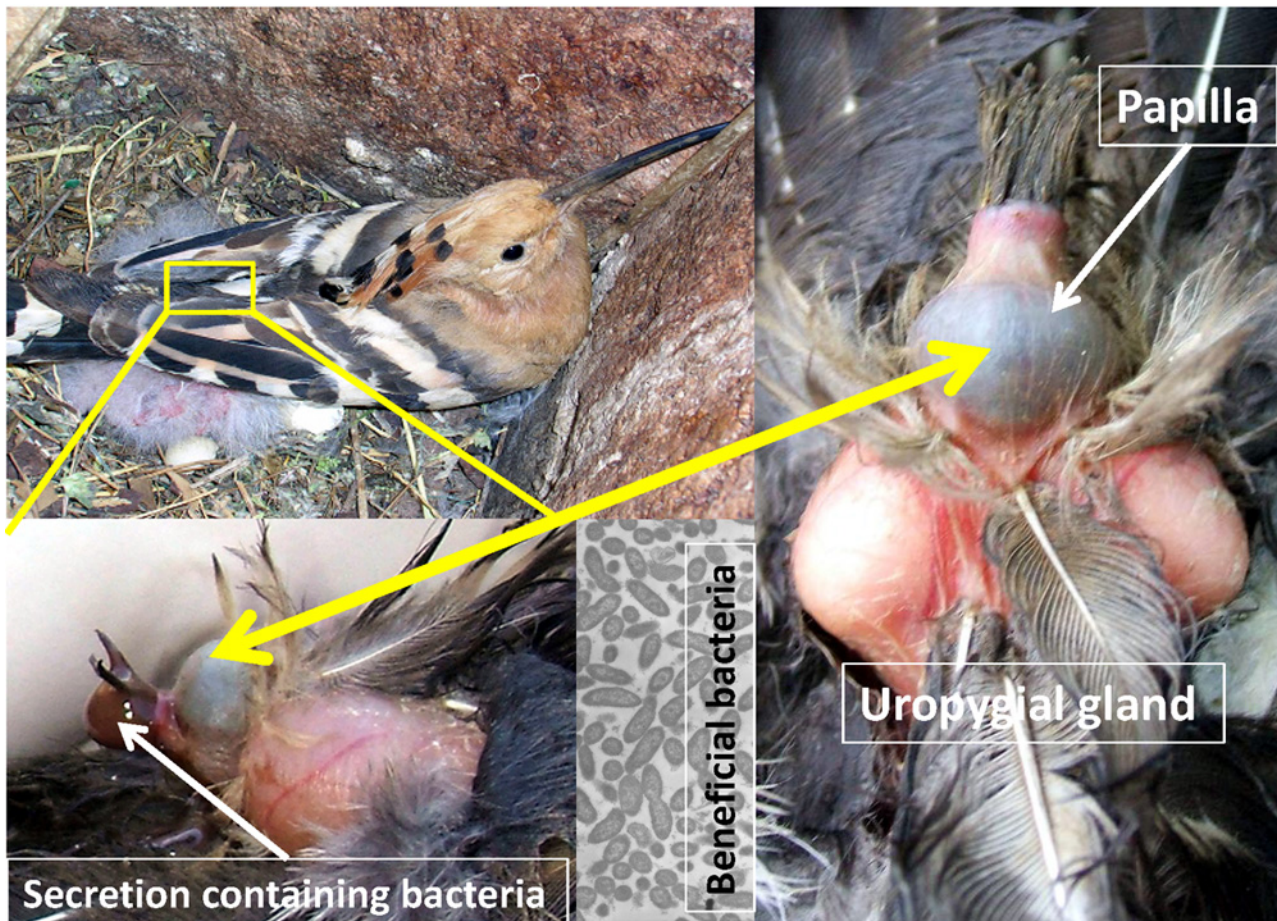


Fig. 1. Dorsal and lateral detail of the uropygial gland of a brooding female hoopoes.

The way bacteria are acquired is fundamental and, in some cases, can determine particularities of

the alliance between them and animals. Beneficial bacteria can be acquired directly from mothers, from the environment, or by a mixed strategy. Strict acquisition of symbionts from mothers assures the transmission of the bacterial strains that helped survival of mothers and grandmothers until reproduction, but prevent the acquisition of some other bacteria from the environment with potentially high beneficial effects. On the other side of the coin, acquisition of beneficial bacteria from the environment would open the door to choose bacteria that fit better with environmental requirements (i.e., risk of pathogenic infection) at the potential cost of not finding the appropriated ones. The third possibility is a mixed strategy that would assure the acquisition of bacteria that previously have helped the mother, but at the same time keeps the doors open to acquire some other beneficial bacteria for particular environments. Even though scientists recognize that modes of symbiont acquisition is pivotal for understanding the evolution of alliances between animals and beneficial bacteria, experimental studies on the subject are almost absent. Our work with hoopoes (*Upupa epops* L.) is therefore one of the first trying to answer this question by means of experimental modification of the environment where nestlings develop.

The hoopoe is one of the very few bird species where this kind of association with beneficial bacteria has been described. These birds harbor in their uropygial gland a complex bacterial community that produce antibiotic substances, protect feathers from microbial degradation, and embryos from trans-shell pathogenic infections. The uropygial gland is dorsally located on the bird's skin, upon the area where tail feather grow (Fig. 1). We knew that some of the bacteria in the uropygial gland of nestlings come from the uropygial gland of their mothers. Then, we wondered whether the bacteria that nestlings acquired during the first days of life could be modified by the contact with other bacteria from the environment (for example, nests) where they develop. We tried to answer this question by exchanging nestlings with already functional glands among nests. Some days later, we sampled the uropygial secretion of nestlings and explored the differences and similarities of the bacterial communities of siblings and of foster siblings reared in the same and in different nests. We also compared bacteria of nestlings with that of their natural and stepmothers. We found that the bacterial community of nestlings experimentally moved between pairs of nests was mainly similar to that of their natural mother and siblings, but also shared some bacteria with those of stepsiblings and stepmothers. Thus, we concluded that hoopoes follow a mixed strategy for acquisition of the symbiotic microorganisms, which suggests the evolution of a flexible alliance with bacterial symbionts that open the possibility of recruiting the most appropriated bacteria for particular environmental conditions of nests.

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