

Cover illustration

In the search for stereopsis

Owls were probably not the first nocturnal avian denizens. After all, they had to evolve from a diurnal species, and this probably required some bridge families. The bridge between the sister taxa of swifts and hummingbirds to the nocturnal owls was probably the order Caprimulgiformes with good cladistic and systematic evidence of this intermediacy. The strange birds in this order are not household names and include the nightjars, oil birds, potoos, owl-nightjars, and frogmouths. All of these birds are characterised by enormous gaping mouths, tiny feet, crepuscular and/or nocturnal activity. The nightjars, oil birds (with perhaps one rare exception), potoos, and swifts are wing feeders and do not take food off the substrate. Only the frogmouths and the owl-nightjars can utilise substrate food sources, and appear to be close to the owls themselves in several ways. The Papuan frogmouth on this month's cover is a good example of this predominately insectivorous order, and will illustrate the evolution from swifts to owls.

The frogmouth family (Podargidae) comprises 12 species and is probably a relic family close to owls. As can be seen, the Papuan frogmouth resembles an owl, but has different feeding habits, and hence different visual mechanisms. This frogmouth has a large hooked beak used to seize invertebrates, a primary food item. Up to 50 cm in height and weighing as much as 550 g, frogmouths have a booming call that can be most disquieting in the Australasian back country that is their home.

Best known for their camouflage techniques, the frogmouths do not forage, or trawl, but rather they sally. Sitting rigidly and still, and resembling a dead branch or stump, the bird will swoop or drop directly to the forest floor for nocturnal insects, spiders, lizards, or even mice. Surprisingly, although relatively swift on the wing, they are poor fliers but, then, extended or aerobic flight isn't really necessary for their lifestyle.

As mentioned they are known for their camouflage, and to find them in daylight requires as much luck as skill. These birds are so well camouflaged



they are almost impossible to see. When approached, they almost never move, but can make a buzzing sound that resembles bees, presumably to ward off predators. Their prey as well as their predators are fooled by the plumage. When a prey moves into range, the bird attacks and dispatches the prey quickly even using the stiff whisker-like feathers (see *BJO* April 2001 for discussion of avian feathers) around their beaks to assist in capture. Their feet are weak and do not assist in capture, but with the large, sturdy, triangular hooked bill, the feet are unnecessary for the kill.

The yawning oropharynx that gives the bird its odd name apparently has a most curious function. The open mouth exudes an odour that attracts insects. Nocturnal flying insects will investigate the source of such a promising scent. This living flytrap, as Jared Diamond (*Natural History* 1994;103:4) called it, may have the ultimate vertebrate sedentary predation method requiring almost no hunting skills. It is doubtful, however, that enough food can be secured by this method, so the sallying described above is probably preferred. Many of the other caprimulgids, such as the night hawks, have large mouths so that they may trawl with their mouths open through swarms of insects to secure food with minimal visual requirements.

The visual mechanisms of the frogmouth are interesting and probably reflect its intermediate position between the diurnal swifts and the nocturnal owls. The frogmouths have a predominantly rod retina, in contrast to the swifts. None the less, there are at least three different cone types with three different coloured oil droplets (to be discussed in a subsequent essay) which

allow satisfactory diurnal acuity for escape or short flights if disturbed. The cone acuity is at least 11 cycles per degree (Snellen equivalent of at least 20/50) and probably better (rods are more densely packed and probably have better nocturnal acuity) with good motion sensitivity. The frogmouth globes are large and together outweigh the brain. The eyes are tubular in shape with bony scleral ossicles supporting the anterior segment, much like those of owls. These large eyes, steep corneas, and large rounded lenses are excellent at light capture to improve their nocturnal image. Swifts have their eyes lateral with large monocular visual fields, but little or no binocular field. Owls have the most frontally placed eyes and probably the largest binocular field of any avian family. Frogmouths have intermediately placed eyes and visual fields to match. These birds spend most of their time with their visual axes confined to a small region of the visual space, with little or no movement. The visual axes of the frogmouth are more divergent than those of the owl, but much less divergent than the swift's. Owls have little to no ocular motility, but frogmouths can align their visual axes to gain stereopsis in a frontal gaze because of better ocular motility, and they do have a binocular "Wulst" (roughly equivalent to the visual cortex in mammals) to provide them with true stereopsis. Curiously, when frogmouths make saccades they are almost always in opposite directions. This evolutionary intermediate position between the swifts and the owls, visually, illustrates the binocular imperative for sophisticated nocturnal predation.

So, in the evolution of truly nocturnal birds, swifts, already crepuscular, probably began the process. As the caprimulgid order evolved, frogmouths discovered the substrate larder of insects and mammals. They became part of the bridge that facilitated the emergence of owls into the dark of night.

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