Quick guides

Bird head stabilization

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What is head stabilization in birds? When the body of a bird is held in the hand and rotated or moved in different directions the head often appears ‘locked in space’ or glued to the spot, and does not move with the rest of the body. To maintain this stable position the bird has, of course, to make complex compensatory movements of the neck. This can be seen clearly in chickens, pigeons, owls and many other bird species. It can also been seen in the natural behaviour of many birds; for example, when they land on a thin branch, or a power or telephone wire, their momentum will often set the branch or wire oscillating back and forth. Yet if one carefully observes their head, by lining it up with a static distant feature of the environment, one can see that it is likewise ‘locked in space’ while compensatory movements of the body and neck are made to balance the bird. Perhaps the most common and obvious example of bird head stabilization can be seen in the ‘head-bobbing’ behaviour of many species of birds as they walk. This is illustrated in Figure 1, where it can be seen in the stroboscopic photo that, while the pigeon’s body moves smoothly forward as it walks, its head is relatively still for several flashes which we call the ‘hold phase’ where stabilization is occurring, and then it is moved rapidly forward (called the ‘thrust phase’) to a new position where again it is stabilized.

What is the function of head stabilization? Its function is to keep the direction of gaze constant or fixed. In principle, an animal can compensate for changes in its body position by moving either its head or its eyes, or both. Some animals do this mainly through eye movements, while others do it mainly through head movements, and a few do it with both. As an animal moves continuously though its environment there is always a limit beyond which it can no longer compensate with a body, head or eye movement, and so it then rapidly moves to a new position to start compensating all over again, much like the ‘spotting’ of ballet dancers as they pirouette. These are called optokinetic head or eye movements, and the stable gaze position permits animals to most efficiently detect if some object (especially another animal) is moving in their environment. Gaze stabilization is almost universal and is seen in invertebrates and vertebrates alike.

Several visual scientists have postulated that the forward thrust of the head of walking birds might function to produce motion parallax, which provides information about the depth and distance of objects. Motion parallax refers to the apparent relative motion of objects in the environment whereby closer objects appear to move faster and in the opposite direction to the animals direction of motion, while objects farther away than the stabilized object will appear to move in the same direction, again with a velocity gradient, where most distant objects move faster than those near the fixation distance. Although this seems like a very plausible hypothesis to date there is no direct evidence for this conjecture in birds.

How good is bird head stabilization? Although head stabilization looks almost perfect to the casual observer, there is always a very small amount of positive movement during stabilization, referred to as ‘retinal slip’. This small amount of motion of the head and eye causes very slow motion of the entire visual image across the retina. This provides the ‘error signal’ that is used to control the compensatory movements that keep the head (almost) still. Stabilization of the head occurs in all three axes of space and for both translation and rotation around these axes. For a walking pigeon the small amount of motion during the hold or stabilization phase is less than 0.5 mm.

Which birds show the best head stabilization? While head stabilization occurs in all birds some of the most remarkable feats of stabilization are to be seen in hovering birds. Humming birds, hovering in front of a flower while feeding show an amazing ability to keep their head stabilized while their body makes considerably larger movement produced by their wing beats and perturbation by the wind. Kestrels and kingfishers, while hovering in mid-air before diving to catch their prey, also show remarkable stabilization of

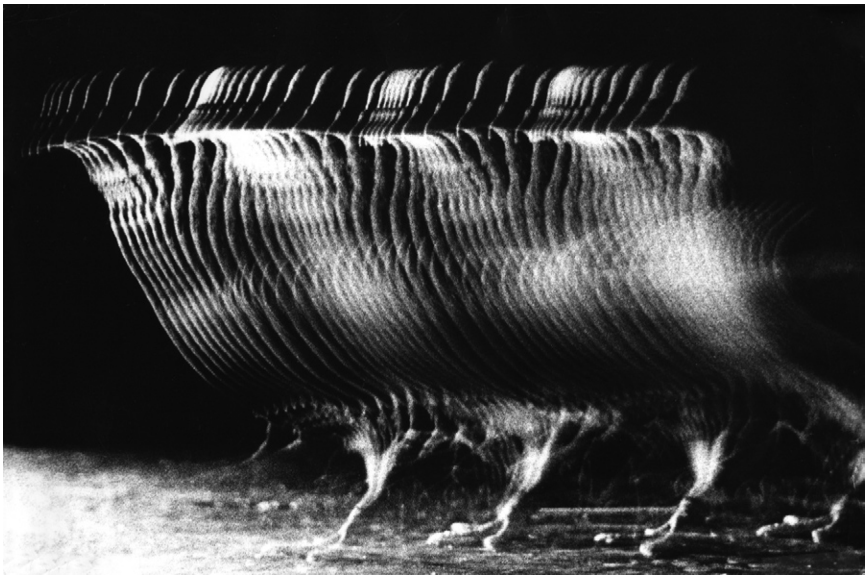

Figure 1. Stroboscopic photograph of pigeon walking illustrating their characteristic head bobbing behaviour, where the head is held relatively still for a few flashes and then moved rapidly to a new position.

the head relative to the much larger movements of their bodies. Films and videos of flying heavier birds, such as geese and swans, show that while there is an upward thrust of their bodies produced with each downward wing-beat their heads maintain a nearly perfect level path.

Is the visual system specialized for this type of image stabilization? Experimental observations on many species have shown that smooth motion of a very large image over an animal's visual field produces optokinetic response of the eye, head and body, where the gaze follows the moving stimulus for a while and then makes a fast resetting movement (saccade), and then another stimulus following movement occurs. These following movements, or pursuit movements as they a usually called, are performing the same task as the head stabilization seen in birds; that is, they are stabilizing the gaze. Not surprisingly there are specialized neurons in the visual system of invertebrates and vertebrates that specifically detect slow motion over very large areas of the visual field, and in birds (and most likely other vertebrate species also) they even have their own special ganglion cells in the retina that begin to carry out this task. These specialized retinal ganglion cells then forward this information to an area of the brain called the accessory optic system, which ultimately connects up with information from the vestibular system or sense of balance, which also plays a role in stabilizing the gaze. Interestingly, birds such as humming birds, kestrels and kingfishers that have remarkably good head stabilization while hovering have an accessory optic system that is relatively several times larger than most other birds.

Where can I find out more about bird head stabilization?

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Anolis lizards

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What is an anole? Anoles comprise one of the most diverse vertebrate genera, with nearly 400 species known and more being discovered every year. They have become a textbook example of adaptive radiation and have contributed greatly to our understanding of evolution, ecology and organismal function. About 150 species occur on islands in the Caribbean; the rest are found in Central and northern South America. Only one species is native to the southeastern United States.

Often quite beautiful, anoles are captivating lizards with a rich behavioral repertoire and extensive variation among species. Most anoles are green, grey or brown; they are generally 35–85 mm in body length and 1–10 g in mass, though some can be substantially larger. They have a generalized lizard body form with robust limbs and a moderately long tail, though there is significant variation among species. The two primary traits that characterize anoles (with a very few exceptions) are possession of expanded toepads and an extensible colorful flap of skin, the *dewlap*, which is attached to the throat.

How much ecological and evolutionary diversity do they exhibit? Studies of anoles have been central to the development of key concepts in ecology and evolution. Two important patterns of diversity have generated substantial ecological and evolutionary research on anoles. First, on each of the islands of the Greater Antilles — Cuba, Hispaniola, Jamaica, and Puerto Rico — sympatric species differ in habitat use, behavior and morphology. For example, species that use broad tree trunks near the ground tend to have long hindlimbs, which they use to run quickly and jump great distances. In contrast, species that use narrow twigs high in the trees have very short legs and tend to creep very slowly to capture prey and escape detection by predators. Species that use the vegetation high in the tree have very large toepads and are green in color. In all, six types of habitat specialists, termed *ecomorphs*, have been defined.

The second important insight from studies of anoles in the Greater Antilles is that, with a few exceptions, the same set of habitat specialists has evolved independently on each island. Phylogenetic analysis indicates that distinct species occupying the same habitat specialist category on the different islands are not closely related.

These anole communities served as a model system for the development of ecological theory in the 1960s and 1970s, and important early work on interspecific competition, niche variation, character displacement and other phenomena were conducted on anoles.

Convergent evolution has long been taken as evidence of adaptation. A hypothesis of adaptation can be further tested by demonstrating that the convergent features are beneficial in the environment in which they occur. Work on anoles was instrumental in developing the idea that ecological adaptation must be studied by examining measures of whole organism performance. These studies indicated that the morphological and physiological variation among species leads to differences in capabilities that are appropriate to the different habitats that species occupy (Figure 1), thus strongly supporting the hypothesis that adaptive radiation has occurred.

What drives evolutionary diversification of anoles? The classic idea of adaptive radiation is that it results from interspecific competition driving initially similar species to diverge in resource use and adapt to new habitats. These predictions are strongly supported for anoles. A wide variety of research— including behavioral observations, comparisons across study sites and experimental manipulations— indicates that anole species interact strongly and that interspecific competition for resources is likely the cause of their adaptive divergence. Moreover, shifts in habitat use as a result of the presence of other species are well-documented, and comparisons across populations demonstrate corresponding adaptive changes in morphology.

These ideas can further be tested directly by measuring natural selection