

Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

MIGRATION



MIGRATING GEESE: NATURALLY ATHLETIC COUCH POTATOES?

Migrating birds accomplish the extraordinary feat of trans-oceanic and even trans-hemispheric treks, a true marvel of the animal kingdom. Prior to these excursions, many bird species display dramatic changes in morphology, withering less crucial organs and increasing essential flight components like heart and flight muscle. Although bulking up muscle in humans necessitates an increase in their use or exercise, recent evidence in birds suggests an additional endogenous capacity for muscle gain, independent of behaviour or the environment. Barnacle geese (*Branta leucopsis*) are known to increase production of key metabolic proteins prior to migration. Wild, flighted birds of this species have significantly higher levels of these proteins than do flightless captive or juvenile geese. This suggests that for this species, flight training may be crucial to migratory readiness. With this knowledge, Steve Portugal of the University of Birmingham (now at the UK's Royal Veterinary College) and his international team set out to further investigate these trends, predicting that long-distance migrants like the barnacle goose might increase flight activity prior to migration to achieve a heftier physique and stimulate essential protein production.

The team caught wild barnacle geese near Norway's Ny-Ålesund research station, implanted custom-made heart rate loggers into the birds' abdomens, and recaptured the birds the following year. The data loggers monitored the heart rate of the birds continuously throughout the year, including both the spring and autumn migrations. As it is known that heart rate increases dramatically during flight, these records allowed the researchers to construct flight activity patterns. Using this strategy, the team calculated the time in flight for each day for each goose in addition to comparing

heart rate patterns during distinct annual phases (pre-migration, migration, breeding and wing-moult). Portugal's crew discovered that, contrary to their original hypothesis, there was no difference in the time spent flying per day in the pre-migratory phase compared with any other period. As a buildup of flight muscle prior to migration has previously been documented in this species, this implies that increased flight activity is not required to achieve their burly physique.

Other bird species show strong relationships between pre-migratory mass gain and increased flight muscle. It is possible, then, that the corresponding increases in wing loading due to the heftier build documented in pre-migration barnacle geese triggers an increase in flight muscle. With this loading effect, the usual amount of time spent flying (just 22 min day⁻¹ for these geese) may be adequate to achieve buildup of flight muscle prior to migration, and potentially induce essential protein production. It is also possible that any endogenous capacity for muscle building in waterfowl may support this pre-migratory couch potato approach. Nonetheless, this study reveals that a flight-training regime is not required to prime the barnacle goose for its impressive long-distance migration. As flight is the most costly form of vertebrate locomotion, 10–20 times more energetically expensive than the resting state, this may also reflect a strategy to conserve vital energy stores for the remarkable journey that lies ahead.

10.1242/jeb.064394

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THERMAL ONTOGENY



LIZARD WITS INCREASE AS PLANET HEATS

We all know an animal is the product of its genes and the influence of the environment. Humidity, food availability and parental care are just examples of factors that can have a strong impact on an animal's characteristics. This is certainly true in the case of reptiles, where incubation temperature can affect several of their physical and physiological characteristics. It is well known, for example, that sex, size and running speed can all be influenced by temperature in various lizard species. But what about other, less-obvious characteristics? It is harder to measure how incubation temperature affects different aspects of behaviour and intelligence. None the less, these are interesting questions and Joshua Amiel and Richard Shine from the University of Sydney, Australia, decided they were worth pursuing.

They wanted to know whether incubation temperature affected young lizards' ability to learn. Moreover, they wanted to know whether an increased ability to learn would be relevant during a life-threatening situation. To do this, Amiel and Shine collected gravid three-lined skinks, which are lizards native to Australian forests. They took them back to their lab in Sydney and incubated their eggs at cold ($16 \pm 7.5^\circ\text{C}$) and hot ($22 \pm 7.5^\circ\text{C}$) regimes. When the babies hatched, it was time for their IQ tests inside their own homes so that they would not have to deal with the additional stress of learning in a strange environment. Each enclosure had two small hiding retreats but the entrance to one of them was blocked with a piece of Plexiglas. For each test a baby lizard was placed right in the middle between the two retreats under a little plastic cover. As soon as the experimenter lifted the cover, he tickled the lizard's tail with a paintbrush, scaring the poor lizard, which ran for a hiding place. The scientists then counted the number of times that the hatchling chose the wrong

hide and the time it took to finally find the available retreat. They repeated these trials for 4 days, four times a day with each lizard and then compared the reptiles' success rates through time. Were they learning?

All the babies were capable of learning and made fewer mistakes the more tests they performed, but as time went by, the hatchlings that had been incubated in the hot environment learned faster and made fewer mistakes than the cold-incubated ones. This was independent of sex, size or running speed.

The fact that warm-incubated lizards turned out to be smarter than cold-incubated lizards gives a glimpse of what might happen during global warming. Amiel and Shine point out that this increased ability to learn will increase the lizard's capacity to respond in the face of environmental changes and therefore increase their chances of survival. The study does not dismiss the possibility that cold-incubated lizards may 'catch up' with their warm-incubated counterparts as they develop, or even compensate for their slower wits with other abilities such as locomotor speed. However, this does not negate the fact that lizards from hot eggs have the edge over their cool-egg friends.

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GROWTH



REDUCED GROWTH IN FIXED FISH

Growth and reproduction are intimately linked by the endocrine system. Pituitary growth hormone (GH) is a major driver of body growth, and modulation of its expression and secretion can be influenced by sex hormones. Despite the established relationship between growth and reproduction, however, the precise role of the gonads in regulating body growth has not been adequately studied, particularly in species displaying sexual growth differences.

Takeshi Miura and his team from Ehime University in Japan began their study with a simple question – what role do the gonads play in body growth? To answer this question, they removed the gonads from Mozambique tilapia (*Oreochromis mossambicus*) 40 days after hatching – when the immature fish can be readily sexed by eye. Then, some fish received their gonads back, although the scientists relocated the gonads between the skin and muscle, and all the fish were weighed 50 days later (at sexual maturity) to determine whether there were any differences in their body masses. Miura and colleagues also measured plasma concentrations of key sex hormones – including 11-ketotestosterone, which is usually produced by the testes and estradiol, which is usually produced by the ovaries – as well as plasma growth hormone and gene expression levels of growth hormone and insulin-like growth factor 1.

The researchers found that fish of both sexes without gonads had significantly reduced body mass compared with fish that had not had their gonads removed. In addition, the fish that had regained their gonads after they were initially removed fully recovered their mass. However, when the team looked at the fish's sex hormone levels (11-ketotestosterone and estradiol) there was no correlation between sex

hormone level and body size, with males and females showing different hormone patterns. Therefore, as the growth patterns of the two sexes responded identically to the loss and return of their gonads, the changes between the sexes indicate that sex hormones alone cannot explain the influence of gonads on growth.

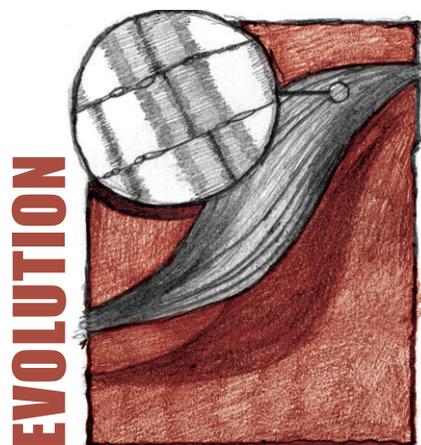
The authors then looked to growth hormone and insulin-like growth factor 1 to explain how gonads directly influence growth. While there were no differences between treatments in the transcript levels of these genes in the pituitary, gonads or liver, levels of growth hormone in the plasma were significantly reduced in male and female tilapia that had lost their gonads. However, the males and females that had received their gonads back fully recovered their plasma growth hormone levels, suggesting that growth hormone produced by the gonads is secreted into the blood to help regulate body growth. This finding is particularly important as it calls into question the long-held assumption that all circulating growth hormone originates from the pituitary. While many other tissues express growth hormone, the conventional thought is that it acts locally and is not secreted into the blood. Miura's study suggests that the gonads are also significant sources of circulating growth hormone, at least in teleosts.

Using a conceptually simple technique, Miura's team clearly show that fish gonads are necessary for normal growth in teleosts, and that growth hormone – not sex steroids – is the major factor governing this relationship. Another important finding is that the pituitary may not be the sole source of circulating growth hormone in non-mammalian vertebrates, opening new avenues of research into the functions of growth hormone from tissues other than the pituitary.

10.1242/jeb.064386

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STRIATED MUSCLES EVOLVED INDEPENDENTLY

Animal life is intimately associated with the ability to move, which allows animals to find food, reproduce or escape predators. Animal locomotion thereby relies on striated skeletal muscles, whose ultrastructure is strikingly similar even in non-related taxonomic groups such as cnidarians (a group of animals including jelly fish) and bilaterians (animals with fronts, backs, tops and bottoms, including all insects and vertebrates). It was this similarity that suggested a common evolutionary origin of striated skeletal muscles, albeit the molecular details of striated muscle evolution have not hitherto been addressed. In a phylogenetic study published recently in *Nature*, Ulrich Technau from the University of Vienna, Austria, and colleagues from various institutions around the world provided evidence for a convergent evolution model of striated muscles, in which newly evolved proteins were added progressively to ancient components of the contractile units promoting independent muscle evolution in cnidarian and bilaterian species.

Striated muscles are made of specialized cells that have fused to form contractile fibrils. These cells contain sequences of sarcomers, which are the smallest contractile units found in muscles. The sarcomers contain thin actin filaments and thick myosin-based filaments that slide against each other in an ATP-dependent manner resulting in contractions, which are meticulously regulated by additional muscle proteins such as the troponin complex. To reassess muscle evolution, the scientists defined a core set of muscle proteins and screened for their presence in various genomes. One of the core proteins that they focused on was a type II myosin heavy

chain (MyHC) motor protein that emanated from a gene duplication event giving rise to two different phylogenetic forms: a striated muscle-specific form (ST MyHC) that functions in muscle contraction, and a non-muscle form (NM MyHC) that serves other cellular functions such as cell division or migration. Technau and his team expected that the gene duplication event that led to the appearance of ST MyHC would coincide with the emergence of striated muscles during the evolution of metazoan animals. To their big surprise, however, they found that ST MyHC was already present in unicellular organisms before the origin of muscles and multicellular animals.

Thrilled by this finding, they analysed the gene expression patterns for ST and NM MyHCs in different non-bilaterian sponges and cnidarians by whole-mount *in situ* hybridization. In muscle-lacking sponges, they found NM MyHC was expressed in a wide range of cells, whereas expression of ST MyHC was restricted to cells involved in controlling the water flow necessary for nutrition. The differential expression suggests that the diversification of ST and NM MyHC forms had already occurred before the emergence of striated muscles. Cnidarians, which possess striated muscles, express the ancient ST MyHC in muscle cells but they lack other components (such as the troponin complex, paramyosin or titin) that are typically found in striated muscles of 'higher' bilaterian animals. This finding in turn suggests that despite the striking ultrastructural similarities, striated muscles have evolved independently in cnidarian and bilaterian animals.

Ulrich Technau and his team showed that the origin of core components of striated muscle cells (such as ST MyHC) predates that of muscle cells, and that other components were added progressively during muscle evolution in different animal groups. The proposed convergent model of striated muscle evolution may also apply to the evolution of other specialized cell types, which also exhibit ultrastructural similarities in different animal groups.

10.1242/jeb.064402

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