Socio-ecology Part 4: Why Are British Badgers Social?

Michael Noonan

Biol 417: Evolutionary Ecology



- 1. Review
- 2. Badger Ecology
- 3. Predator Avoidance Hypothesis
- 4. Information Center Hypothesis
- 5. Mate Guarding and Group-Living
- 6. Resource Dispersion Hypothesis
- 7. Safe Havens and Natal Philopatry

Biol 417: Evolutionary Ecology

Review



We have covered 5 mechanisms underpinning the formation **and** maintenance of stable spatial groups.

Mate guarding, predator avoidance and information sharing brings individuals together, but often fall short when providing a mechanism for the maintenance of **stable** spatial groups.

The resource dispersion provides a mechanism for the passive formation of spatial groups but empirical support is limited.

The safe haven model accounts for both the relative costs and benefits of dispersal and philopatry but the parameters are 'catch-alls' without specific mechanisms ($\alpha, \beta, \mu_F, \mu_S, T_F, T_S$).



No single hypothesis is likely to explain the propensity for group living in any species.

A species' ecology, and local conditions are critical for dictating how these hypotheses interact to tip the cost-benefit balance in one direction or the other.

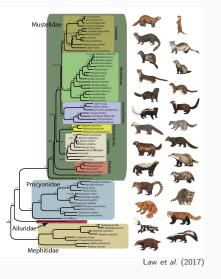


Today we will see how these 5 hypotheses help us understand group-living in British badgers (*meles meles*) as a case study.

Badger Ecology

Phylogeny





European badgers are carnivores of the Melinae subfamily that diverged from the rest of the mustelids ca. 14.8 million years ago (Law *et al.*, 2017).

Mustelids are a diverse group of small to medium sized predators that form the largest family in the order Carnivora.

Most are solitary.



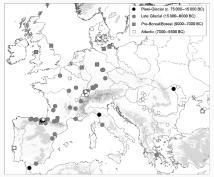
Badgers have an extensive biogeographic distribution and experience varying degrees of seasonality, foraging conditions, predation threat, sett use, and sociality across their range.



Source: Wikipedia



In the Late Glacial (15000–9000BC), *M. meles* was the most frequent mustelid species in the European fossil record and appear relatively tolerant of climatic extremes (Sommer & Benecke, 2004).



⁽Sommer & Benecke, 2004)



Badgers are generalists, feeding opportunistically on berries, nuts, cereals, earthworms, carrion, and small mammals (Roper, 1994).

... but in Britain, they tend toward trophic specialisms, feeding extensively, though not exclusively, on one species of earthworm, *Lumbricus terrestris* (Kruuk & Parish, 1981).



Over their range, badger densities vary from <1 badger/km² across Continental Europe to >36 badgers/km² in high density regions of the United Kingdom (Johnson *et al.*, 2002).

Across mainland Europe they are solitary/pair-living, in Britain large groups of 25+ animals are common (Macdonald *et al.*, 2015)



	Continent	Britain
Predators	Wolves, Lynx, Bears (rare)	None
Diet	Generalists	Flexible Specialists
Climate	Variable	Mild
Sett Use	Variable	Variable
Sett Size	Variable (small common)	Variable (large common)
Litter Size	1-5	1-5
Density	${<}1~{ m badger/km^2}$	>36 badger/km ²
Sociality	Solitary/Pairs	Large Groups

Predator Avoidance Hypothesis



Mechanism: Aggregations serve to dilute the individual level predation threat.





Predation threat: Badgers have few predators and all are restricted to Continental Europe.

Verdict: Predator avoidance is unlikely to play a role in badger socio-ecology.

Biol 417: Evolutionary Ecology

Information Center Hypothesis



Mechanism: Aggregations provide individuals with information on the foraging activities of conspecifics.



Source: Wikipedia



Continental badgers are opportunistic omnivores (clumped unpredictable food sources), British badgers are vermivorous specialists (homogeneously distributed food source).





Source: The Glam Pad

ICH and foraging ecology: Continental badgers would benefit most from learning about ephemeral food sources.

Verdict: Information sharing is unlikely to drive bad. socio-ecology. Biol 417: Evolutionary Ecology 17

Mate Guarding and Group-Living

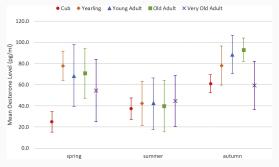


Mate guarding brings individuals together and provides a path towards group-formation if aggregations can be maintained outside of the breeding season (Lukas & Clutton-Brock, 2013)

... but badgers have superfetation and delayed implantation in order to precisely time the birth of offspring with spring resources/weather (Yamaguchi *et al.*, 2006).



Mating can happen at any time in the year and mate guarding is inefficient.

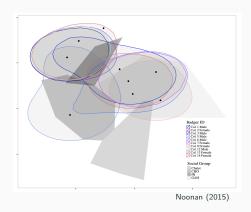


Sugianto et al. (2020)



Badgers have a polygynanandrous mating system (Annavi *et al.*, 2014), resulting in:

- $\bullet\,$ ca. 2/3 of cubs being fathered by males from different groups.
- $\bullet\,$ ca. 10% of litters contain cubs from multiple fathers.



B

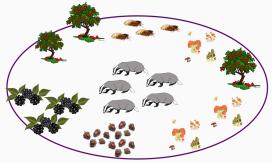
Badger spacing is consistent with predictions of the mate guarding hypotheses (females with non-overlapping home ranges and males overlapping multiple females), but genetic and behavioural data provide no evidence of mate guarding.

Verdict: Unclear. No evidence of mate guarding, but spatial structure hints at the ghost of a mate-guarding past.

Resource Dispersion Hypothesis



Mechanism: If the dispersion and renewal rate of local resources result in a territory that can viably accommodate multiple individuals, groups can arise without any specific benefits, assuming there are minimal costs to the 'primary territory holder'.





Continental

Diet: Omnivory Densities: <1 badger/km² Group size: 1-2



Britain

Diet: Specialists w/ omnivory Densities: $>36 \text{ badger/km}^2$ Group size: 25+



Badgers' flexible sociality is correlated with resource abundance and feeding ecology

Biol 417: Evolutionary Ecology



RDH assumes no (or minimal) costs to the primary territory holder.

Badgers suffer from severe parasitic infestations and group size is correlated with parasite loads (Johnson *et al.*, 2004). Cub mortality is high (up to 70%) and driven by parasitic infections (Macdonald & Newman, 2002).



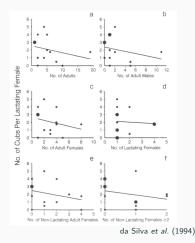
Source: Francis J Taylor Photography



(Macdonald & Newman, 2002)



RDH assumes no (or minimal) costs to the primary territory holder.



There is also a (weak) negative relationship between group size and reproductive success (da Silva *et al.*, 1994).

Verdict: Unclear. Resource abundance and feeding ecology correlate with group size, but group-living incurs costs.

Safe Havens and Natal Philopatry

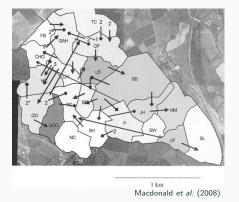


Mechanism: Natal territory acts as a 'safe haven' for waiting for breeding opportunities assuming the benefits of philopatry (P) outweigh the benefits of dispersal (D).

$$D = \frac{\beta T_F}{\mu_F} \qquad \qquad P = \frac{\alpha T_S}{\mu_S}$$

 β = competitive ability of floater $T_F = \#$ of terr. floater can obs. μ_F = Mortality of floater α = competitive ability of sub. $T_S = \#$ of terr. sub. can obs. μ_S = Mortality of subordinate





In a high-density population in Wytham Woods, only ca. 10% badgers disperse from their natal group (Macdonald *et al.*, 2008).

Energetic benefits of burrows





Source: Milton Keynes FM



Source: Wikipedia

Setts vary in thermal stability. Large established setts are more stable than small setts.

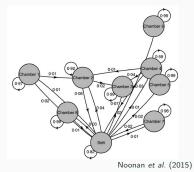
Cubs born in setts with the warmest, most stable conditions over winter had greater survival than cubs born in colder, less stable setts (83.3% vs. 27.3% Kaneko *et al.*, 2010).

Cubs born in large main setts were also more philopatric than those born in small setts.

Energetic benefits of burrows cont.







Noonan *et al.* (2015) found that in mid-winter, badgers were never away from the sett for more than ca. 3-4 hrs and exhibited a preference for deeper, warmer chambers.

Setts play a role in maintaining an energetic balance through adulthood.

Verdict: Philopatry is common and related to natal group survival.

Biol 417: Evolutionary Ecology



PAH Verdict: Predation threat is unlikely to govern badger socio-ecology.

ICH Verdict: Information sharing is unlikely to govern badger socio-ecology.

Mate Guarding Verdict: No mate guarding, but spatial structure suggests that mate guarding may have been important historically.

RDH Verdict: Resource abundance and feeding ecology correlate with group size, but group-living incurs costs.

Safe Haven Verdict: Philopatry is common and related to natal group survival.

Biol 417: Evolutionary Ecology



Multiple mechanisms play a role in determining badger socio-ecology.

The gulf stream (mild, rainy conditions), combined with the conversion of large tracts of land to agriculture (70%) are likely key drivers (RDH).

Intense agriculture occurred around 3,000 BC, so badger societies are very new and explains why they exhibit very little cooperative behaviour.

References

- Annavi, G., Newman, C., Dugdale, H.L., Buesching, C.D., Sin, Y.W., Burke, T. & Macdonald, D.W. (2014). Neighbouring-group composition and within-group relatedness drive extra-group paternity rate in the European badger (*Meles meles*). Journal of Evolutionary Biology, 27, 2191–2203.
- Johnson, D.D.P., Jetz, W. & Macdonald, D.W. (2002). Environmental correlates of badger social spacing across Europe. Journal of Biogeography, 29, 411–425.
- Johnson, D.D.P., Stopka, P. & Macdonald, D.W. (2004). Ideal flea constraints on group living: unwanted public goods and the emergence of cooperation. *Behavioral Ecology*, 15, 181–186.
- Kaneko, Y., Newman, C., Buesching, C.D. & Macdonald, D.W. (2010). Variations in badger (meles meles) sett microclimate: differential cub survival between main and subsidiary setts, with implications for artificial sett construction. *International Journal of Ecology*, 2010.
- Kruuk, H. & Parish, T. (1981). Feeding Specialization of the European Badger Meles meles in Scotland. The Journal of Animal Ecology, 50, 773.
- Law, C.J., Slater, G.J. & Mehta, R.S. (2017). Lineage Diversity and Size Disparity in Musteloidea: Testing Patterns of Adaptive Radiation Using Molecular and Fossil-Based Methods. Systematic Biology, 67, 127–144.

Lukas, D. & Clutton-Brock, T.H. (2013). The Evolution of Social Monogamy in Mammals. Science, 341, 526-530.

- Macdonald, D.W., Macdonald, D.W., Newman, C., Newman, C. & Buesching, C.D. (2015). Badgers in the rural landscape - conservation paragon or farmland pariah? Lessons from the Wytham Badger Project. In: Farming and Wildlife. Conflict in the countryside (eds. Macdonald, D.W. & Feber, R.E.). Oxford University Press, Oxford, pp. 65–94.
- Macdonald, D.W. & Newman, C. (2002). Population dynamics of badgers (*Meles meles*) in Oxfordshire, U.K.: numbers, density and cohort life histories, and a possible role of climate change in population growth. *Journal of Zoology*, 256, 121–138.

Macdonald, D.W., Newman, C. & Buesching, C.D. (2008). Male-biased movement in a high-density population of the Eurasian badger (*Meles meles*). Journal of Zoology, 89, 1077–1086. Biol 417: Evolutionary Ecology 35

- Noonan, M.J. (2015). The socio-ecological functions of fossoriality in a group-living carnivore, the European badger (Meles meles). Ph.D. thesis, University of Oxford.
- Noonan, M.J., Newman, C., Trigoni, N. & Buesching, C.D. (2015). A new Magneto-Inductive tracking technique to uncover subterranean activity: what do animals do underground? *Methods in Ecology and Evolution*, 6, 510–520.
- Roper, T.J. (1994). The European badger Meles meles: food specialist or generalist? Journal of Zoology, 234, 437–452.
- da Silva, J., Macdonald, D.W. & Evans, P.G.H. (1994). Net costs of group living in a solitary forager, the Eurasian badger (*Meles meles*). *Behavioral Ecology*, 5, 151–158.
- Sommer, R. & Benecke, N. (2004). Late-and post-glacial history of the mustelidae in europe. Mammal Review, 34, 249–284.
- Sugianto, N.A., Newman, C., Macdonald, D.W. & Buesching, C.D. (2020). Reproductive and somatic senescence in the european badger (meles meles): Evidence from lifetime sex-steroid profiles. *Zoology*, 141, 125803.
- Yamaguchi, N., Dugdale, H.L. & Macdonald, D.W. (2006). Female Receptiveity, Embryonic Diapause, and Superfetation in the European Badger (*Meles Meles*): Implications for the Reproductive Tactics of Males and Females. *The Quarterly review of biology*, 81, 33–48.