Specialising on Change Part 4: Burrowing

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Biol 417: Evolutionary Ecology

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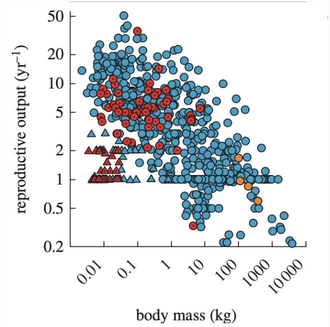
Review

Dormancy allows organisms to ‘ride out’ unfavourable periods, but there is upper limit on how long species can stay dormant, which increases with body size in mammals, meaning large mammals are more suited to long periods of hibernation.

...but hibernation occurs mostly in small to intermediate sized mammals.



(Turbill & Bieber, 2011)

We also covered how animals are subject to the physics of energy transfer, and adaptations to cold environments involve minimising

$$\frac{dE}{dt} = -kA\frac{\Delta T}{L}.$$

We saw how large body sizes and short limbs decrease A, fat layers increase L, and summer vs. winter fur coats give mammals the capacity to modify k, and we stopped at ΔT.

Eocene-Oligocene Boundary

Eocene Climatic Optimum

The Eocene epoch occurred between 56 and 33.9 million years ago.

The Eocene was characterised by a warm and relatively stable period known as the 'Eocene Climatic Optimum', with mean annual temperatures in North America, ranging from 9-24 °C, and winter temperatures well above freezing.

Source: American Museum of Natural History

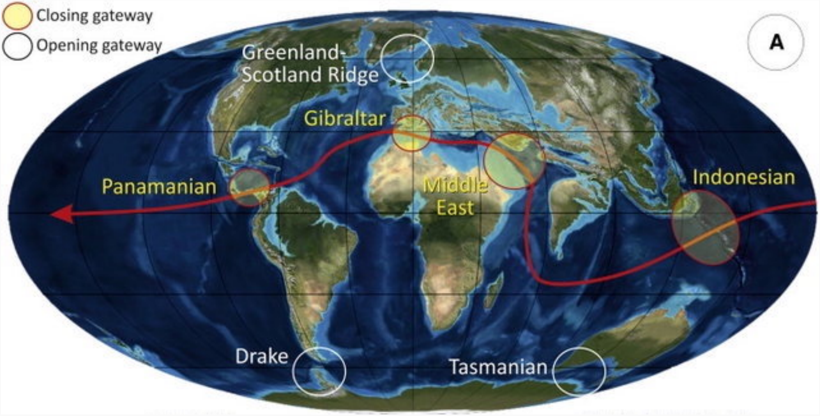
Eocene Climatic Optimum cont.

Landscapes were dominated by tropical forests and many new mammalian groups started appearing in the fossil record (e.g., perissodactyls, artiodactyls, proboscideans, rodents, primates, and carnivores).

Source: Crater Lake Institute

Then came the Oligocene...

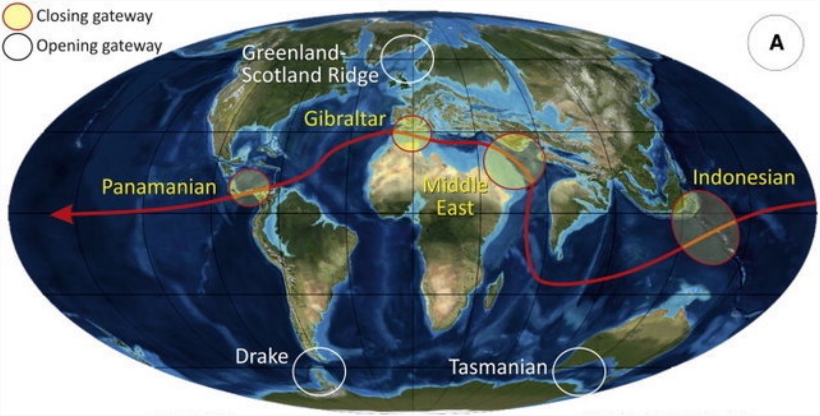
During the Eocene-Oligocene transition, warm ocean currents were disrupted, cold ocean currents began to flow between the newly separated Antartica and Australia, and the polar ice caps expanded.



(Rebesco *et al.*, 2014)

Oligocene cont.

The Earth underwent a shift to globally cooler (7-10 °C), drier, and variable conditions with pronounced seasonality, resulting in mass extinctions (i.e., the 'Grand Coupure').



(Rebesco *et al.*, 2014)

Oligocene cont.

The climatic changes over the Eocene-Oligocene boundary favoured plants using C4 photosynthesis only found in angiosperms, predominantly poaceae grasses.

Middle-Eocene forests gave way to late-Eocene dry woodlands, then to early-Oligocene wooded grasslands, and finally to mid-Oligocene grasslands.

Oligocene Selection Pressures

During this hypothermal transition organisms had to achieve an energetic balance under colder conditions (i.e., a new, and greater ΔT) and increased variability in foraging conditions due to pronounced seasonality.

Natural selection therefore favoured taxa more able to adapt to these challenges (i.e., minimising $\frac{dE}{dt}$) either via the adjustment of their conductive properties (k, A, and L), or by occupying environments that minimised ΔT.

This triggered a pronounced radiation in mammalian burrowing behaviour (Nevo, 1999) and 447 of 777 genera of extant terrestrial mammals include burrowing species (Kinlaw, 1999).

Palaeocastor

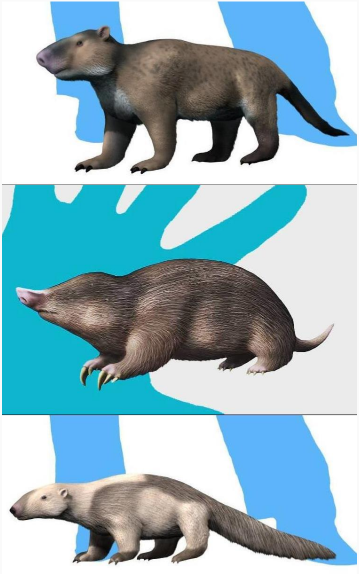
Source:Wikipedia

Source:Wikipedia

Palaeocastor fossor: A late Oligocene beaver that lived in the North American Badlands in a helical burrow called the '*daimonelix*'.

Palaeontologists believe that the corkscrew shape helped maintain consistent temperatures and humidities (Meyer, 1999).

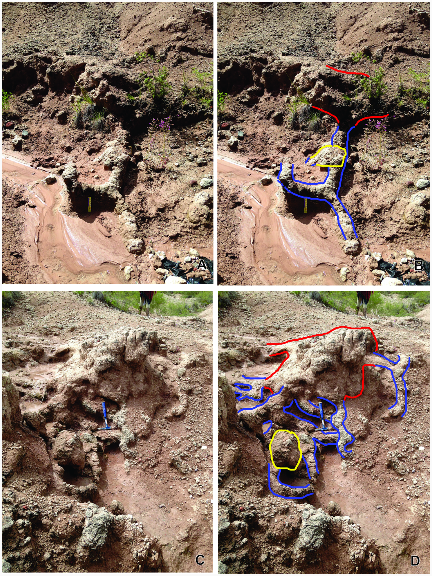
Pseudochrysochloris



Source:Wikipedia

Pseudochrysochloris: An early Oligocene burrowing palaeanodont that lived in Wyoming.

Had strong forelimbs that evolved for rapid scratch digging (Turnbull & Reed, 1967).



Source: Guerrero-Arenas *et al.* (2020)

Yaviichnus inyooensis: A late Eocene/early Oligocene burrowing geomyid rodent that lived in southern Mexico.

Their burrow systems were complex with tunnels, main chambers, and secondary chambers, and likely evolved as an adaptation to facilitate thermoregulation (Guerrero-Arenas *et al.*, 2020).

Eocene-Oligocene Take Homes

Dramatic cooling and aridisation occurred the Eocene-Oligocene transition period and energetic balances were challenged by a new, and greater, ΔT.

Seasonality and cooling resulted in mass extinctions (opening niche space), and strong selection pressure (spurring change).

Burrows and burrowing species were mostly absent in the 'Eocene Climatic Optimum', but dominate the fossil record during/after this transition period.

Burrowing behaviour likely saved many taxa from extinction (Nevo, 1999) and 447 of 777 genera of extant terrestrial mammals include burrowing species (Kinlaw, 1999).

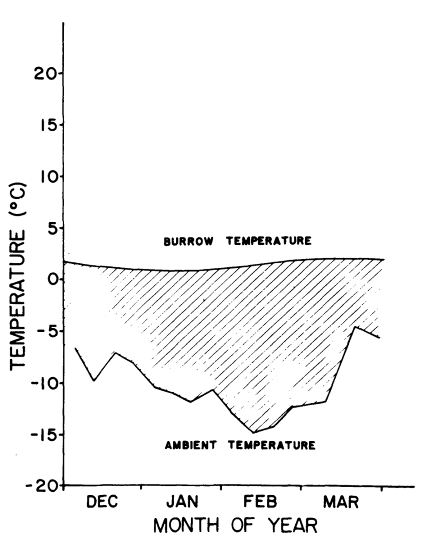
Energetics of Burrowing

Energetic roots of burrowing

Fossil evidence tells us that energetics are at the root of the radiation in burrowing behaviour (tightly correlated with the advent of seasonality and atmospheric cooling).

...but why burrowing?

Burrow conditions



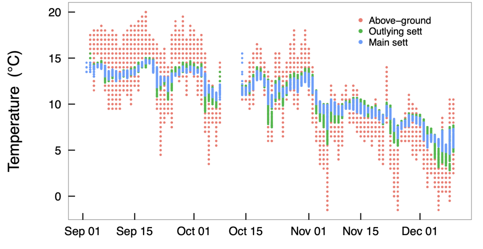
Source: Harlow (1981)

Source: Wisconsin Dept. of Nat. Res.

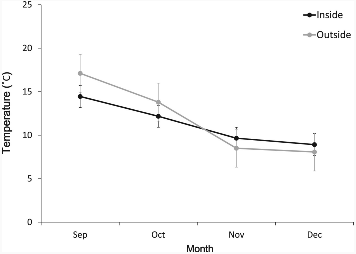
Taxidea taxus: Undergo seasonal torpor in burrows during winter months.

Burrow temp. is extremely stable and can be 20°C warmer than temperatures above-ground.

Burrow conditions cont.



Source: Noonan *et al.* (2018)

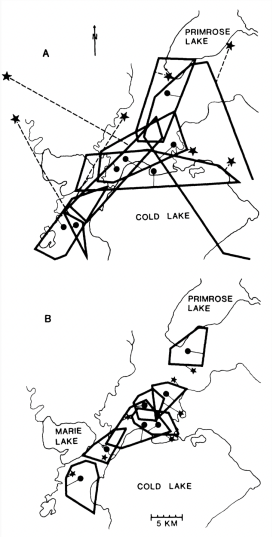


Source: Tsunoda *et al.* (2018)

Meles meles: Sett temp. is less variable (i.e., predictable) than temperatures above-ground.

Setts buffer against hot conditions in the summer and cold conditions in the winter.

Energetic benefits of burrows



Source: Tietje & Ruff (1980)

In overwintering black bears (*Ursus americanus*) in Alberta, males that remain in a single hibernaculum could conserve 84% of their body mass.

If disturbed, and forced out of their den, the amount of body mass conserved was reduced to 75% (Tietje & Ruff, 1980).

Energetic benefits of burrows cont.

Source: Milton Keynes FM

Source: Getty images

Kaneko *et al.* (2010) looked at the relationship between the thermal stability of European badger setts, and offspring survival.

Setts varied in size and thermal stability.

Cubs born in setts with the warmest, most stable conditions over winter had greater survival than cubs born in colder, less stable setts.

Energetic benefits of burrows cont.

Temperatures in burrows are stable and predictable vs. variable and unpredictable conditions above-ground ground (i.e., provide thermal refugia (i.e., minimising the impacts of ΔT).

This thermal buffer minimises energetic losses to the environment, and decreases thermoregulatory costs, allowing organisms to survive longer unfavourable periods.

So why don't all species burrow?

Cost of burrowing

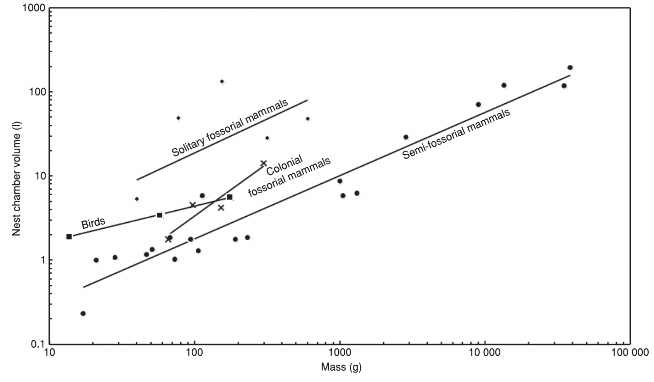
Constructing a burrow is expensive.

For a 150g pocket gopher (*Thomomys bottae*), burrowing a 1m tunnel requires up to 3,400 times more energy expenditure than traveling the same distance above-ground (Vleck, 1979).

Source: Wikipedia

Constructing a burrow is expensive.

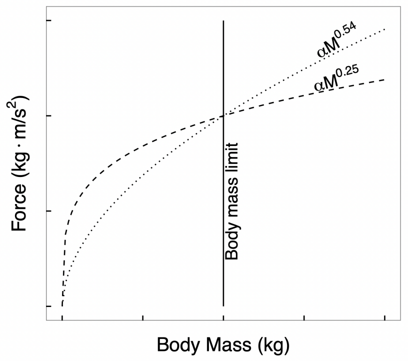
The energetic costs of burrow construction increases with body size (White, 2005).



Source: White (2005)

Constructing a burrow is expensive.

The energetic cost of digging scales with body size with an exponent of 0.54, wheres the amount of muscular force available scales with an exponent of 0.25 (Noonan, 2015).



Source: Noonan (2015)

Cost of burrowing cont.

As a consequence, there are lots of small (<1 kg) burrowing species (Nevo, 1999), but large fossil burrows are rare (Voorhies & Toots, 1970), and the largest extant burrowers, aardvarks (*Orycteropus afer*), weigh ∼50 kg (McNab, 1979).









Fossorial exaptations

There is also the non-trivial question of how to dig?

Of the vertebrates, the principal burrowers are the mammals, which have the dentition, claws strong forelimbs, and muscle mass large enough to exert the force required to dislodge soil (Kinlaw, 1999).


Take home messages

Environmental change opens up niche space.

Specialising on predictable environmental change via migration, dormancy, burrowing, storing energy reserves, moulting, etc... allows species to capitalise on otherwise open niche space.

... but it also generates new challenges (e.g., reliance on energy reserves, exposure to variable weather, increased predation risk during dormant periods, seasonal mating opportunities, migrating over large distances, etc...).

We will discuss some of the downstream impacts of these specialisations next lecture.

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