How birds became airborne

The evolutionary scenario that led to powered flight in birds, or rather proto-birds, has been the focus of controversy for more than a century. The enigmatic blend of reptilian and avian characters in *Archaeopteryx* – the oldest known bird fossil – has certainly resulted in strongly diverging interpretations among scientists[1]. Two main theories explain how flight evolved: (1) the arboreal, or trees-down, scenario; and (2) the ground-up theory. The arboreal scenario hypothesizes that flight evolved in animals that climbed trees or rocks. These animals then simply parachuted down to the ground, and increased aerodynamic adaptations (such as lift-generating surfaces on forelimbs) enhanced gliding performance, eventually leading to the evolution of powered (flapping) flight[2]. In this scenario, powered flight evolved via gliding flight, which is less complicated than flapping flight. The ground-up theory assumes that the bird ancestor, proavis, was a cursorial dinosaur (i.e. adapted for running), probably a maniraptor, that evolved distal-lifting surfaces for increased control when running and catching flying insects[1,3]. Subsequently, the aerofoil function developed further to allow extended jumps and eventually self-powered flight evolved.

Recent fossil finds in China, of apparently feathered dinosaurs, have reopened the debate concerning the phylogenetic origin of birds[4]. By combining morphology and aerodynamic theory, researchers have argued in favour of both of the two main scenarios for the evolution of flight[1–3]. *Archaeopteryx* had flight feathers showing the asymmetrical vane that is typical of modern flighted birds[5], but this feature is typical of both gliding and powered flapping flight. The main argument for the arboreal scenario is that gliding flight is a natural transition to flapping flight because it is less complex[2,6], whereas the phylogenetic origin in cursorial theropods (some of which are now also known to have been feathered) favours the ground-up theory. A ground take-off requires a running speed equal to the minimum speed that can support the animal's weight in air (possibly adjusted for the ground-effect, which might reduce the lift required). Top running speed is believed to have been lower than the required take-off speed[7], but the speed might have been enough for take-off if *Archaeopteryx* was flapping its wings when taxiing[8]. Be that as it may, *Archaeopteryx* could probably fly fairly well. The basic question remains: what was the main selection pressure for the evolution of flight (i.e. how did a non-flying animal, probably a maniraptoriform dinosaur, begin to acquire the necessary adaptations for increased aerodynamic performance)? A team of zoologists from Oxford now offers a new hypothesis for how proavis became airborne.

The pouncing proavis

In a new study, Garner *et al.*[9] introduce the 'pouncing proavis hypothesis', which suggests that the bird-to-be was a predator specialized in ambush attacks from elevated sites. Garner *et al.* envisage that lifting surfaces initially developed distally on the forelimbs to increase control and manoeuvrability during the aerial part of the attack. If pounces were initiated from slightly elevated sites, gravity would have assisted the leaping attacks, facilitating the evolution of flight. The pouncing proavis hypothesis therefore combines elements from both the arboreal theory (attacks from elevated sites) and Caple *et al.*'s[3] version of the cursorial theory, in which a bipedal animal developed incipient flight surfaces to control leaps from the ground. Pounces gradually became longer swoops and eventually the animal developed true flight.

A strength of the pouncing proavis theory is that the acquisition of flight adaptations can be mapped onto the current cladogram of theropod dinosaurs (including birds), which indicates a sequence in agreement with the new theory. This approach represents a clearer and more rigorous analysis than most previous studies of the evolution of flight. Garner *et al.*[9] use five features (ancestral state, feather asymmetry, placement of wings, weight reduction and transition from theropodan to avian gait) with which to compare the predictions of the competing theories for the evolution of flight. Not surprisingly, only the pouncing proavis theory correctly predicts the evolutionary order of all five characters. The cursorial theory (both run–jump glide and flapping start versions) is second, whereas the arboreal theory predicts only that the transition to avian gait occurs late in avian evolution[9]. In this respect, the present consensus that the cursorial scenario is more likely than the arboreal scenario appears to be supported (cf. Ref. 1).

But what should we conclude from this new hypothesis? Scientific history in this field has been dominated by two rival theories that have divided scientists into two camps – cursorial versus arboreal – where the main focus has often been criticism of the other theory[1]. However, because the pouncing proavis model combines features of both previous theories, it will be interesting to see how the new idea will be received by the scientific community. The recently found feathered dinosaurs have settled the question of avian ancestry. It is also clear that the aerodynamic function of feathers is a secondary adaptation (or an exaptation in the terms of Gould and Vrba[10]). However, the evolutionary route to active flight is difficult to disentangle because behaviours do not leave fossils.

Will we ever know?

Evolutionary ecologists tend to think in terms of adaptive function. This is also true about the evolution of flight (with some amusing exceptions[1]). In both the cursorial and pouncing proavis theories incipient distal wings evolved to increase the control of running–leaping and attack success, respectively. It is easy to see how enhanced accuracy of ambush attacks is favoured by selection. Modern birds require less energy for transport than terrestrial running animals[11], hence, the cost of transport could have been an important currency for natural selection in a central place foraging proavis[12]. Theoretically, however, this would work in both an arboreal and cursorial context[2,3]. Therefore, comparing the predictions of the different theories in relation to various characters is perhaps the best way to proceed, even if the selected features compared by Garner *et al.*[9] are contested or more features are added to the analysis. One potential problem with a pouncing proavis is that we do not know why a cursorial dinosaur became a sit-and-wait ambush predator.

Evolution of flight is a fascinating field and the last word has by no means been said. New and interesting fossils are being reported at an increasing rate, and refined phylogenies combined with biomechanical considerations are definitely taking us closer to the solution of a great scientific conundrum. But perhaps we will never know for certain how birds took off, whether from the ground, a tree or because of a predatory habit.

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Mosaic landscapes, family structure and evolution

Many species populations consist of small groups of genetically related individuals rather than randomly arrayed entities of related and unrelated individuals. This has many important consequences for the evolutionary dynamics of these species, but we need to know the mechanisms responsible for such clustering, how common a phenomenon it is, and how it affects evolution of natural populations. For these reasons, the scales at which patterns and processes interact are attracting increasing attention from both ecologists and geneticists. The best known examples of such studies concern the analyses of metapopulations and their subdivisions[1]; however, it is becoming increasingly evident that predictably organized mosaics also exist at smaller scales.

Recently, Giles, Goudet, Ingvarsson and colleagues[2–4], who have studied the population ecology and genetics of the bladder campion [*Silene dioica* (Caryophyllaceae)], have documented a remarkably dynamic system involving metapopulations on arrays of newly arisen islands. These metapopulations are so heterogeneous in distribution and genetic constitution that clustering of plants into groups of genetically related individuals can be detected. This organization provides opportunities for evolutionary change that might occur as a result of intergroup selection.

The landscape

The Skeppsvik Archipelago, in the Gulf of Bothnia off the coast of Sweden, covers an area of about 20 km[2], and is composed of about 100 islands formed from morainic deposits accumulated following the melting of glaciers ~7700 years ago. New islands are constantly created, because the deposits are uplifted rapidly (almost one metre per century). This rate of uplift and the height of islands above sea level can be used to estimate island age.

In this ever-changing environment, Giles and colleagues[2–4] have been studying the process of colonization of the islands by *S. dioica*, a dioecious, perennial herb that reproduces when 2–3-years old and has a life expectancy of ~ten years. *Silene dioica* is pollinated by bumblebees (*Bombus* spp.); its seeds drop out of capsules near the female parent and most of these then form a group of seedlings around their mother. Seeds mix with plant debris and can be subsequently transported by the sea to other islands in drift material. New demes (local interbreeding groups) can become established after a few adjacent individuals of both sexes have flowered simultaneously and their progeny have germinated nearby. Knowledge of island age and local successional rates can be used to estimate individual population ages. The short generation time of the plants, coupled with rapid ecological change on the islands, means that family groups and local populations have high turnover rates.

These conditions are ideal for studying the interplay between population establishment, persistence, size, age and genetics, to determine the contributions of colonization and extinction to genetic architecture and differentiation. In a series of studies, Giles and colleagues[2–4] used increasing ecological magnification to analyze progressively smaller scales of spatial patterns and associated genetic differentiation. At the largest scale, 52 islands were sampled and analysed indicating the existence of significant restriction of gene flow (and associated departures from random mating) and differentiation. Colonization of islands by new seeds can occur from more than one source, and the genetic differences among colonizers account for much of the differentiation observed. There is also considerable variation in patterns of mating, distribution of genotypes within islands and genetic constitution of island populations[2].

Mechanisms of genetic clustering

The specifics of intra-island genetic architecture and the exact size of breeding units were studied on four neighbouring islands. Detailed studies of seed dynamics and genetics in *S. dioica* showed that breeding units, within which mating is random, are typically between 0.2 and 6.0 m[2], and often consist of three to four reproductive individuals (a total of 9–21 plants). This pattern was consistent among the four islands, indicating that the dynamics of *S. dioica* are predictable in these habitats.

These results help to explain why the large amount of genetic differentiation observed among patches within islands was markedly greater than that among the four islands. This is somewhat counter-intuitive because, given the limits of gene flow and patterns of landscape heterogeneity, the usual expectation is that genetic differences increase with geographic distances. Giles and colleagues[2,3] hypothesize that this pattern occurs as a result of repeated movement of seeds and pollen among islands over a few generations, causing islands to receive mostly the same alleles. Conversely, individual patches are founded by few individuals.

To understand better the interplay between ecological and genetic details of patch dynamics, Ingvarsson and Giles[4] analysed a single population established less than ten years ago, consisting of ~700 mature individuals divided into 34 patches. Mapping and genetic analyses

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