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ZSL LIVING CONSERVATION

NEW

Editorial Board Member's Choice

By Alan McElligott

(Queen Mary, University of London)

The contribution of source–filter theory to mammal vocal communication research

Taylor, A.M. and Reby, D. (2010) *Journal of Zoology* **280**: 221-236.

For as long as I can remember, I have been interested in how animals communicate with one another, and in particular how vocal communication or vocal information transfer occurs. Some of my own earlier work examined how investment in calling affects reproductive success and the social factors linked to variation in short-term rates of vocalisation. However, I was often confused when examining the literature on the structure of calls and how information was conveyed by the many components. Authors wrote about various seemingly complex frequencies (e.g. fundamental or formant) and harmonics, showed puzzling spectrograms in figures etc., without clearly explaining what these were or how an animal produced them. I believe that one can only really comprehend the kind of information transfer that is going on when an animal utters a call, when there is some understanding of the production mechanism and how that is related to qualities of the caller.

This is where the source-filter theory of voice production comes in useful, and it was originally developed as a framework for studying human speech in the 1960s. According to the source-filter theory, vocalizations are generated by vibrations of the vocal folds ('source') and are subsequently filtered by the supralaryngeal vocal tract ('filter'). The source determines the fundamental frequency of the call (the term pitch is usually used when referring to human speech), whereas the filter shapes the source signal by selectively amplifying certain frequencies and dampening out others. This filtering mechanism produces peaks called formant frequencies. Furthermore, the source and filter can potentially vary independently of each other.

Our understanding of the evolution of vocal communication in animals (particularly mammals) has benefited greatly from the adoption of the source-filter theory of voice production, because it has allowed researchers to develop hypotheses within a testable framework for investigating the origin and function of vocal signals. This did not begin until the 1990s and the last 10 years have seen the number of studies using this framework increase greatly. This why the review of Taylor and Reby (2010) is very timely. The authors provide an excellent and easy to read review of the increasing literature in this rapidly developing field, which should attract the attention of both specialists and non-specialists alike.

Editorial Board Member's Choice

By Trent W.J. Garner

(Institute of Zoology, Zoological Society of London)

Hurt yourself to hurt your enemy: new insights on the function of the bizarre antipredator mechanisms in the salamandrid *Pleurodeles waltl*.

Heiss E, Natchev N, Salaberger D, Gumpenberger M, Rabanser A, Weisgram J, (2010) *Journal of Zoology* **280**: 156 - 162

Is this going to hurt me more than it's going to hurt you?

Amphibians are generally better known for barks rather than bites. Even less known is the ability of some species of amphibians to protrude bones through the epidermis as a means of predator deterrence. David Blackburn and coworkers (Blackburn et al. 2008) published an in-depth morphological examination of African frogs that use modified phalanges for defence. In this issue of Journal of Zoology, Egon Heiss and colleagues (Heiss et al. 2010) examine another example of amphibians using bony protuberances as antipredator defences. Heiss and co. report on an example in the other well-known amphibian clade, the caudates, and describe in detail how the Spanish ribbed newt, *Pleurodeles waltl*, project sharpened ribs. Newts initially exhibited escape behaviour when confronted with simulated predator stimulus, but newts adopted one of two defensive postures when experiencing prolonged stimulation and produced skin secretions as well. Both common tactics utilized by amphibians, but unlike other amphibians, newts also rotated their ribs forward, puncturing the skin where lateral trunk warts occurred. While the presence of protruding ribs was noted as early as the 19th century, Heiss et al. (2010) show clearly that ribs are not simply unsheathed through pores but instead pierce the skin when projected outside the body.

While the use of bones as defensive weaponry is fascinating on its own, this study is particularly relevant given the current focus on infectious diseases of amphibians as a conservation issue (Daszak et al. 1999). The skin is the first line of innate immune defence, and penetrating skin is a bad idea if you want to prevent microparasites from crossing this barrier. Yet the example described by Heiss and co seems rather well entrenched, evolutionarily speaking, since it incorporates behaviour, physiology and morphology. So why don't ribbed newts suffer constantly from infections? Evidence does exist that, at least in some circumstances, ribbed newts are killed by amphibian pathogens (J. Bosch pers. comm.) but immune response in this species does seem more complex (Schaerlinger et al. 2008). Perhaps *P. waltl* holds the key to developing an immunological approach to mitigating amphibian infectious disease? Or does it give insight into a mechanism through which multitrophic disease regulation may occur (Holt 2008)? As bizarre as Heiss and co say this antipredator mechanism is, their stimulating study may open the door to even more unpredictable and newt biological phenomena.

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Heiss E, Natchev N, Salaberger D, Gumpenberger M, Rabanser A, Weisgram J (2010) Hurt yourself to hurt your enemy: new insights on the function of the bizarre antipredator mechanisms in the salamandrid *Pleurodeles waltl*. *Journal of Zoology*

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Editorial Board Member's Choice

By Philip Bateman

Sexual selection is not the origin of long necks in giraffes

G. Mitchell, S. J. van Sittert & J. D. Skinner*,*
Journal of Zoology, Volume 278 Issue 4, Pages 281 – 286

The distinctive form of the giraffe – the long neck and legs, sloping back, chequered pelage and deep lustrous eyes with long eyelashes make it possibly one of the most iconic animals in the world. One of the first giraffes to be seen in modern Europe was the one presented to Lorenzo de'Medici of Florence in the late 1400s, causing a sensation, as did Zarafa the giraffe presented to Charles X of France in the 1800s when even clothes and hairstyles were based on the giraffe's coat pattern and the willowy neck. The Arabic word '*zarafa'* from which we derive 'giraffe' means, appropriately, 'the beautiful one'.

Of all the attributes of the giraffe, it is the long graceful neck that is most enigmatic. Darwin suggested that the long neck was a good example of natural selection, allowing individuals with longer necks to reach foliage inaccessible to competing species of browser. While this is undoubtedly an advantage, it has since been suggested that browse-competition may be an exaptation and the origin of the elongation of the neck lies in sexual selection through male-male competition. 'Necking' by competing male giraffes is a spectacular sight; each one lashes its head and neck like a club against that of its rival. As older males tend to have very heavy, solid heads carunculated with short horns and a bony roman nose it is easy to see how they could be formidable weapons wielded at the end of a long, muscular neck. A paper by Simmons & Scheepers (1996) examined and compared the necks of male and female Namibian giraffes and claimed support for the sexual selection hypothesis as male heads and necks were significantly heavier than they were in females of the same size and male head and neck mass increased throughout males' lives whereas in females they did not.

One of the wonderful things about the scientific method is that it revels in uncertainty and the retesting of hypotheses and potential undermining of previously supported ideas. A recent study in *Journal of Zoology* does just this with the compelling sexual selection hypothesis for giraffe neck elongation. Mitchell, van Sittert and Skinner examined the bodies of culled male and female Zimbabwean giraffes to see if head mass, neck mass, neck and leg length and the neck length to leg length ratio supported an origin in sexual selection. To show convincingly that part of a body is under sexual selection it should (1) be more exaggerated in one sex than the other; (2) used in dominance contests; (3) have no immediate survival benefits; (4) incur survival costs; (5) show positive allometry and (6) during its phylogenetic history show increases in size that are not correlated with size increases in other parts of the body. Mitchell *et al.*, however, found no significant differences in any of the body dimensions between males and females of the same mass, although mature males, whose body mass is half as great again as mature females, did have significantly heavier (but not longer) necks and heavier heads than did mature females; neither was there any real evidence for costs to fitness or survival through having a long neck. While the neck of the male giraffe evidently is used in male- male competition, the morphological differences between the sexes are minimal, and sexual selection does not seem to be the origin of a long neck in giraffes.

Empirical testing of hypotheses is the cornerstone of science; retesting of apparently established hypotheses are just as important and a vital part of how scientific knowledge moves forward.

Editorial Board Member's Choice

By Noga Kronfeld-Schor

(Tel Aviv University, Israel).

[The effect of perceived predation risk on pre-and post-metamorphic phenotypes in the common frog]

C.E. Stamper, J.R. Downie, D.J. Stevens & P. Monaghan, Journal of Zoology 277 (2009) 205-213.

Environmentally affected phenotypes were considered less important by evolutionary biologists, who were interested in the genetic basis of phenotypes. It is now widely accepted, however, that phenotypic plasticity (variation in environmental conditions eliciting variation in the traits expressed by a given genotype) is an evolutionary trait with genetic basis, subjected to selective pressure. As such, it has costs and benefits, and of course, ecological consequences. It can affect interaction between species, dispersal and distribution of species, community structure, and the way organisms maximize fitness in the face of both changing and variable environments.

Prey organisms have been the subject of studies of many researchers interested in phenotypic plasticity. Many prey species show a phenotypic plasticity in response to perceived predation risk, in traits such as behavior, morphological defense, physiological defense or any combination of the above. The potential benefit of the expressed phenotype may be offset by a cost. These costs were less frequently addressed.

In their paper, Stamper *et al.* studied the effect of perceived predation risk not only on tadpoles of the common frog (which are subjected to predation by the common hawker – *Aeshna juncea*), but also on the froglets, 4, 8, and 12 weeks post metamorphosis. As expected, they found that tadpoles developed deeper tail fins and muscles, and swam faster and further in response to predation risk. Interestingly, since Stamper *et al.* extended their study to the post-metamorphosis stages, they were able to show that there may be a long-term cost for tailoring the tadpole phenotype to the perceived predation risk: 12 weeks post metamorphosis, froglets that developed from predator-exposed tadpoles swam more slowly and less far than those that developed from tadpoles reared in the absence of predators, and had narrower femurs. To date, the fitness costs of the phenotypic response to predators are less clear than the benefits. Such a link between inducible trait and its cost is rare, especially in organisms such as amphibians that have complex life histories and the costs may occur long after the benefits.

Editorial Board Member's Choice

by Heike Lutermann

(University of Pretoria, South Africa)

[Female secondary coloration in the Mexican boulder spiny lizard is associated with nematode load]

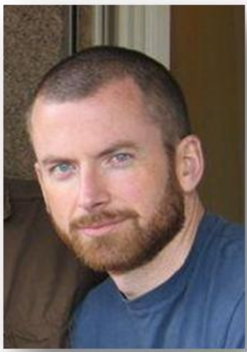
Calisi, R.M., Malone, J.H. & Hews, D.K. (2008)
Journal of Zoology **276:** 358–367

The exaggerated tail of the peacock is probably one of the most striking examples of sexual selection in vertebrates; however, this does not just catch the eye of his female conspecifics but comes at a cost. Traits such as the peacock's tail are often testosterone-mediated and although high testosterone levels may help to achieve larger fitness returns, a large body of literature has dealt with the entailed costs in terms of pathogens and parasites. The study of sexual selection appears to be a 'sexist' topic since although ultimately applicable to both sexes it is rarely considered in females, and such studies are largely restricted to species with reversed sex roles. Based on the notion that testosterone is a 'male' sex hormone even fewer studies consider its role in females. The study by Calisi *et al.* 2008 represents an exception to this and shows that not only may testosterone play an important role in female sexual selection but the associated costs appear to be similar to those experienced by males. Females of the Mexican boulder spiny lizards exhibit a conspicuous colouration that indicates their reproductive condition but also correlates with nematode infection. This colouration appears to be testosterone-mediated and the authors found a correlation between testosterone and parasite load in the females. The study by Calisi *et al.* 2008 thus demonstrates that females are well worth the attention of scholars of sexual selection. Furthermore, though there are similarities in the testosterone pathways among the sexes there are also striking differences suggesting that the study of this 'male' hormone in both sexes may be useful to further elucidate the effects and mechanisms triggered by it.

Editorial board member's choice

By Alan McElligott

(Queen Mary, University of London)



Age-specific feeding cessation in male red deer during the rut

Mysterud, A. Bonenfant, C., Loe, L.E., Langvatn, R., Yoccoz, N.G. & Stenseth, N.C. (2008)

Journal of Zoology **275:** 407–412

Why do male ungulates in temperate climates greatly reduce their food intake or indeed stop feeding during the rut? It seems counter intuitive because to increase fitness, males need to accept a large loss of body condition just before the start of winter when the risk of death becomes higher. This phenomenon has been known for a very long time, but has also puzzled those who tried to explain it. Some early explanations included the suggestion that males simply did not have time to eat when they are also trying to gain access to mating opportunities, while others suggested that it was simply an unavoidable by-product of the physiological changes that males undergo at this time of year.

Recently, a number of studies have contributed to our understanding of this phenomenon by examining weight loss during the breeding season in a variety of species, including alpine chamois (*Rupicapra rupicapra*), bighorn sheep (*Ovis canadensis*), fallow deer (*Dama dama)* and red deer (*Cervus elaphus*). Not surprisingly perhaps, the weight lost by males is related to their age, body condition and breeding activities. For example, prime-aged, mature males lose a great deal more weight than immature males, with immature males usually excluded from breeding activities in naturally age-structured populations. However, very successful males (in terms of matings) do not necessarily lose more weight than other prime-aged males that are not successful.

The new study by Mysterud *et al.* (2008) is noteworthy because it provides direct data on how much food a large sample size of animals of various ages were consuming during the breeding season. The authors analysed data on rumen fill taken from a culled sample of male and female red deer, collected over many years. The main finding was that rumen content during the breeding season declined steadily with age until around 6 years of age, and rumen fill at that age was similar to the levels in all the older age classes (up to 13 years old). In addition, rumen fill was lowest when the mass lost by males and the number of females in oestrous peaked.

Mysterud *et al.* (2008) propose two new hypotheses to explain their results. The "physical rest hypothesis" suggests that males need rest in order to compete for access to females and therefore this constrains feeding time, because most active time is spent involved in breeding-related behaviours. Their second ultimate hypothesis for explaining a reduction in food consumption during the breeding season I find even more intriguing, and this they called the “parasite hypothesis”. This hypothesis suggests that males must avoid eating during the breeding season in order to avoid consuming parasites at a time when their immune systems are compromised. The immune system in rutting males is probably reduced because of all the breeding-related activities, as well as the surge in testosterone levels (a well-known immunosuppressant), that occur at this time of year. This links the suggestion of Mysterud *et al.* (2008) with the study of the immunocompetence handicap hypothesis, an area of research that is of interest to many evolutionary biologists and others. The new hypotheses should help stimulate research aimed at finally resolving the question of why male ungulates need to reduce their food intake during the breeding season, a strategy that might otherwise be seen as one that compromises their future survival.

Editorial board member’s choice

By Michael Scantlebury

Effects of culling on badger abundance: implications for tuberculosis control

R. Woodroffe, P. Gilks, W. T. Johnston, A. M. Le Fevre, D. R. Cox, C. A. Donnelly, F. J. Bourne, C. L. Cheeseman, G. Gettinby, J. P. McInerney & W. I. Morrison
Journal of Zoology (2008), Volume 1, pages 28-37

The Eurasian badger (*Meles meles*) is considered the key reservoir of bovine tuberc ulosis (bTB) in the UK and Ireland and has been culled for several decades in an attempt to control the disease. However, there is controversy over the efficacy of culling, which has been linked to both a reduction and an increase in bTB prevalence in cattle. Though generally assumed that reducing a host population will lower disease transmission in a linear manner, badger culling does not show this pattern and the impact of badger removal on population density is likely to be an important factor in the efficacy of culling as a bTB control strategy.

This paper measures the impacts of two culling strategies on badger population density in Britain, in order to better understand the effect they have on cattle TB and improve future control strategies. The impact of ‘proactive’ and ‘reactive’ culling during Britain’s Randomized Badger Culling Trial (RBCT) on badger abundance were measured using field data including sett activity, latrine density and frequency of road-kills.

Proactive culling (widespread removal of badgers across entire trial areas in order to maintain low badger densities by carrying out annual culls) resulted in a 69% reduction of active setts, a 73% reduction in badger latrine density and a 73% reduction in the number of road-killed badgers. Whilst this method had a significant impact on badger population densities, only a reduction in cattle TB of 19% was observed within culled areas and there was an *elevated* prevalence of bTB in surrounding unculled areas. By comparison, reactive culling (localized removal of badgers inhabiting land shared with cattle suffering a bTB outbreak) resulted in a reduction of 32% of active setts, 26% in latrine density and 10% road kills and was linked to overall *elevated* incidences of bTB in cattle.

The study shows that culling is an effective method of reducing badger population densities. However badger population density may not be the over-riding factor influencing transmission of bTB to cattle, making it difficult to justify the massive effort required to carry out intensive culling programs. Instead, social perturbation caused by culling (in the form of disruption to social structure and behaviour and immigration into removal zones) is likely to result in higher contact rates within badgers and between badgers and cattle, increasing bTB prevalence. Although intrinsically appealing, culling does not therefore represent a viable option for the long-term control of bTB in Britain, highlighting the need to develop alternative control strategies.

Editorial board member's choice

By Philip Bateman

Secret lives of maned wolves (*Chrysocyon brachyurus* Illiger 1815): as revealed by GPS tracking collars.

L.F. Bandeira de Melo, M.A. Lima Sábata, E.M. Vaz Magni, R.J. Young and C.M. Coelho, ***2007, Journal of Zoology 271: 27–36.***

What is the difference between science and technology? Science is, of course, an objective method of discovery, and technology is what scientists use when applying the method to empirical discovery. Advances in science and technology tend to go hand in hand. Any new technological advance is soon used for empirical discovery, and new theories soon appear to manifest the required technology to test them. One technological advance that we now probably take much for granted in field-based zoology is that of collaring or otherwise tagging animals in order to track them, or discover their home ranges or territories. Whilst this used to mean radio-telemetry requiring constant triangulation to pinpoint the animal GPS technology now means that collars can provide us with even more information and on species that previously we knew very little about without disturbing the animals apart from initially putting the collar on them. Bandeiro de Melo and colleagues used GPS collars to track three maned wolves, a shy and nocturnal species about which very little was previously known, in a Brazilian savanna habitat. What I find appealing about this sort of study is that it gives us insights into, often quite basic, natural history and zoology of species that, while sometimes familiar to us for centuries we tantalisingly have known barely anything about. Discovering that maned wolf pairs have a strong bond, often sleeping very close to each other during the day, but hunt entirely separately, all of which has been learned from position data recorded every two hours by their collars, strikes me as being the 21st Century equivalent of the observations of the naturalists of the previous two, or more centuries, who had to rely on the technology of their eras but were filled with delight and excitement at what they found. People like David Douglas and John Kirk Townsend (who wrote of a naturalist's ecstatic delight at new discoveries) in North America and W.H. Hudson and Gilbert White (who identified new species of warbler with a small telescope and a keen ear and observation skills) in Britain. For me, it emphasises that we are the heirs of these pioneers of field studies of animal behaviour and that we have discoveries ahead of us, thanks to advances in technology, which may be as apparently simple as theirs but are just as exciting and satisfying.

Editorial board member's choice by Russell Hill:

Effects of culling on badger abundance: implications for tuberculosis control

R. Woodroffe, P. Gilks, W. T. Johnston, A. M. Le Fevre, D. R. Cox, C. A. Donnelly, F. J. Bourne, C. L. Cheeseman, G. Gettinby, J. P. McInerney & W. I. Morrison ***Journal of Zoology (2008), Volume 1, pages 28-37***

The importance of the European badger (Meles meles) in the spread of bovine tuberculosis (bTB) in Britain has been hotly debated. The role of culling badgers in controlling the disease has been equally contentious. On the one hand, the farming industry is supportive of culling, citing infected badgers as responsible for the vast majority of bTB outbreaks. At the other extreme, environmental and animal welfare groups argue that culling badgers does little to reduce the incidence of TB and cite cattle movements as playing a greater part in the spread of bTB. Detailed scientific study clearly has a key role to play in approaching a resolution to this debate, and following the recommendation of the Krebs report in 1997, the Randomised Badger Culling Trial (RBCT) was established to determine how bTB spread between cattle, badgers and other wildlife. Here, Woodroffe et al. present detailed field data from the RBCT on the effects of culling on the badger populations included in that study.

The design of the RBCT divided study areas into triplets, with proactive culling (widespread, repeated culling), reactive culling (one-off, small scale culling) and experimental control (no culling) treatments randomly assigned within each triplet. Woodroffe et al. report the widespread proactive culling to have the greatest impact on badger populations; latrine use, set density and frequency of badger road kills substantially reduced in the face of repeated badger trapping. Significantly, however, the intense culling effort was associated with only a slight reduction in bTB incidence in the culling areas.

Furthermore, there was an increased incidence of bTB in the surrounding unculled areas. Similarly, although localised reactive culling achieved modest reductions in badger activity, incidences of bTB actually increased in the culling areas. The relationship between badger density and bTB transmission is clearly not straightforward and the disruption caused by culling on badger behaviour appears to have a detrimental impact on transmission rates. As a result, Woodroffe et al. conclude that culling has little to contribute to the control on bTB in Britain.

The conclusions of Woodroffe et al. are not confined to badgers and bTB in Britain. For example, jackals are the main vector responsible for the transmission of rabies to domestic stock in southern Africa. In earlier work, published in the Journal of Zoology (2001, vol 253, pages 101–111), Loveridge and Macdonald highlighted that although eradication of jackals was the main method of vector control, this culling could lead to increased rabies incidence. Again, perturbation of the social system, increased contact at territorial boundaries and movement of animals into vacant territories underlie the high levels of rabies in areas of greatest jackal persecution. Woodroffe et al. add valuable data to the debate on the role of culling in controlling wildlife diseases that can also infect livestock and humans. Clearly the problem of future disease management must be approached through a detailed understanding of the behavioural ecology of the host species. Alternative approaches to culling, such as oral vaccines, may represent useful tools for the future but from the culling perspective the emerging picture is that greatest control will be achieved through allowing vector populations to co-exist with livestock undisturbed.

Editorial board member's choice by Heike Lutermann:

Altered prevalence of raccoon roundworm (Baylisascaris procyonis) owing to manipulated contact rates of hosts

M.E. Gompper and A.N. Wright, ***2005, Journal of Zoology, 266:215-219***

Parasites and pathogens are an ubiquitous threat to organisms and can cause substantial reductions in reproductive success and survival of their hosts. Hence, they constitute a powerful selective agent. Transmission of parasites is a key process in host-parasite interaction and is often related to contact rates among hosts. However, such contact rates are difficult to assess and most studies and theoretical models have used population density of the host as a proxy for contact rates. In marked contrast, the study by Gompper and Wright manipulates actual contact rates in racoons (Procyon lotor) by providing food resources in either a clumped or dispersed manner and measures the associated infection with a common nematode parasite before and after manipulation. Clumped resources lead to drastic increases in infected individuals despite population densities being similar in both groups. Remote photography confirmed that this was probably due to higher contact rates among individuals that aggregated at clumped food sources. Their study illustrates that parasite transmission is not a simple density-depend process and hence models based on population density alone are rather over simplistic. Racoons have successfully exploited resources provided by humans such as rubbish dumps and this is associated with even higher parasite prevalence than in the rural population studied. These dramatic effects of human activity have staged a new host-parasite dynamic and it will be exciting to watch this evolution in action.

Editorial board member's choice by Lars Podsiadlowski:

Genetics and animal domestication: new windows on an elusive process

K. Dobney and G. Larsen, ***2006, J. Zoology, 269:261-271***

The domestication of wild animals was not only a crucial achievement in human prehistory: starting with Darwin, it has also served as an illustration of the evolutionary changes which selection can cause. Even today, in the genomic age, artificial selection is an important topic in evolutionary biology. In this review, K. Dobney and G. Larsen summarise several important studies from past and present research and raise important questions for future work.

Darwin noticed the conspicuous morphological and physiological similarities between domesticated animals from different species – and the similarity of the morphological and physiological changes that domesticated animals have undergone relative to their wild counterparts, such as the appearance of dwarf and giant varieties, piebald colour and even floppy ears. Subsequent studies have demonstrated that complex genetic networks control almost every aspect of an organism, e.g. selection for behavioural traits also alters morphology: Belyaev's fox-farm experiment, dating back to the 1950s, in which the previously undomesticated silver fox was selected for tameness, led him to suggest that tiny genetic changes affecting the balance of hormones and neurochemicals may be the cause for some of the characters shared in various domesticated mammalian species: fascinatingly, a suite of characters not selected for, including piebald coats and dropping ears, also appeared in the foxes. Probably, comparative genomic and transcriptional analyses of domesticated animals and their wild counterparts will provide more and more important insights into the developmental and genomic control of morphological and behavioural changes in general.

Dobney and Larsen's review addresses another important issue in the reconstruction of the history of domestication for individual species. The time and place of domestication and the wild ancestors of domesticated animals can now be estimated with molecular data. However, the authors also demonstrate that some results, like the dating of domestication with molecular clocks, have to be interpreted with caution. Complex histories of domestication are revealed in some studies with dogs and cattle, and many questions are still unresolved, requiring larger datasets of different genomic sources (and probably also from ancient samples).

All in all this is an excellent review, illuminating many different aspects of the biology of domestication and giving a broad overview of the relevant literature. In addition the authors provide important hints to open questions and further topics to be studied in this field. It is apparent that many results of modern domestication research may serve as good models in understanding fundamental principles of evolution – just as they did in Darwin's time.