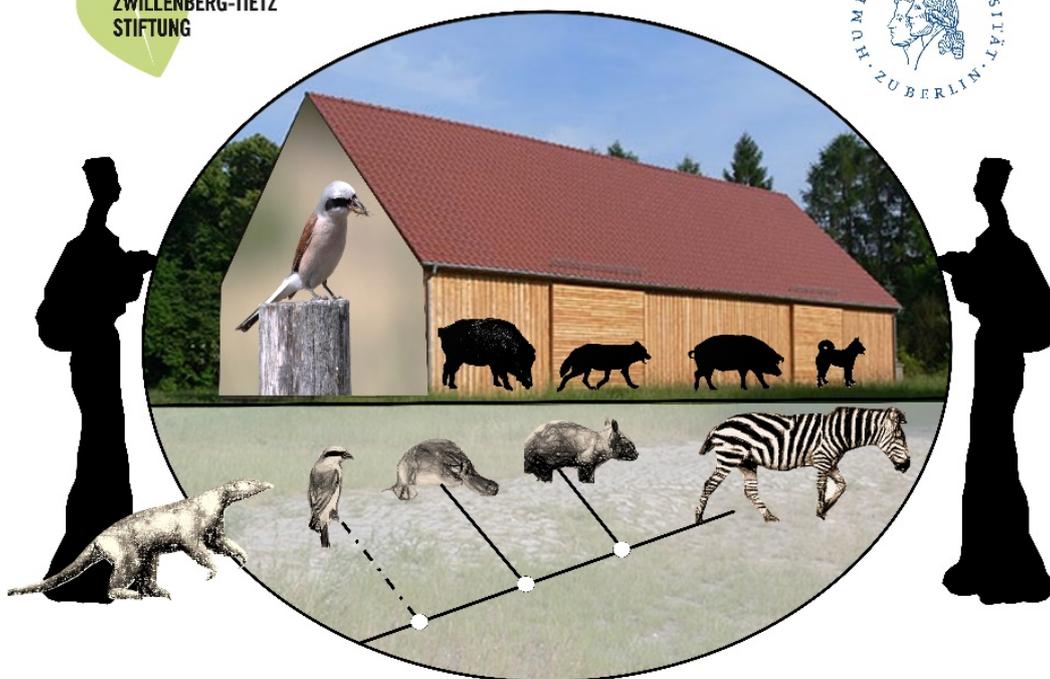


# Organisms in nature – evolutionary perspective and ecological significance

Ulrich Zeller, Gad Perry, Nicole Starik, and Thomas Göttert (eds.)

## Organisms in nature – evolutionary perspective and ecological significance

Linde, September 9-12, 2019



Fourth international workshop within the project

*“Land use conflicts and edge effects – a comparative approach”*

## Workshop

### “Organisms in nature – evolutionary perspective and ecological significance”

**Linde, 9<sup>th</sup> – 12<sup>th</sup> September 2019**

**Organisation:**

Systematic Zoology Division  
Albrecht Daniel Thaer-Institute of Agricultural and Horticultural Sciences  
Faculty of Life Sciences  
Humboldt-Universität zu Berlin  
Unter den Linden 6, 10099 Berlin

Zwillenberg-Tietz Stiftung  
Forschungsstation Linde  
Brunnenweg 2  
14715 Märkisch Luch /OT Linde

**Links:**

<https://www.agrar.hu-berlin.de/fakultaet/departments/dntw/index.html/index.html>  
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**Logo:**

S. Bengsch, Photos: T. Göttert, U. Zeller, Zwillenberg-Tietz Stiftung

**Doi:**

<https://doi.org/10.18452/21181>

## Content

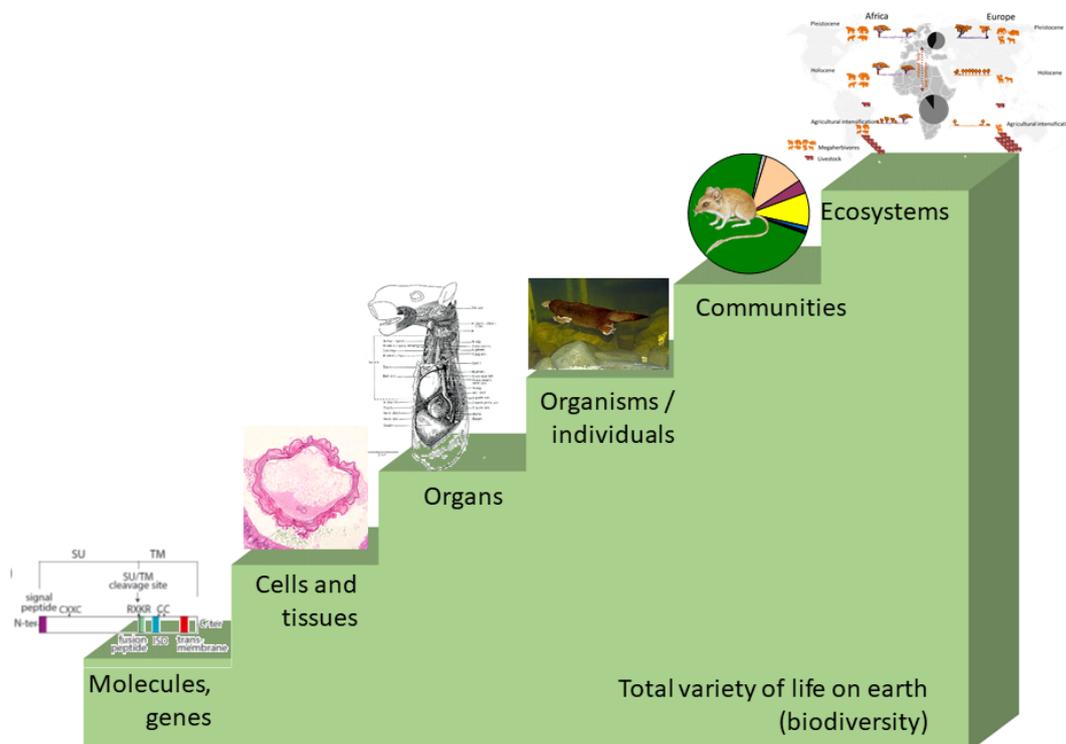
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## Synopsis

*Ulrich Zeller, Gad Perry, Nicole Starik & Thomas Göttert (editors)*

Between the 9<sup>th</sup> and 12<sup>th</sup> of September 2019, the Systematic Zoology Division (Faculty of Life Sciences, Humboldt-Universität zu Berlin) hosted the fourth annual international workshop within the project “*Land use contrasts and edge effects – a comparative approach*”. The event was entitled “*Organisms in nature – evolutionary perspective and ecological significance*”. Similar to the previous workshops of the project, the venue was the Linde research station in Brandenburg, Germany (<https://www.zwillenberg-tietz-stiftung.de/category/veranstaltungen/>). The aim was a mutual reflection about concepts, approaches, results and experiences from a global network of scientists dealing with the topic of organismic biology in a comparative context but through the unifying lens of evolution. Participants represented a broad range of scientific disciplines, such as paleontology, functional morphology, and ecology.

The first session was opened by U. Zeller, who reflected about the inherent diversity of organismic life and the necessity to approach organismic biology from a variety of perspectives (Figure 1). He synthesized findings of his own research, conducted over the past four decades, related to various stages of organismic maturation including gene expression, ontogenetic and structural development, and adaptive radiation of phenotypes to ecological conditions.



**Figure 1.** Different organizational levels of biodiversity allow for/result in various perspectives to approach the phenomenon of organismic life and reflect the historic idea of a hierarchy of biological sciences arranged according to these different levels. Slide from presentation given by U. Zeller

This enables the reconstruction of the stem species patterns of the common ancestor of all living mammals (Zeller 1999, Freyer et al. 2003, Zeller et al. 2007). Rooted in this framework of organismic and comparative analysis, Zeller pointed towards assessments of ecological stability / fragility through the study of organismic abilities / limitations that shape natural communities and consequently ecosystems. He suggested the straightforward application of organismic thinking in ecological conceptualization to reveal deeper insights into the laws of natural organization and ecological function as a basis for a more sustainable use of natural resources (Zeller et al. 2017). The subsequent presentations gave evidence that interlinking studies on structural and ecological expression of organismic life can provide a powerful tool for the study of evolution.

### What exactly do we mean by “organismic approach”?

The consideration of organisms is a prerequisite for the conceptualization of biodiversity. The perception of an organism as a source of inspiration - a “starting point” for the systematization of life - is a common feature of the thinking of several pioneers of biological conceptualization (Zeller & Göttert 2019), including Carl von Linné (bottom-up approach based on organism/specimen, typological thinking) and Willi Hennig (organisms representing crown groups).

Although “the organism” is widely used as an integrative unit in biology, one aspect that emerged in the course of the event is the breadth of scope for interpretation associated with the term “organismic” and the notion of how the organism is actually conceptualized. First, an organism may be used as a representative of a larger category, e.g. a monophylum (U. Zeller, X.-I. Luo, R. Asher, T. Stach). Another interpretation stresses individual variability within a taxon. Examples are the “breeding nuclei” of few individuals that provided the basis for successful reintroductions of mammal taxa rescued from the brink of extinction (T. Göttert) or the phenotypic plasticity in water loss rates related to microgeographic variation in an environment (G. Perry). A third perspective puts emphasis on species-specific ecological amplitudes and response-scales resulting from this intra-specific spectrum of organismic abilities and limitations (N. Starik, P. Temple-Smith, S. Eiseb). Against this background, M. Sobral reflected on the relationships between phenotypic traits and fitness highlighting that these complex relationships are defined within continuously varying contexts (e.g. within individual or population environment, community or ecosystem level) implying that traits within an organism cannot be understood independently from each other. To develop a basis of common understanding, M. Gutmann argued for an “*indispensable systematic role of the concept ‘organism’ for evolutionary transformations*” (p. 23) arising from reflections about presuppositions related to explanations for anagenetic transformations and the philosophy of systems biology (Gutmann 2011). Gutmann suggested a “multi-level-description of living entities as working units that are composed of functional elements” in terms of “organismic subsystems” as operationalized tools for the reconstruction of evolutionary transformation-lines.

### Combining paleontological and organismic data - a powerful tool to reconstruct evolutionary scenarios

Another point of discussion was the link between the work of paleontologists and the phenomenon of organismic diversity. To cite R. Asher: “*The decay inherent in fossilization greatly reduces the amount of information available for understanding extinct species.*” (p. 15). Fossils disclose insight to structural components of organisms that disappeared a long time ago but from a current perspective, it seems difficult to obtain a precise picture of the entire complexity of these organisms.

Z.-X. Luo demonstrated how current insight from fossil discoveries (e.g. hand-foot structures, limb bones), in combination with data gained from ecological investigations of extant species, contribute to the debate about contingency vs. determinism in mammalian evolution (Zhou et al. 2019). By highlighting the link between paleo-zoological and morphological-ecological approaches, Luo reflected on the relations between Jurassic & early Cretaceous mammalian ecomorph diversity and replicated evolution of Mesozoic mammals resulting in re-assemblies of early mammal ecological communities – a finding that furthermore highlights the resilience of natural systems. It became evident that the interpretability of paleontological data greatly increases when being integrated into an organismic concept including the study of extant taxa (e.g. mapping of ecological disparity in extant clades or comparisons between characters of Mesozoic mammal fossils and extant mammals). Luo showed that the combination of current and historical data is crucial for the reconstruction of evolutionary scenarios, e.g. repeated evolution of locomotor modes in different mammalian groups or the convergence of tongue-feeding & digging adaptations in various mammalian clades (Luo et al. 2017).

This line of thought was deepened by R. Asher, who raised the question: “*Is it possible to build an accurate Tree of Life using fossilizable data?*” and who showed that “*phylogenies based on morphology alone can capture genomic phylogenetic signal by using `predicted ancestors` in well-corroborated trees of living species*”. Asher’s use of the term “predicted ancestor” instead of “stem species” (Hennig 1950, Ax 1985) is worth special consideration. He referred to this “predicted ancestor” in terms of “*an animal hypothesized to have existed in the geological past, constrained by the optimization of anatomy observed in modern species reconstructed onto ancestral nodes of a well-corroborated tree*”. The use of the term “predicted ancestor” obviously stresses the organismic dimension behind the stem species concept. A take-home message was that it is possible to build an accurate Tree of Life using fossilizable data - but only against the background of information gained from the organismic variety of still existing species (Asher 2018, Asher et al. 2019).

### Adaptationist approaches – functional morphology & evolution

A further focus was on adaptationist approaches and the conceptual framework of functional morphology for reconstructing evolutionary scenarios (D. Homberger, A. Panyutina). In contrast to the explanatory approach of “optimal design” (evolution exclusively orientates towards character optimization), the functional morphology framework is based on the theory that the relationships between form and function remain stable during the change of characters, since the laws underlying these relations are independent of evolutionary processes (Kummer 1962).

Against this background, A. Panyutina reflected on the phenomenon of mammalian flapping flight. She showed that the mechanical properties of organismic structures provide a valuable instrument for understanding the ecological and evolutionary perspectives when considering an organism in the sense of a mechanical system (Panyutina et al. 2015, Panyutina 2018). By using Dermoptera as examples for locomotor specialization equally benefitting gliding flight as well as quadrupedal ascent on thick trees (the ability of limbs to move between parasagittal and frontal position), Panyutina established a series of successive morphological transformations and identified the musculoskeletal features of bats as an intermediate specialization to arboreal-gliding locomotion.

D. Homberger used the evolutionary history of Gondwanan parrots and cockatoos to illustrate the significance of functional morphology for the reconstruction of morphological and ecological characteristics of a common ancestor (Redd et al. 2012, Homberger 2017). This was another important example of the study of organisms from different perspectives, including: i) functional-morphological analysis of structural components (feeding apparatus) of captive animals, ii) ecological analysis (“natural experiments”) considering organismic expressions of wild animals in their current ecological context, and iii) analysis of floristic, geological and paleoclimatic data. This synthesis of morphological, ecological, and environmental dimensions allows for the detection of diversifying or stabilizing aspects of evolutionary processes and also highlights the value of long-term comparative eco-morphological studies to consider effects of seasonal variations, climatic changes, urbanization and other anthropogenic-induced disturbances.

T. Stach used the examples of different organ systems of what is called Rarely Considered Organisms demonstrating the contribution of precise morphological analyses towards an integrative understanding of evolution of tunicates (Braun et al. 2019).

#### Different perspectives on the organism-environment interrelation

Some participants holistically approached the overall theme by making the organism the center of the framework. For example, P. Temple-Smith’s comprehensive overview “*On the biology of the platypus*” included aspects of evolutionary history, anatomical-morphological characters, distribution and habitat use, venom system and envenomation, electroreception and feeding behavior, reproduction and captive breeding, as well as conservation measures. S. Eiseb adopted an equivalent perspective while reporting on aspects of reproduction, predation, sexual dimorphism and diet in the lizard *Agama anchietae* in Namibia.

Other participants approached the organism via the environmental conditions and characteristics of their natural habitats and focused on the behavioral interactions between the organism and the relevant part of its environment. As organisms respond to information from the environment through their (unique) sensory systems, they can have different perceptions of the same environment and may react in different ways to the same environmental factors (e.g. by habitat selection). This viewpoint on habitat recognition and habitat selection from an organism’s perspective is thus of high significance for conservation biology.

G. Perry highlighted the increasing knowledge and appreciation of the degree of sophistication and diversity of mechanisms underlying behavioral components that allow lissamphibians and squamates to cope with the inhospitable conditions of arid and semi-arid environments (Gao & Perry 2016, Anderson et al. 2017). N. Starik used the evolutionary ecology framework to deal with conservation issues and reported on the response patterns of insectivorous bat communities and particular bat species to local land use types and intensities (Starik et al. 2018). Starik argued that structural habitat reflects the functional habitat of an organism suggesting a high significance for animal conservation. Starik discussed that resource distributions and relevant conditions may change already with little alteration of the general vegetation structures and refers to adopting a “bat’s eye view” on the environment to aid with conservation decisions. Another example of organism-environment interactions discussed was the spatial ecology of megaherbivores in their natural environment. Special emphasis was placed on the organismic dimension behind reintroductions and the influence of seasonal conditions on home range and movement patterns of African elephants (*Loxodonta africana*) in a humid-tropical environment in Mozambique (V. Macandza) and black rhinos (*Diceros bicornis*) in a semi-arid environment in Namibia (T. Göttert).

### Concluding remarks

In a time of increasing abstraction of scientific concepts and a tendency to value the simulation of biological phenomena higher than the observation of organismic expressions (Ríos-Saldaña et al. 2018), the discussed approaches and viewpoints stimulated reflections how organismic biology (represented by taxa ranging from tunicates to elephants) can contribute to the understanding of evolutionary scenarios and ecosystem interactions, not least to support a more sustainable management of biodiversity and natural resources.



**Figure 2.** Workshop participants, from left to right: N. Starik, T. Göttert, Z.-X. Luo, J. Hartmann, P. Temple-Smith, V. Macandza, T. Rottstock, G. Perry, A. Behrendt, S. Eiseb, U. Zeller, M. Gutmann, M. Sobral, A. Kuznetsov, A. Panyutina, C. Slaton, T. Stach, D. Homberger, J. Hendricks, R. Asher; photo: M. Wicke

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## Program

### Monday, 9<sup>th</sup> of September

#### *Arrival*

17.00h *Musical introduction*, Humboldt-Quartett (violin: Miriam Götze & Michael Yokas;  
viola: Renate Germer; violoncello: Katja Kerstiens)

**U. Zeller (Germany, Humboldt-Universität [HU]):** Welcoming notes

*Come together and refreshments*

18.00h **P. Temple-Smith (Australia, Monash University):** On the biology of the  
platypus (*Ornithorhynchus anatinus*)

19.00h *Dinner*

## Tuesday, 10<sup>th</sup> of September

- 09.00h      **U. Zeller (Germany, HU):** Organisms in nature – evolutionary perspective and ecological significance – an introduction
- 10.00h      **W. Maier (Germany, Universität Tübingen):** Organism concept and evolutionary biology<sup>1</sup>
- 10.45h      *Coffee and Tea*
- 11.15h      **D. G. Homberger (USA, Louisiana State University):** A case study using natural experiments and long-term eco-morphological investigations to generate evolutionary scenarios: The evolutionary history of Gondwanan parrots and cockatoos
- 12.00h      *Discussions*
- 12.45h      *Lunch break*
- 14.00h      **R. J. Asher (UK, University of Cambridge):** Is it possible to build an accurate Tree of Life using fossilizable data?
- 14.45h      **M. Gutmann (Germany, Karlsruher Institut für Technologie):** The concept of organism and the Extended Synthesis
- 15.30h      *Coffee and Tea*
- 16.00h      **S. J. Eiseb (Namibia, University of Namibia):** Reproduction, predation, sexual dimorphism and diet in *Agama anchietae* (Reptilia: Agamidae) from Namibia
- 16.45h      **G. Perry (USA, Texas Tech University):** Adaptations of “reptiles” and amphibians to arid and semi-arid environments
- 17.30h      *Discussions / Posters*
- 18:30h      *Dinner*

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<sup>1</sup> unable to attend

### Wednesday, 11<sup>th</sup> of September

- 9.00h            **Z.-X. Luo (USA, University of Chicago):** Iterative Ecological Diversifications of Mammaliaforms in Early Mammal Evolution
- 9.45h            **T. Stach (Germany, HU):** Phylogenies and morphologies - on the evolution of Rarely Considered Organisms
- 10.30h           *Coffee and Tea*
- 11.00h           **V. Macandza (Mozambique, Universidade Eduardo Mondlane):** Seasonal home range and movement patterns of elephants in a humid tropical environment in Mozambique
- 11.45h           **T. Göttert (Germany, HU):** Species-specific requirements vs. intra-specific variability - on the organismic dimension in large herbivore reintroductions and its importance for species conservation and landscape development
- 12.30h           *Lunch break*
- 14.00h           **A. A. Panyutina (Russia, Russian Academy of Sciences):** Adaptationist approach to construction of evolutionary scenarios. Mammalian flapping flight as an example
- 14.45h           **N. Starik (Germany, HU):** Organismic responses of insectivorous bats to local land use
- 15.30h           *Coffee and Tea*
- 16.00h           **M. Sobral (Spain, Universidade de Santiago de Compostela):** Relationships between phenotypic traits and fitness
- 16.45h           **P. Temple-Smith (Australia, Monash University):** Phylogeny and ecology of the enigmatic microbiotheriid marsupial, the monito del monte *Dromiciops gliroides*
- 17.30h           *Discussions / Posters*
- 18.30h           *Barbeque*

### **Thursday, 12<sup>th</sup> of September**

- 9.00h            Excursion to Westhavelland Nature Park, visiting Brandenburg State Bird Conservation Centre (Dr. T. Langgemach)
- 12.30h            *Lunch*
- From 13.30h    *Departure*

### **Posters**

- G. Perry et al. (USA, TTU):** Wildlife trafficking, its impacts on global biodiversity, and efforts to reduce harms
- T. Rottstock et al. (Germany, HU):** Livestock-wildlife interactions: a synthesis of four case studies from central Europe and Sub-Saharan Africa
- N. Starik et al. (Germany, HU):** Similar is not the same - Case study on long-eared bats in Brandenburg reveals challenges for their conservation

## **Abstracts and extended abstracts of presentations<sup>2</sup>**

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<sup>2</sup> in alphabetical order of authors' surnames; presenting author underlined when > one author

## **Is it possible to build an accurate Tree of Life using fossilizable data?**

*Robert J. Asher, United Kingdom*

The decay inherent in fossilization greatly reduces the amount of information available for understanding extinct species. The possibility that such decay influences phylogenetic reconstruction in a non-random way is worth serious consideration. At least for some clades, characters phylogenetically informative for key nodes may be the first ones to decay when an animal dies. The extent to which such bias is widespread has major, potential effects on any biological investigation seeking to understand extinction, diversity, and character evolution over the course of Earth history. Here, I discuss the vertebrate Tree of Life which benefits from a well-corroborated topology and a rich fossil record and use datasets that sample across partitions that are decay-resistant (e.g., the dentition) and decay-prone (e.g., DNA). I ask if taxa with well-corroborated phylogenetic affinities exhibit properties of bias (e.g., long branch attraction, stemward slippage) with the removal of decay-prone partitions. Results so far indicate that bias is indeed apparent in some datasets, but not others, and is not an inherent property of hard-tissue characters across vertebrate groups. I further discuss techniques of character sampling, implied weighting, and data-combination that can potentially maximize the ability of paleontologists to accurately infer the branching pattern of the Tree of Life, even for fossils which are missing most or all of the soft tissues and molecular data available for living species.

## **Reproduction, predation, sexual dimorphism and diet in *Agama anchietae* (Reptilia: Agamidae) from Namibia**

*Bertha Buiswalelo*<sup>1,2</sup>, *Seth J. Eiseb*<sup>1,2</sup>, *Jacqueline Goedhals*<sup>3</sup>, *Joaquín Verdú-Ricoy*<sup>4</sup> and *Neil Heideman*<sup>4</sup>

<sup>1</sup>University of Namibia, Windhoek, Namibia

<sup>2</sup>National Museum of Namibia, P O Box 1203, Windhoek, Namibia

<sup>3</sup>University of the Free State, P.O. Box 339, Bloemfontein, South Africa

<sup>4</sup>Department of Zoology & Entomology, University of the Free State, P.O. Box 339, Bloemfontein, South Africa

The agamas of southern Africa comprise eight species, some with overlapping distribution ranges (Griffin, 1994), and show substantial variation in size, social organisation, colour patterns and microhabitat utilization. *Agama anchietae* has an expansive distribution in the western parts of Namibia, extending from northern Namibia to South Africa in the South. In this study, preserved specimens of *A. anchietae* were analysed to describe its (a) sexual size dimorphism (SSD, in terms of body, head and limb size), (b) reproductive strategy (timing, fecundity and clutch traits), (c) predation pressure (using damaged or regenerated tails as possible indicator) and (d) diet preferences (bases on stomach and intestinal content analysis).

Males were found to be slightly larger than females, having a longer body as well as a relatively longer tail. The head of males was relatively longer, wider and slightly higher than that of females. Males also had relatively longer fore- and hind limbs than females. The degree of SSD in *A. anchietae* is very similar to that found in *A. etoshae* (Heideman, 2001), and to a lesser degree to that found in *A. a. aculeata* and *A. p. planiceps* (Heideman, 1995a).

*Agama anchietae* females are reproductively active during the hot rainy season of Namibia, (spring and summer, Namibian Weather Bureau) similar to *A. a. aculeata* and *A. p. planiceps* (Heideman, 1994), and *A. etoshae* (Heideman, 1998). This is a period characterised by vegetation blooms and an increase in arthropod diversity and abundance. *Agama anchietae* males are also reproductively active during this season, suggesting that the gonadal activities of the two sexes are synchronised, as also found in *A. a. aculeata* and *A. p. planiceps* (Heideman, 1995b).

The incidence of broken tails was 6.25% in females and 4.26% in males, similarly low as that of *A. etoshae* (0% for both sexes, pers. obs.), but much lower than 16.8% and 16.4% in *A. a. aculeata*, and 32.6% and 31.5% in *A. p. planiceps*, respectively (Heideman, 1993).

The high occurrence of ants in *A. anchietae* (average 88.61% of items in the gut) is similar to the amounts found in *A. a. aculeata* (87.5%–100.0%) and *A. p. planiceps* (74.4%–96.8%) (Heideman, 2002), suggesting that ants are the main food item of these agamas and that they are primarily sit-and-wait foragers.

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## **Species-specific requirements vs. intra-specific variability – on the organismic dimension in large herbivore reintroductions and its importance for conservation and landscape development**

*Thomas Götttert and Ulrich Zeller, Germany*

Reintroduction is “*the intentional movement and release of an organism inside its indigenous range from which it has disappeared*” aiming at re-establishing “*a viable population of the focal species within its indigenous range*” (IUCN/SSC 2013, p.3). Reintroductions have become a powerful tool to support the survival of endangered species. There are various examples for reintroduction as a key-measure in preventing the extinction of large herbivore species or taxa (Table 1, Figure 1). These reintroductions can be considered as organismic approaches by nature, because current *in-situ* populations of these taxa descent from “breeding nuclei” of few individuals only (Table 1). Since the overall goal is the establishment of self-sustaining populations in what is considered “the wild”, survival and reproductive performance are important criteria to assess the success of reintroduction programs (e.g. Saltz 1998). Different reintroduction strategies are in use depending on species and country (soft-release vs. hard-release, repeated removals from a permanent local breeding-core vs. direct translocations of selected organisms among various reserves). However, the interrelations between introduced herbivores and their novel environments are complex and the factors affecting the reintroduction success are focus of ongoing investigations (e.g. Berger-Tal & Saltz 2014, Perzanowski et al. 2019). Based on own data on spatial behavior of reintroduced black rhinos (*Diceros bicornis*) to former livestock farmland in Namibia (Götttert et al. 2010, Schwabe et al. 2015), possible factors affecting post-release acclimatization of individuals will be discussed from an organismic perspective. Among others, we discuss the influence of pre-existing social bonds among released individuals (e.g. Anderson 2013), animal temperament (e.g. McDougall et al. 2006), selecting of individuals for release (e.g. Reading et al. 2013), and behavioral persistence in captive animals (e.g. Vickery & Mason 2003). Besides its importance for species conservation, large herbivore reintroductions are also a measure for landscape development and ecological restoration (Zeller et al. 2017). Against this background, we critically discuss the “rewilding” concept and pay attention to the use of domesticated ungulate species as “surrogate” taxa to maintain cultural landscapes (Zeller & Götttert 2019).

**Table 1.** Info about the *in-situ* population development of selected large mammal species or taxa

Scientific name	Extinct in the wild	Population bottleneck	Nucleus of reintroduction program (founders)	Year of initial release into wild	Area of initial release into wild	Current in-situ population <sup>1</sup>
<i>Dama mesopotamica</i>	-	25 animals, 1956 <sup>2</sup>	Iran: 6 animals, 1964-1965 <sup>3</sup> Israel: 7 animals, 1976 <sup>2</sup>	From 1977 <sup>3</sup> 1996 <sup>2</sup>	Different sites in Iran <sup>3</sup> Nahal Kziv Nature Reserve <sup>2,4</sup>	>250 adults
<i>Elaphurus davidianus</i>	>1500 years ago <sup>5</sup>	11 animals, 1900-1910 <sup>5</sup>	77 animals, 1985-1987 <sup>5</sup>	1987 <sup>5</sup>	Dafeng Milu Nature Reserve <sup>5</sup>	~1725 fenced + ~600 unfenced
<i>Oryx leucoryx</i>	1972 <sup>6</sup>	14 animals, 1962-1967 ("World Herd") <sup>7</sup> +few animals from private collections <sup>8</sup>	Oman: 40 animals, 1980 - 1995 <sup>9</sup>	1982 <sup>9</sup>	Arabian Oryx Sanctuary <sup>9</sup>	850 mature individuals
			Jordan: 14 animals, 1978-84 <sup>10</sup>	1983 <sup>10</sup>	Shaumari Nature Reserve <sup>10</sup>	
			Israel: 7 animals, 1978 <sup>8</sup>	1997-1998 <sup>8</sup>	Shahak Spring <sup>8</sup>	
			Saudi Arabia: 35 animals, 1989 <sup>11</sup>	1990-1993 <sup>12</sup> 1995-2003 <sup>12</sup>	Mahazat as-Sayd <sup>12</sup> Uruq Bani Ma'arid <sup>12</sup>	
			UAE: 90 animals <sup>13</sup>	2007 <sup>13</sup>	Um El Zumool <sup>13</sup>	
<i>Bison bonasus</i>	1927 <sup>14</sup>	54 animals <sup>15</sup> , 1920s	18 animals <sup>14</sup>	1952-1966 <sup>14</sup>	Puszczka Bialowieska <sup>14</sup>	~1000 mature individuals
<i>Equus ferus przewalskii</i>	1960s <sup>16</sup>	53 animals <sup>18</sup> , 1920s	16 animals, 1900-1947 <sup>17,18</sup>	1992-2004 <sup>18</sup> 1992-2000 <sup>18</sup>	Great Gobi B via Takhin Tal <sup>18</sup> Hustai National Park <sup>18</sup>	178 mature individuals
<i>Ceratotherium simum simum</i>	-	20-50 animals <sup>19</sup> ~200 animals <sup>20</sup> , 1900	South Africa: 330 animals <sup>21</sup>	1961-67 <sup>21</sup>	Different reserves in South Africa <sup>21</sup>	20,170 animals

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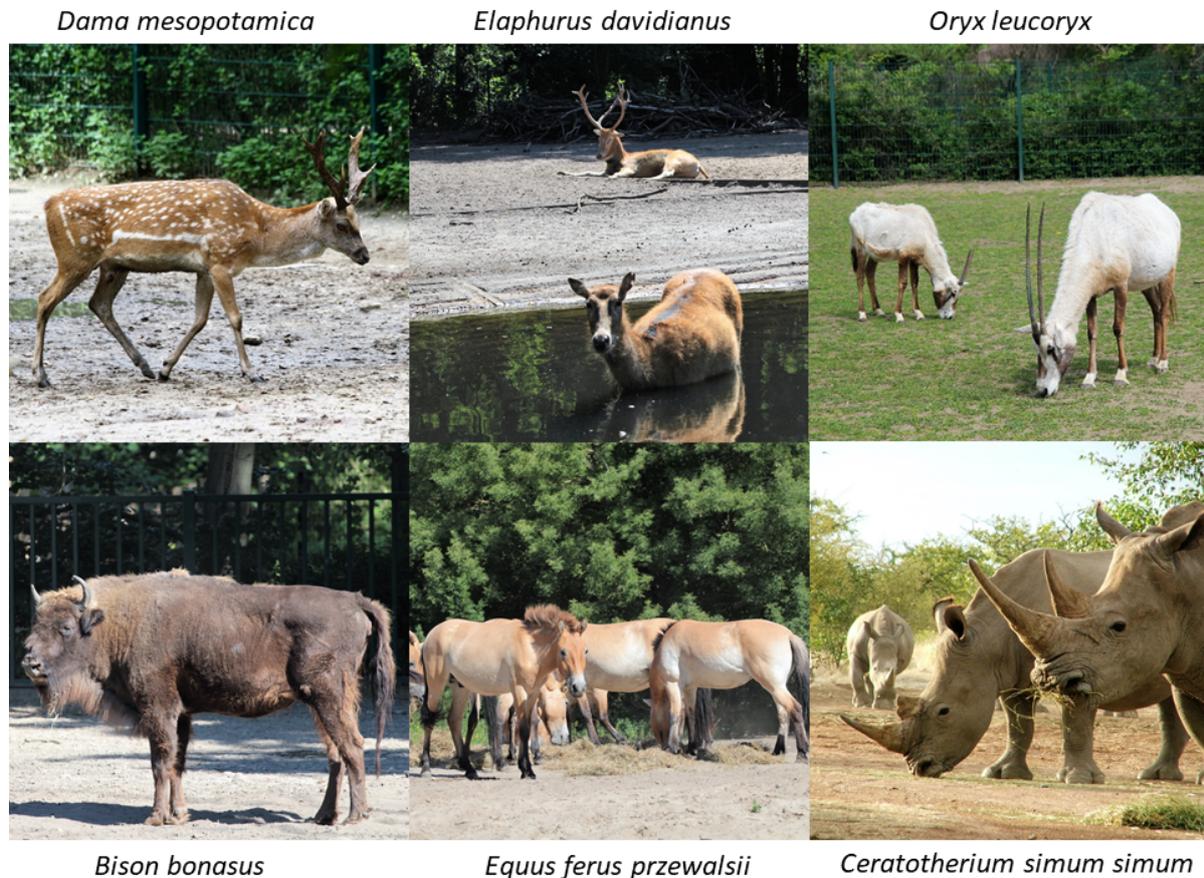


Figure 1. Selected large mammal species / taxa referred to in Table 1, photos: T. Göttert

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## **The concept of organism and the Extended Synthesis**

*Mathias Gutmann, Germany*

The question how to determine biological individuals – as a necessary point of reference of biological structuralisations - is one of the most intriguing problems of and in biology. This question is usually answered by applying concepts of either “life”, “organism” or “system”, and became increasingly crucial during the last three decennia in the light of the latest transformation of the “Synthetic Framework”.

The integration of virtually all sources of knowledge on virtually all levels of biological descriptions into this framework provided the most universal basis for the presentation of evolutionary transformations. Populations-genetic models, the application of game theory and relational ecological and epigenetic concepts finally lead to several approaches of Extended Evolutionary Synthesis, which became seemingly independent of the central position, held by the reference to organisms. This independence allowed the *systemization* of biological descriptions, within which regulative feedback loops, reciprocal causality and emergent effect constitute a fine-grained causal network. This network is thought to overcome inadequate and insufficient “mono-” or “oligo-causal” explanations; however, this indisputably important advantage comes with some unexpected costs:

1. On the one hand, the integrative structure of systemic approaches provides the best available source for the description of the constitution and interaction of biological organization.
2. On the other hand, it is this very *same systemic descriptions*, which do not allow explanations proper – at least when they are assumed to avoid vicious circles and truisms. In short, explanation is replaced by causal-factor analysis.

These methodological problems become most sever, by facing the challenge of evolutionary explanations of the transformation of biological units, which are usually addressed by discerning ana- from cladogenetic transformations. Whereas causal-factor analysis is relevant in cladogenetic contexts, the presentation of anagenetic transformation requires much more complex presuppositions. This paper aims to provide some overview on these (empirical, methodic and methodological) presuppositions, particularly from the side of several “extended” versions of the “new” synthesis. Referring to this reconstruction, I am arguing for an indispensable systematic role of the concept “organism” for evolutionary transformations. It can be shown, that “organisms” provide – in terms of even but not only morphological structuralisations- the methodological starting point as well as – at least some of – the principles that guide the actual evolutionary reconstruction itself.

## **A case study using natural experiments and long-term eco-morphological investigations to generate evolutionary scenarios: The evolutionary history of Gondwanan parrots and cockatoos**

*Dominique G. Homberger*, United States

The Psittaciformes are a distinctive, diverse and species-rich avian order with over 350 species distributed mainly across the Southern Hemisphere and inhabiting diverse environments. They are characterized by their curved beak whose shape and structural details, however, vary in adaptation to diets ranging from insect larvae to seeds, nuts, fruits, bulbs, corms, and nectar. This geographical and ecological diversity creates logistical and methodological challenges for the study of the evolutionary history of these birds in adaptation to the changing environmental conditions during and after the breakup of the Gondwanan landmass into the current southern continents. But this diversity is also a rich source of data for natural experiments and eco-morphological studies. In general, the basis for these studies involves a morphological and biomechanical analysis of the feeding apparatus of captive individuals. To understand the selective regime controlling the feeding apparatus, the interactions of natural populations with their environment need to be observed over several years to consider the effects of seasonal variations, climatic changes, urbanization, and invasions of exotic plants. The evolutionary history of particular lineages is then reconstructed (1) through natural experiments that compare the collected data while reducing the number of variables to answer specific questions, and (2) by integrating floristic, geological and paleoclimatic data. To illustrate this complex method, two studies will exemplify the diversifying or stabilising aspects of evolutionary processes. (1) Red-tailed Black-Cockatoos (*Calyptorhynchus banksii* and *C. lathami*) occur as geographically separate populations across Australia. Their similar plumage points to a common evolutionary origin, but the individual populations differ by their body size, the length of their toes, and the size, shape and internal structure of their beaks. The integration of functional-morphological and ecological observations and floristic, geological and paleoclimatic data revealed that the red-tailed Black-Cockatoos lived originally in Gondwanan temperate rainforests and adapted to forest refugia or woodland and grassland regions during Australia's "drying" and movement toward the equator. (2) The Austral Parakeets (*Enicognathus ferrugineus*) occur in the southernmost temperate rainforests of South America, which have retained the floristic elements of the original Gondwanan temperate rainforests and have remained protected from exotic plants by their remoteness and challenging climate. Hence, the interactions between the parakeets and their environment can be surmised as having remained comparable to those of their Gondwanan ancestors. With their generalized feeding apparatus, they feed year-round on various seeds, leaf buds, and insect larvae within the seeds of Gondwanan Southern Beeches (*Nothofagus* species). A recently discovered population of Crimson Rosellas (*Platycercus elegans*) with analogous ancestral morphological and ecological characteristics in a remnant Gondwanan temperate rainforest in eastern Australia supports the Gondwanan origin of parrots. Hence, natural experiments and long-term eco-morphological investigations of parrots and cockatoos allow the reconstruction of (1) their evolutionary history, and (2) the morphological and ecological characteristics of the original parrot and cockatoo populations in Gondwana.

## **Iterative Ecological Diversifications of Mammaliaforms in Early Mammal Evolution**

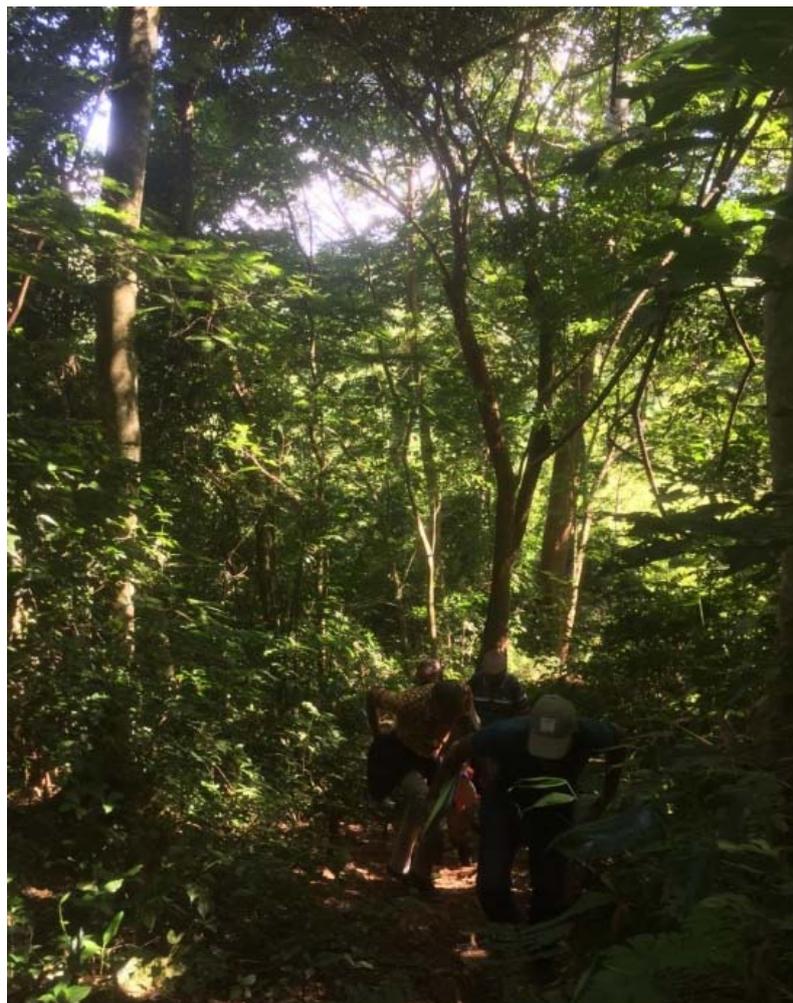
*Zhe-Xi Luo*, United States

New discoveries of Mesozoic mammal fossils in the last 20 years have revealed a spectacular diversity of their locomotor functions associated with fossorial, semiaquatic, terrestrial, arboreal, and volant adaptations. The early mammaliaforms, the evolutionary predecessors to modern Mammalia, were ecologically diverse. Their ecomorphological diversification during the Jurassic was driven by distinctive clades, phylogenetically independent of the Cretaceous clades of crown mammals, and also independently of the therian radiation in the Cenozoic. The ecological diversity of stem mammaliaforms during the Jurassic is now nearly matching that of extant marsupials, and suggesting an iterative paleoecological evolution by successive episodes of mammaliaform diversification during the Mesozoic. This represents a new evolutionary pattern of early mammal history.

## **Seasonal home range and movement patterns of elephants in a humid tropical environment in Mozambique**

*Valério Macandza & Faruk Mamugy, Mozambique*

In African environments, the quantity and quality of food resources for large herbivores vary spatially and temporally. When resources are abundant and spatially concentrated, foraging herbivores use small and overlapping home ranges during successive seasons. However, when food resources become patchily distributed and spatially unpredictable, herbivores adaptively expand or shift home range location and increase diel displacement in search for the scarce resources. In addition, when food resources are abundant, foraging herbivores remain in the same home ranges during successive seasons, whereas when resources are scarce, herbivores shift home range location. The aim of this study was to investigate the spatial ecology of elephants and identify their adaptive responses to the seasonal variation in the spatial distribution of resources in the predominantly evergreen forest of the Moribane Forest Reserve in central Mozambique (Figure 1).



**Figure 1.** Evergreen vegetation of the Moribane Forest Reserve in Mozambique

GPS satellite collars were fitted on two adult elephants, one female, representing the matriarchal herd, and one bull. The collars were scheduled to record GPS coordinates every six hours, which provided 1630 locations for the matriarchal herd and 1018 location for the elephant bull from May 2011 to January 2013. We used the a-LoCoH method to estimate the core and total home range size for each of the collared elephants during the annual cycle and in different seasons distinguished on the basis of rainfall received, to represent distinct periods regarding the availability of food and water for elephants. We calculated proportional overlap between seasonal home ranges and estimated diel displacement of each collared herd. Median diel displacements were compared among seasonal subdivisions using the non-parametric Kruskal-Wallis tests. Both elephants doubled the size of the core and total range used from the dry to the wet season.

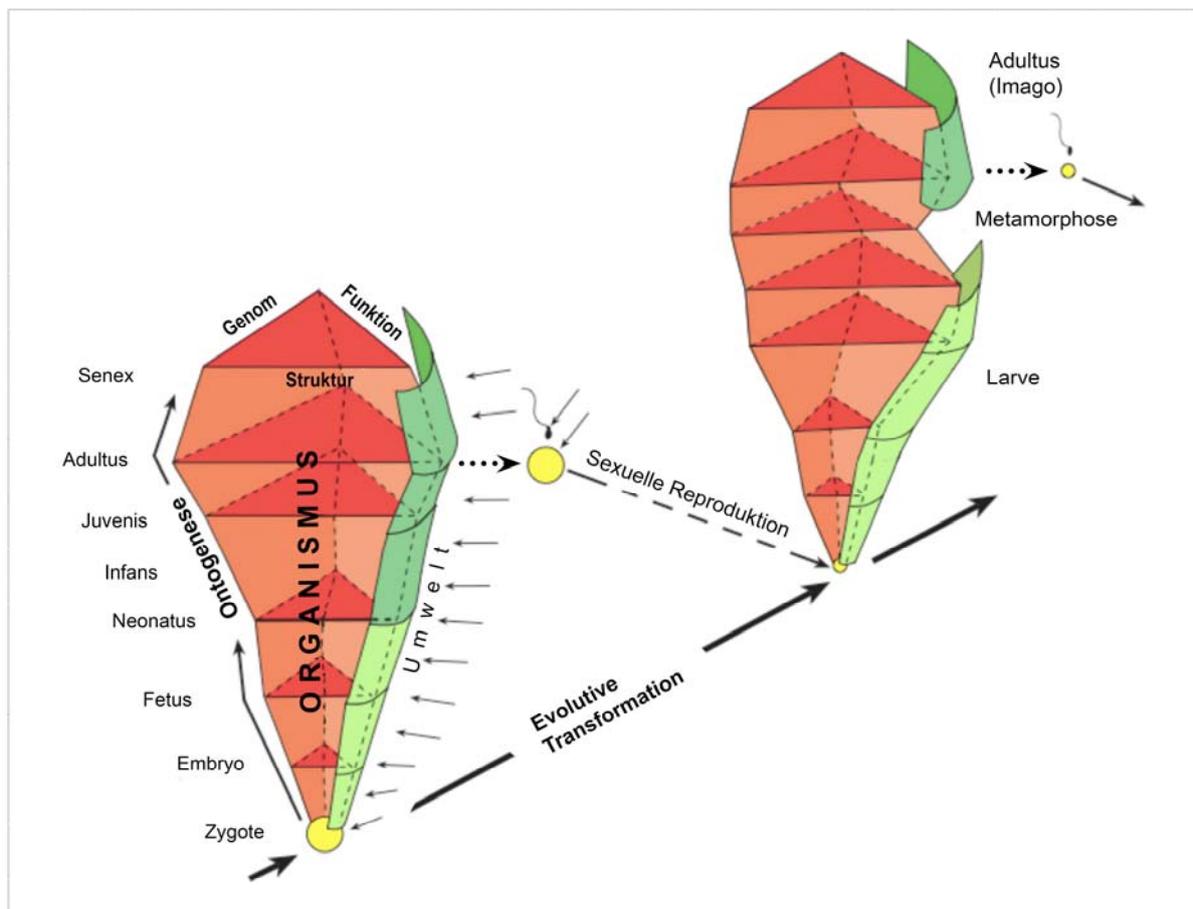
The matriarchal herd used the smallest range during the late dry (August-October) and the largest during the late wet season (February – April). This suggests that when food and water resources are widely available in the landscape elephants expand the home range use. Wider movements in the wet season resulted in less overlap between home ranges used in early and late wet season than during the early and late dry season when resources become restricted to few locations. The diel displacement of both matriarchal and bull herd declined during the wet season and increased in the dry season. Matriarchal herds showed shorter diel displacement (mean= 800 m/day) than bulls (mean= 1000 m/day). Our results show that when green vegetation and water are abundant and widely distributed, elephants move widely in the landscape, but they adaptively reduce the home range used when these resources become restricted to discrete areas of the landscape, such as riparian habitats. The increase of the home range used from early to late dry season, combined with high range overlap, indicates range expansion in response to decline in resource density throughout the landscape as the dry season progresses.

Key words: seasonal variation, spatial heterogeneity, home range, movement patterns, elephants

## Organism concept and evolutionary biology

Wolfgang Maier, Germany

Russell (1930) was one of the prominent advocates of organismic biology: "Biology should be the science of individual living organisms ... everything depends of course upon what conception we form of organism" (p.167). Partially influenced by this notion, I designed a scheme to visualize my understanding of the individual organism as an ontogenetically and phylogenetically changing system. This living system is determined on the one side by its phylogenetic history as manifested by its genome, and is, on the other hand, exposed to manifold conditions of actual life on all ontogenetic levels. The confrontation with internal and external conditions is eventually evaluated through reproductive fitness. In sexually reproducing species, the fitness of the individuals of each generation is summed-up by population genetics as modified evolutionary adaptation through natural selection. The result is micro-evolutionary transformation and macro-evolutionary change in the long run.



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## **Adaptationist approach to construction of evolutionary scenarios. Mammalian flapping flight as an example**

*Aleksandra A. Panyutina, Russia*

### ADAPTATIONIST APPROACH

Interactions of an organism with the environment are performed at a plurality of different levels: mechanical, ecological, physiological etc. Analyzing the interaction framework at each of these levels and comparing it in different organisms, we can reconstruct an outline of the evolution of adaptations. To understand the functioning and the formation of morphological forms of macroscopic organisms, mechanical interactions are most demonstrative. Considering an organism as a mechanical system, we can understand how one or another of its structures are responsible for the interaction with the environment and for optimal fitness. Based on knowledge of these interactions, we can build lines of successive adaptations on the grounds of the mechanical properties of the structures of organisms under comparison. Subsequently, relying on the environmental paleodata and knowledge of phylogenetic relations, we can reconstruct those evolutionary scenarios of morphological transformations that meet the ecological conditions of the formation of specific groups, as well as their initial morphological basis. In this case strict adherence to mechanical consistency and functionality allows us to develop scenarios with uninterrupted adaptation to the environment and justification for improving the fitness of each subsequent evolutionary stage.

In animals, the locomotor apparatus, which is a purely mechanical system, is best suited for solving such problems of all organ systems. Moreover, it is the evolution of the locomotor apparatus that is the most challenging to interpret in terms of preserving the fitness of transitional forms during major evolutionary transformations associated with the change of the locomotor environment, such as the land or air conquest.

In such an analysis, it is important to be guided not by kinship, but by the mechanical coherence of each stage, i.e. the organisms used to construct evolutionary scenarios need not necessarily be close relatives, but rather should be adequate models.

However, to select an appropriate model it is important to consider the level of kinship. For mammals, the level of kinship within a cohort is optimal. The matter is that at the moment of the modern orders divergence, the groups that formed the bases of the further explosive radiation were more or less similar to each other, so they hadn't yet have the features of locomotor specializations that modern mammals subsequently acquired. However, they had that basic design which made it possible to build all the resulting locomotor forms. Therefore, the model of a locomotor form, which some placentals could have passed in their evolution, should be looked for among other placental mammals; if there are no good candidates among recent placentals, then a marsupial is best suited, etc. In the worst case reptiles and even amphibians can be used as a model if there are appropriate forms among them. However, the more distant phylogenetically is the model form, the rougher the reconstruction will be because of escalating difference in the basal musculoskeletal designs on which the compared specializations are built.

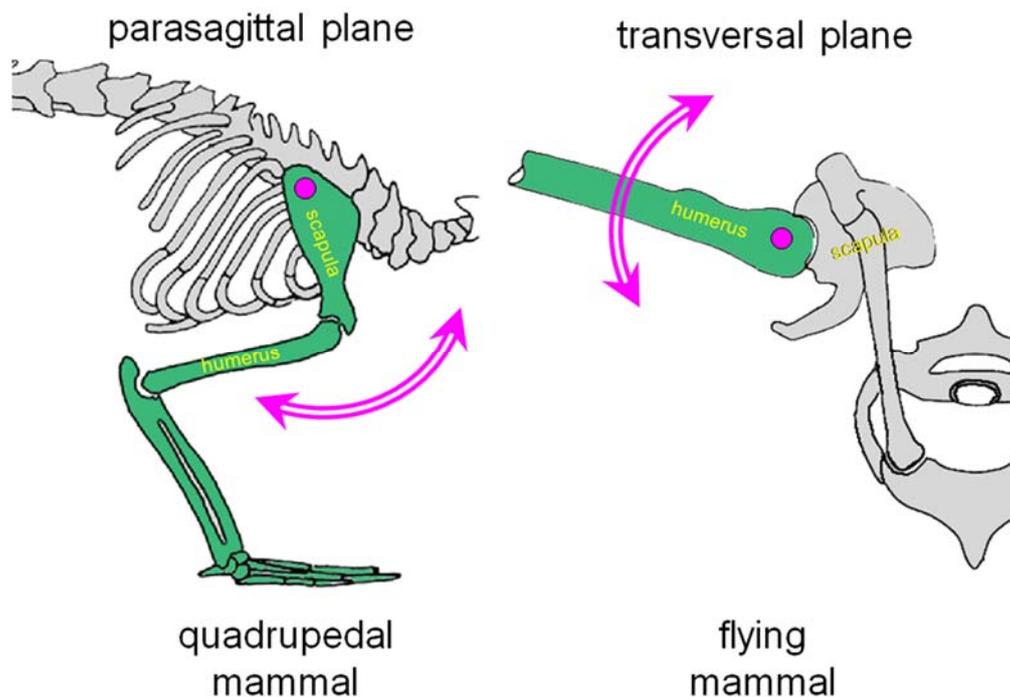
For similar reasons, it is optimal to use a recent organism rather than a fossil as a model, since a living specimens can be totally studied and allows to better establish the main parameters of the locomotor apparatus, in particular the attachment points of the muscles and their mechanical properties. This is very important in the context of assessing the redistribution of muscle mass when changing locomotor environment. Fossil forms, due to partial preservation, can be only used as auxiliary illustrating particular details of evolutionary stages. As a result of this approach, it becomes possible to address the key problems of evolutionary biology, for holistic consideration of which paleontological data is sorely insufficient.

#### MAMMALIAN FLIGHT FORMATION

We have reconstructed an evolutionary scenario for the flight formation in the bat lineage of mammals. The forelimbs were analyzed in detail as the major basis for the mechanical model; however, the hind limbs and the features of the axial skeleton were addressed as well for completeness. For the model, data on the structure of muscles, bones and ligaments of tree shrews, colugos and bats, as well as auxiliary data on a number of other groups of mammals were used.

As a result, a series of successive morphological transformations has been built, which should have taken place during the formation of a flapping flight. The series includes the following locomotive forms: terrestrial-arboreal, arboreal-gliding, and active-flying. All transformations at each evolutionary transition were considered both at the preadaptation stage and at the stage of full-fledged functioning.

As a key structural transformation that paved the way for a flapping flight in mammals, we have identified the transition of the extremities from the parasagittal plane to the frontal one (deparasagittalization). The parasagittal leg operates in the same parasagittal plane, while the frontally oriented wing operates in the transverse plane. Like the parasagittal plane, the transverse plane of operation is vertical, because the main mechanical work outside the aquatic environment is the work against gravity. With a change in the plane of work of a limb, its kinematic pattern also changes (Fig. 1). The forelimb of quadrupedal therians moves together with the scapula, the scapula operates as a proximal segment functionally similar to the femur of the hind limb – this is a three-segment Z-shaped pattern (Kuznetsov, 1985; 1995). In bats, the pivot for the flapping movement of the forelimb is in the shoulder joint (Panyutina et al., 2013). The limb moves relative to the scapula, so in contrast to the three-segment terrestrial limb, the scapula is not included in the moving part and does not form an additional segment of the limb. The scapula shifts but a little and not in the transverse plane in which the limb is flapping. Formally, the kinematic model of the bat wing (like of bird wing too) can be called a single-segmented, because the mobility in the elbow and in the carpal joint does not much participate in the overall wing excursion.



**Figure 1.** Scheme of operation planes and kinematic pattern of mammalian forelimbs. Left – quadrupedal therian, right – bat. Green – moving limb segments, pink dots – major pivot of the limb, pink arrows – major swing direction.

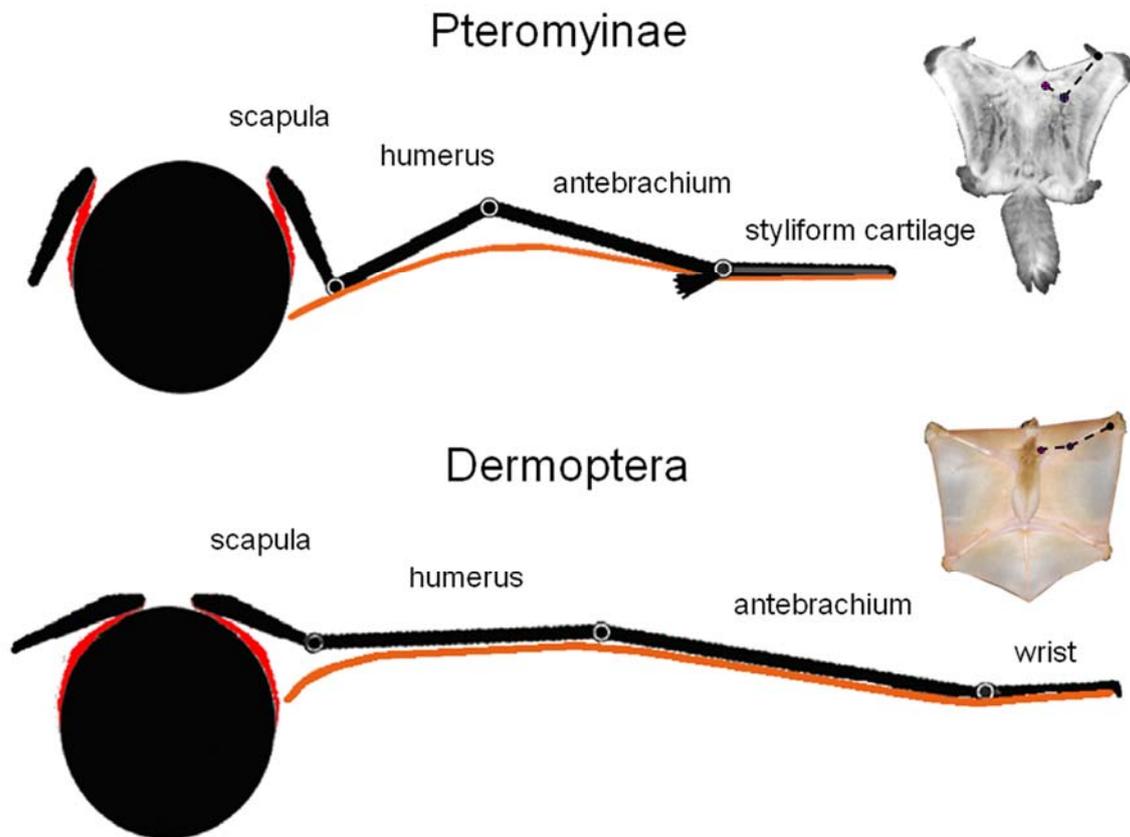
Such a shift of the forelimb movement plane and a change in the kinematic pattern of the limb require a great reformation of the shoulder girdle, its muscles, and reorientation of the shoulder joint. To understand how this transition could have happened in evolution, we need a model of the locomotor apparatus which is clearly viable and fitted, and which could open the way to changing the plane of limb operation, as opposed to the main-stream parasagittalization of the therian locomotor apparatus. We will concentrate on emergence of features, which could at the same time constitute a set of preadaptations for the limb operation in the transverse plane.

Since the key locomotor specialization of bats is the flapping flight, and besides among recent mammals there are at least six independently emerged groups using the air support passively (gliding), the search for a suitable model for the bats' ancestor should first be conducted out among these lineages. Only the absence of a suitable model among recent mammals, which could convincingly demonstrate the viability of the core set of preadaptations necessary for the development of flapping flight, would be the reason for devising some hypothetical locomotor model not actually found in nature.

An analysis of gliding mammals shows that the deparasagittalization of the forelimbs is most fully expressed in the colugo. During gliding, the scapula of the colugo is located in the frontal plane (Panyutina et al., 2015), due to which the glenoid became laterally oriented (which otherwise would have been impossible without changing the design of the therian scapula).

This creates the prerequisites for the frontal position of the humerus (as in humans) and its movements in the transverse plane as in bats.

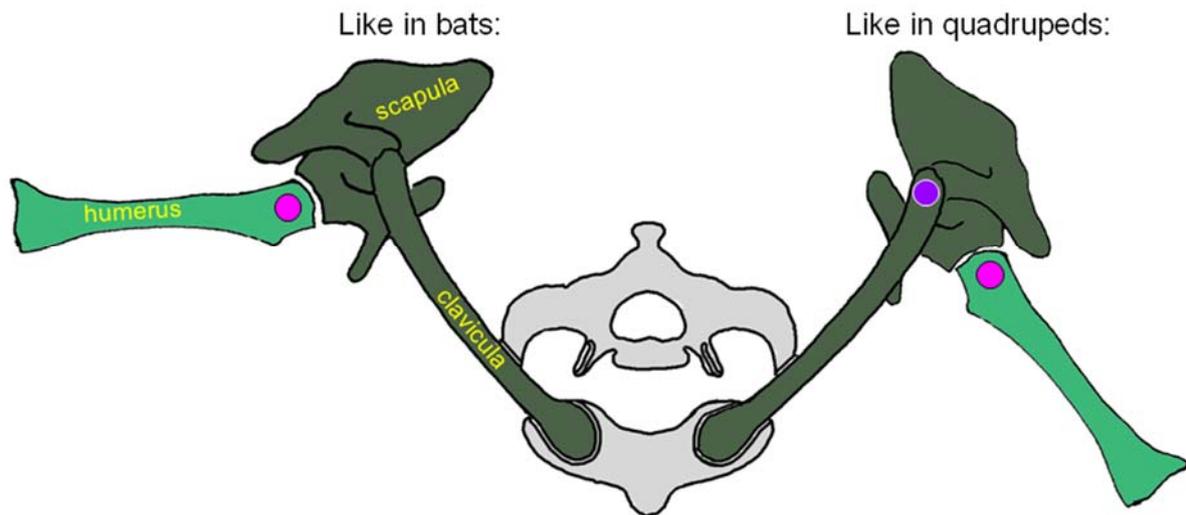
The advantage of such configuration of the shoulder girdle and forelimb is that the limb length is more fully involved in spreading the flying membrane and, accordingly, in the wing span (Fig. 2).



**Figure 2.** Forelimb position in mammalian gliders. Left – scheme of transverse section: orange line – flying membrane, red – ventral serrate muscle. Right – photos from the ventral side: dashed segments – humerus and antebrachium, dots – shoulder, elbow, and antebrachiocarpal joints.

In those mammals which glenoid is facing ventrally, as in quadrupedal therians, the humerus cannot be fully driven to the frontal plane during gliding, i.e. when stretching a membrane the limb remains half-flexed. On the example of flying squirrels (Pteromyini) it can be seen that to build the leading edge of the membrane they have to use specific distal add-ons – stiliform cartilages, while the colugos do not need such structures (Fig. 2). Considering other mammalian gliders from the point of view of the shoulder girdle repositioning it can be noted that marsupials demonstrate more advanced deparasagittalization. Apparently, it was easier for them to return to widely set limbs for gliding, because quadrupedal metatherians didn't yet achieve such a perfect parasagittalization as eutherians. According to preliminary data, in the scaly-tailed squirrels (Anomaluridae), the shoulder girdle is closer in design to that of flying squirrels – no pronounced morphological features of scapula deparasagittalization were detected.

So, based on the analysis of the shoulder girdle transformations among placental gliders, it seems that colugo provides the most suitable model for the reconstruction of the locomotor form of the bats' ancestor, which have taken the path of deparasagittalization of the locomotor apparatus. However, the difficulty lies in the fact that the mobility pattern of the colugo's limbs varies (Panyutina et al., 2015). Depending on type of locomotion, the shoulder girdle of colugo can take two positions: with a scapula lying frontally on the back like in bats and with a scapula standing almost parasagittally on the flank like in quadrupedal mammals (Fig. 3).



**Figure 3.** Scheme of colugo's shoulder girdle repositioning in transverse plane. Left – position in climbing tree trunks and gliding, right – position in suspension-running under branches. Pink dots – major pivot of the free limb, violet dot – center of mobility between the scapula and the clavicle, ensuring the scapula repositioning from the frontal to the parasagittal plane and back again.

The position of the scapula is frontal in gliding and climbing large-diameter tree trunks. In such climbing, the main pivot of the limb mobility is in the shoulder joint – the humerus moves relative to the scapula more or less in the frontal plane. In gliding, the frontally-spread limb bears statically the aerodynamic force of the aerial support, which force acts vertically and tends to elevate the limb even higher. So, the shoulder girdle already occupies a position similar to that of bats, but the mobility of the humerus in the transverse plane is not yet activated in aerial locomotion. In moving under the branches, the position of the scapula is most probably close to parasagittal, as in quadrupedal therians. But, there is no evidence that the scapula is involved as additional segment in the limb movement. Available videos suggest that the main mobility takes place in the shoulder joint too. To move the scapula from the parasagittal plane to the frontal and vice versa, a pronounced mobility between the clavicle and the scapula is used. Thus, the colugo has several preadaptations to the reorientation of the operation plane of the forelimb: firstly, the specific mobility between the clavicle and the scapula necessary for the displacement of the scapula to the frontal position; secondly, the reduction in the number of the free limb segments, i.e. exclusion of the scapula from a set of movable segments; thirdly, moving (gliding) with the static counteraction to an external force tending to abduct the forelimb in the transverse plane (which require the appropriate development of humeral adductor muscles needed subsequently for active strokes in the same plane). The above list of preadaptations can be considered sufficient to admit that colugo is a suitable model for reconstructing the locomotor stage passed by the ancestors of bats on the path to the formation of flapping flight.

In what conditions such a locomotor form could have emerged? The analysis of the biology and locomotion of the colugo shows that mechanical conditions for this transition arise when dwelling the biotope of a mature forest with large tree-to-tree distances.

At the initial stage of the transition from the terrestrial-arboreal niche to arboreal-gliding, the main skeletal segments of the limbs operated predominantly in the parasagittal plane. As the parachuting and then gliding from tree to tree developed, the elements of the shoulder girdle began to acquire more and more horizontal position bringing the limb to the frontal plane. This repositioning contributed to the wingspan. The ability to spread the limbs apart plays also an important role in running up large-diameter tree trunks, as it helps keeping the body closer to the trunk in order to reduce the torque which tends to overturn the body. The additional benefit is that the flattened pose on the tree together with a "camouflage cloak" made of the membrane – make colugos so invisible on the trunks, that they do not need shelters.

As a result, locomotor specialization is formed, equally beneficial for two ways of traveling at once: gliding flight and quadrupedal ascent on thick trees with the forelimbs set widely apart. Such locomotor specialization leads to the acquisition of the ability of limbs to move from parasagittal to frontal position and back again, that is to move up and down in the transverse plane, which eventually turns out to be a preadaptation to the next step in the chain of specializations – the development of flapping motions.

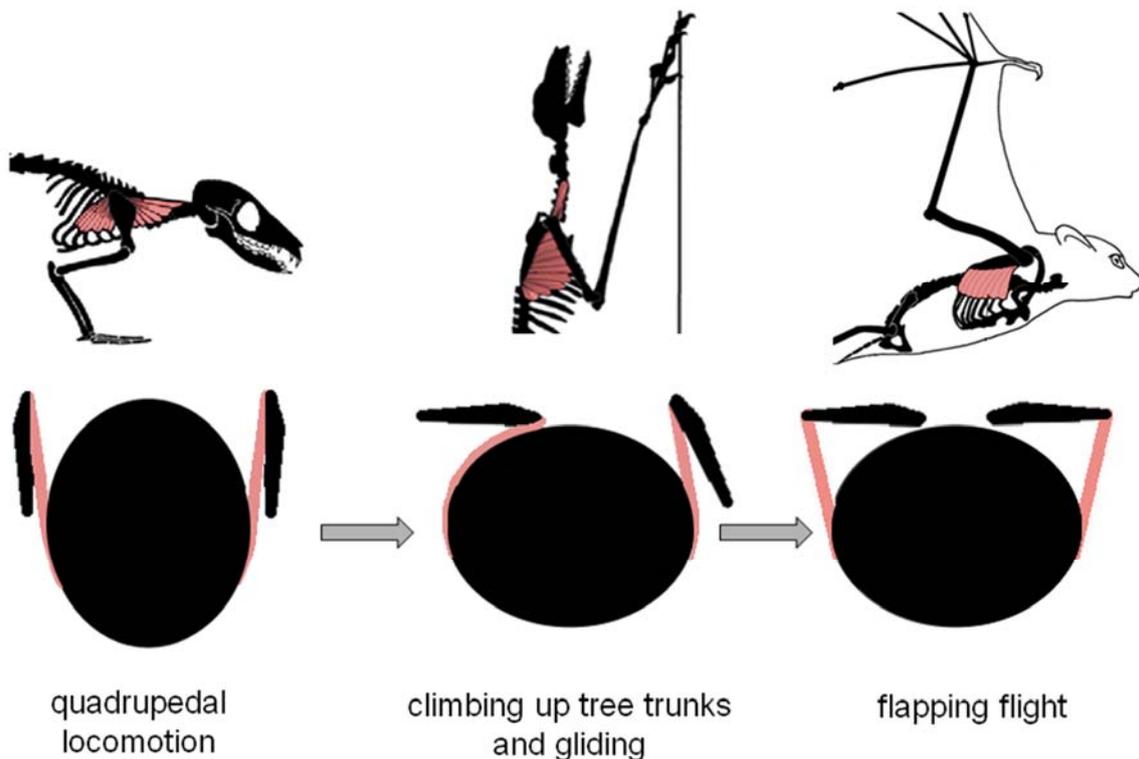
Using the colugo model as an intermediate stage in the formation of active aerial locomotion, we can consider a number of important transformations that ultimately ensure the development of flapping flight of bats.

In the series "quadrupedal therian – glider like colugo – active flyer like bat" the role of the clavicle as a strut for the forelimb increases. The clavicle acquires distinct articular surfaces with the scapula and the sternum, and becomes an analogue of the avian coracoid. Some specialization of this kind is already expressed in the clavicles of various groups of gliding mammals, among which it reaches its maximum in the colugo. In bats the clavicle is the most complete analogue to the coracoid of birds.

Reorientation of the main mobility and position of the limbs, and respective change of action of external forces on the limbs, is accompanied by changes in the mass distribution among the forelimb muscles. Depending on the external forces involved in locomotion, the mass of muscles acting in the corresponding direction increases and the mass of other muscles decreases. In the shoulder girdle, in quadrupedal parasagittal locomotion, retractors and, to a lesser extent, protractors play the main role, whereas when gliding locomotion becomes more and more developed, the adductors begin to dominate gradually taking away part of the mass from retractors. During the development of flapping flight in mammals, quadrupedal locomotion becomes secondary, and the adductors gain dominance in the muscular system; in fact retractors are forced out by adductors, and protractors are forced out by abductors.

Some of the key muscles are those suspending the trunk to the shoulder girdle (Fig. 4). The main muscle in this group is the ventral serrate muscle (musculus serratus ventralis). In quadrupedal parasagittal mammals, it suspends thorax to the vertebral border of the scapula. So the trunk is hanging between vertically placed scapulae as in a hammock. In colugo, the ventral serrate muscle is inserted, as in the vast majority of mammals, on the vertebral border of the scapula (Panyutina et al., 2015). But its insertion is not concentrated around one point – it spreads widely along the entire vertebral border. In bats, the bulk of this muscle, the thoracic part of the ventral serrate muscle (musculus serratus ventralis thoracis) also spreads along the whole scapula, but along its caudal border – instead of the vertebral one. The bat pattern of this muscle is exceptional.

Even the most complex ventral serrate muscle found in monotremes (and that of reptiles and amphibians) is structurally much closer to the pattern of quadrupedal therians. It is necessary to note that the bats have retained a "piece" of the ventral serrate muscle, which inserts in its original place, namely, on the vertebral border of the scapula. This small portion is homologous to the cervical part of the ventral serrate muscle (*musculus serratus ventralis cervicis*) and it shows how the whole ventral serrate muscle would be attached in bats if its thoracic part has not been shifted. In order to understand why such a transposition of the muscular suspension of the body was required and how it could happen in evolution, we need to analyze forces, which the ventral serrate muscle transmits to the trunk.



**Figure 4.** Repositioning of the ventral serrate muscle associated with the change of locomotor specialization. Top row – right side view, bottom row – scheme of transverse section through the thorax.

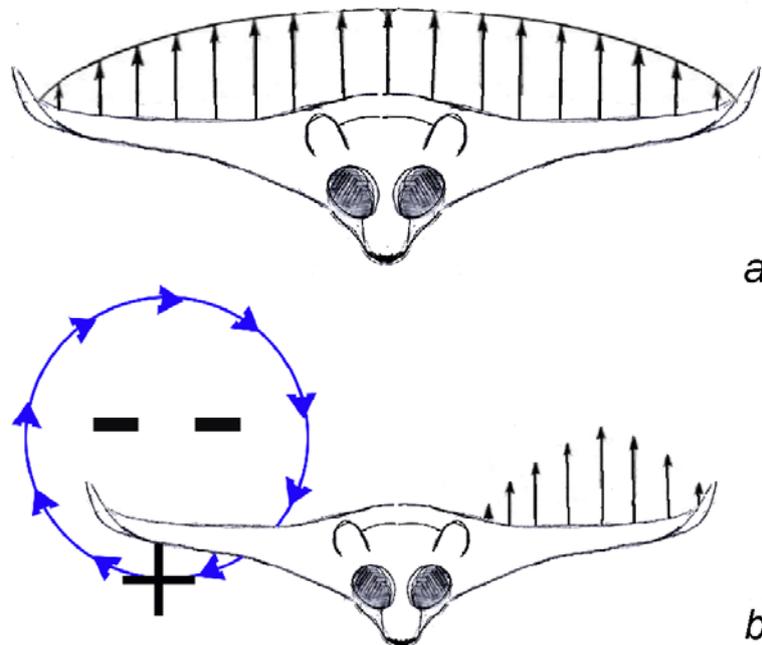
In quadrupedal parasagittal mammals, the ground reaction force acts more or less along the parasagittal limb. Accordingly, the humerus presses on the scapula from below in the vertical plane. The ventral serrate muscle, transmits the force further, from the parasagittally-placed scapula to the trunk, and thus, holds aloft the rib cage against the force of gravity. In colugo – in case of frontal position of the scapula – the ventral serrate muscle is somewhat wrapped around the rib cage, gaining a significant horizontal component. During gliding, the straight limb of colugo acts within the membrane as a spoke in umbrella – it is loaded by longitudinal compression (Panyutina et al., 2015, Fig. 4.12). In the wing plane, the tension of the anterior and lateral parts of the membrane creates force acting along the limb. This force presses the limb together with the scapula medially (posteromedially in fact). And the only one muscle that can act against and balance this force in the frontal plane is the ventral serrate muscle wrapped around the rib cage.

This is a unique situation: normally, no muscle is able to pull the scapula laterally. And, due to its attachment along the whole scapula, the colugo's muscle can balance the limb against membrane tension in a wider range of conditions. So, the main morphological modification of the ventral serrate muscle in colugo is that its attachment is widely spread along the scapula. And the main functional innovation is that – when the scapula is in the frontal position – the muscle's force gains a significant horizontal component.

To understand the functional basis for the shift of the ventral serrate muscle to the caudal border of the scapula in bats – it is necessary to analyze how the flying membrane of bats acts on the limbs in the air. In a glider, e.g. colugo, the tense membrane acts on the fore and hind limbs with approximately equal forces, tending to bring them together and elevate. Similarly acts the part of the bat membrane that is located between the fore and hind limbs. We propose to call it "archaeopathagium" (Panyutina et al., 2015). This term has a functional sense because homology is not full here. However, by "archaeo-" we mean that this part of the bat membrane is evolutionarily older. In addition to the archaeopathagium, bats have a huge distal part of the membrane not attached to the hind limb, which is supported only by the forelimb. We call this part of the membrane "neopatagium". The archaeopathagium, being stretched between the fore and hind limbs, tends to bring them together and elevate. The sum of the forces acting on the limbs from the archaeopathagium is transmitted through both limbs to the trunk and, like in gliders, balances the force of gravity. More exactly, in the case of bats, the forces from the archaeopathagium balance only a smaller part of the force of gravity. The aerodynamic force acts on the neopatagium upward and forward, tending to elevate and protract the wing. And all this force is transmitted only to the forelimb. The neopatagium force is much greater than that of the archaeopathagium, because the neopatagium has a significantly larger area and moves due to the wing flapping with a greater speed relative to air. So, the forelimb is loaded not only by the smaller force coming from the air through the archaeopathagium, like in the hind limb, but in addition by the greater force from the neopatagium. As a result, the body is balanced against gravity mainly by the forelimb in bats. However, if all the forelimb force is transmitted to the body through the pectoral muscle passing in front of the center of gravity of the body, the force of pectoral muscle together with the force of gravity would couple in a torque pitching the body head up. To keep the body horizontal in flight, some part of the force from the neopatagium must be transmitted to the thorax by the forelimb muscles posterior to the center of gravity of the body. Such a mechanism in bats really exists. It is due to the specific position of the thoracic ventral serrate muscle. Because this muscle is spread along all the lateral border of a very elongated scapula, it is mainly located considerably posterior to the center of gravity, opposing the pectoral muscle. The force of the thoracic ventral serrate muscle of bats pulls the rib cage upward posterior to the center of gravity of the body. So, the specific structure of this muscle in bats helps balance the body supported predominantly by the forelimb with the neopatagium.

Rearrangements of the hind limb mobility are much less radical, since the hip joint of mammals initially allows for much greater freedom of movement than the shoulder joint. However, at the stage of improving the gliding apparatus some special accommodations were formed in it. Inter alia, the dorsal bony lip of the acetabulum, which normally restricts the elevation of the femur in the transverse plane, is reduced to varying extent in all mammalian gliders.

Speaking about transformations of the locomotor apparatus that took place in the evolution of bats, we can't leave aside the reasons for wing elongation in ancestor gliders. Increased aspect ratio significantly improves the glider quality by reducing induced drag. However, the aspect ratio of mammalian gliders does not much exceed 1, which means that the wing span is equal to the mean wing chord (Bishop, 2006; our data), while in actively flying vertebrates it is usually higher than 4 (Stegmann, 1954; Alexander, 1995; Pennycuik, 2008). An increase of the aspect ratio in gliders faces at least two obstacles. Firstly, the need to maintain the quadrupedal locomotion remains. Secondly, it was shown experimentally (Torres, Mueller, 2001; Shyy et al., 2005) that, in low aspect ratio wings at Reynolds numbers relevant to vertebrate flight, aerodynamic performance declines with increasing aspect ratio from 1 to  $\approx 2$ , particularly at the high angles of attack used by the mammalian gliders. This surprising experimental fact, which contradicts the general principle of reducing induced drag with increasing aspect ratio, can be explained by the secondary source of lift arising from the spillage airflow over the wing tip (Bishop, 2008; Fig. 5).

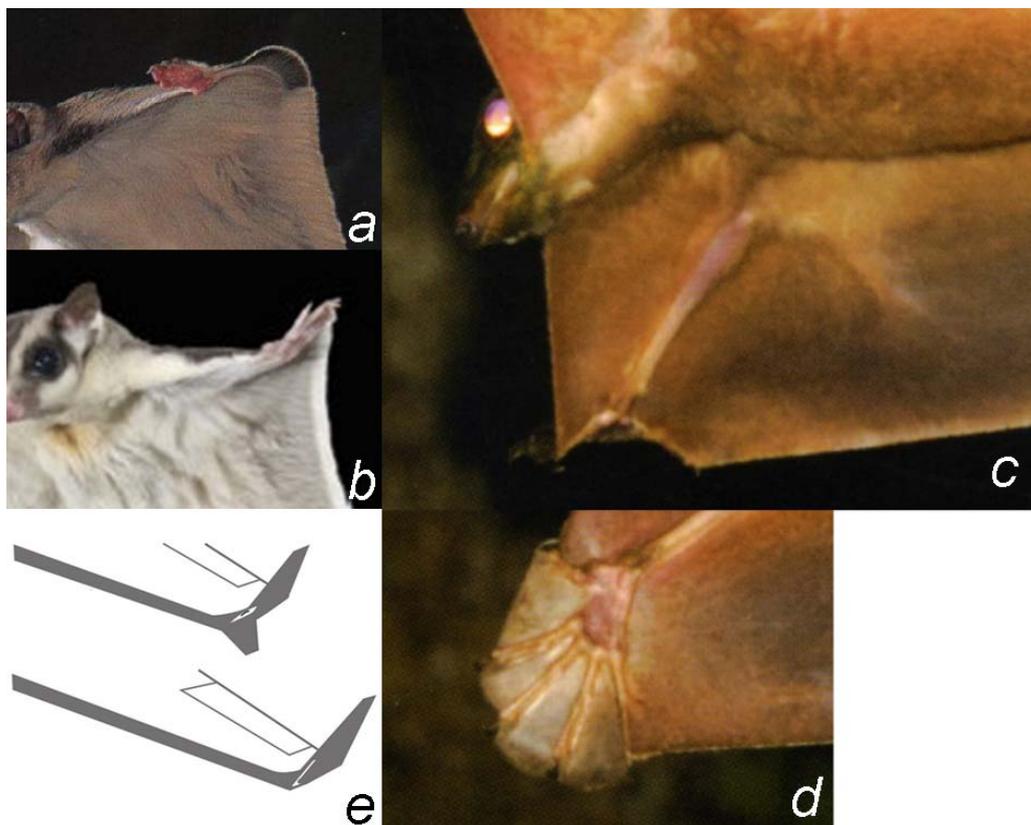


**Figure 5.** Scheme of the lift force distribution along the wing span in a gliding mammal, anterior view. a – the primary lift due to "classic" airflow along the chord of the airfoil, b – the secondary lift (right side of the image) due to location of the low-pressure core of the tip vortex (blue arrows on the left side of the image) above the wing tip.

A feature of this tip vorticity is that its low pressure core is situated on the upper surface of the wing tip and, hence, increases the pressure difference between upper and lower surfaces and contributes to the lift force on the wing (Torres, Mueller 2001; Shyy et al. 2005). This secondary source of lift becomes stronger with increasing angles of attack, and in low aspect ratio wings the effect is enough to compensate for the loss of the primary source of lift associated with flow separation (i.e., stall) along the wing span at these angles. As a result, the total lift generated by low aspect ratio wings does not drop until much larger angles of attack are reached than in the usual high aspect ratio wings (Torres, Mueller 2001). Therefore, the wings of very low aspect ratios ( $\approx 1$ ), such as those possessed by gliding mammals, have better lift generating performance at high angles of attack than the wings with intermediate aspect ratios ( $\approx 1-2$ ) which should have been passed in the ancestors of bats.

Thus, combined with the need to maintain the proportions of the extremities suitable for the quadrupedal locomotion (at least for climbing tree trunks), the loss of this secondary source of lift at the wing tip, when the angle of attack is very large, can be a critical barrier for the elongation of wings and acquisition of perfect aerodynamic quality in mammalian gliders.

However, the wing elongation initially could follow the path of winglets development. Winglets located on the lateral (distal) edge of the wing serve as physical barriers to the air spillage and significantly improve the aerodynamic characteristics of the wing reducing the energy of the tip vorticity and, hence, the induced drag (Whitcomb, 1976; Faye et al., 2002). In the majority of gliding mammals there are winglet-like structures (Fig. 6).



**Figure 6.** Winglet-like structures in gliding mammals (a-d) vs winglets of aircraft (e). a – *Glaucomys sabrinus* (photo by Stephen Dalton), b – *Petaurus breviceps* (photo by Joe McDonald), c, d – *Cynocephalus variegatus* (photo by Norman Lim).

Most similar to a double-sided winglet is the manus of colugo. Its first and fifth digits are depressed, and digits second to fourth are elevated relative to the main wing plane. As soon as until now the aerodynamic characteristics of mammalian gliders have not been studied experimentally, we can not say for sure if the manus of colugo, or other gliding mammals, actually works as a winglet. Alternative interpretation is that this is not a winglet, but simply an extension of the main wing plane, increasing the aspect ratio. To find out its actual role, it requires testing the colugo's wing in a wind tunnel and making particle image velocimetry. But in any case, such an add-on is useful for the aerodynamic quality of the wing. If the manus of colugo really works like a winglet, then, firstly, it reduces spillage, thereby increasing the lift force at the tip of the wing, and secondly, deflects the wing-tip vortex upward so that its low-pressure core shifts on top of the wing tip, which can additionally increase the secondary source of lift at large angles of attack.

If it does not work as a winglet, it gives an additional elongation which as well reduces the induced drag. In any case, the development of such a tip manus-based structure opens the way to the wing elongation. The membrane between the digits allows the manus to create considerable aerodynamic interaction with the air. Strong reinforcement provided by the digits, in turn, enables in the future a significant enlargement of this structure (which is impossible, for example, on the basis of compliant cartilaginous structures such as the styloform).

If analyzed thoroughly from the adaptationist point of view, almost the entire set of specific musculoskeletal features of the locomotor apparatus of bats can be interpreted through an intermediate specialization to arboreal-gliding locomotion. Most of the features acquired at this stage appeared to be key preadaptations for the further development of flapping flight.

With this approach, the structure of organisms gives the key not only to evaluation of the environmental constraints, but also to understanding the ecological and evolutionary perspectives of a particular structural type.

#### FITNESS TRADE-OFF PROBLEM

As a result, the widely spread and elongated limbs of colugos are an excellent structural basis for a wing of glider. This wing can significantly reduce the energy cost of transport (Schmidt-Nielsen 1972; Tucker, 1975; Norberg, 1985). On the other hand, it gives a complete set of preadaptations for the formation of flapping flight. But why then Dermoptera is the only group with such an advanced gliding apparatus? And further, why bats represent the only case of flapping flight in mammals?

Considering morphological transformations of the locomotor apparatus on the way to the formation of flapping flight, it is necessary to take into account the problem of evolutionary trade-offs at each key stage of specialization. For example, the modification of the muscles for the body suspension, which allows the colugo to glide on limbs spread in the frontal plane, makes the quadrupedal parasagittal running troublesome. Occasional videos of colugos on the ground (eg, NG Live! web resource; N. Lim, personal video) show that they can not maintain the parasagittal posture of limbs. They spread the limbs in the frontal plane over the ground, as if embracing a large-diameter tree trunk. The energy consumption of colugo while running is still unknown. But we can confidently assume that it is greater than in flying squirrels. And in flying squirrels, in turn, the cost of running is known to be greater than in tree squirrels (Flaherty et al, 2010). Colugos compensate for the loss in running ability by gliding at smaller angles, which significantly reduces the distance that must be covered quadrupedally up the next tree trunk. For the smallest recorded angle of the colugo gliding, the height loss is about 1 meter per 10 meters of the distance traveled (Jackson, 2000). This makes it possible to compensate for the rejection of quadrupedal running and even the decrease of ability for quadrupedal climbing. However, the further aerodynamic upgrade through wing elongation is strictly prohibited by the necessity to retain the ability to climb. This is one of the key fitness trade-off points in the formation of the flapping flight of mammals. The destruction of climbing ability is the only way to a perfect wing (in birds too). But when the climbing can become unnecessary? Only in case there is no loss of altitude in flight, and only flapping movements can abolish the altitude loss! The conclusion is that the flapping flight was the direct replacement of quadrupedal climbing tree trunks. So, the wing upgrade above the degree of colugo became possible after the appearance of flapping motions.

The bat ancestors began to flap with bad short wings. Even moderate occasional wing strokes could reduce the altitude loss – subsequently making the flight horizontal and then even ascending. Due to the fact that the body when gliding moves fast through the air, a moderate wing stroke is able to give substantial increase in lift (Norberg, 1985; Panyutina, 2018). Due to the emergence of “proto-strokes”, the bat ancestors were able to overcome just the very extremum of the fitness trade-off, at which a gliding specialization began to destroy too strongly and quickly the ability to climb. This is possible only in case the new type of locomotion provides energy profit that compensates for the losses. Then, the quadrupedal locomotion (its energy economy and speed) could be dismissed. But, there could not be a complete loss of the quadrupedal locomotion, and it never took place in the early evolution of bats. This happened only at the peak of the flapping-flight specialization in some super-advanced aerial hunters (like Rhinolophidae). Unable to climb, they even lost the ability to use slit-type roosting places which cannot be entered by flight. And this was another extremum of the fitness trade-off that only a few bat species in several families managed to pass.

#### ACKNOWLEDGMENTS

The author is grateful to Dr. Kuznetsov for useful discussion and criticism. E. Yakhontov much assisted in English translation of the manuscript. The major impulse for this writing came from the invitation by Professor Zeller, Dr. Göttert and Dr. Starik to participate in the fascinating workshop in Linde.

This study was supported by the Russian Foundation for Basic Research (grant 17-04-00954).

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## **Adaptations of “reptiles” and amphibians to arid and semi-arid environments**

*Gad Perry*, United States

Modern “reptiles” (popularly considered to include crocodylians, turtles, tuataras, lizards, and snakes, but excluding birds) and amphibians are found in almost every habitat around the globe, including many that are somewhat or even extremely dry. Detailed scientific analyses of how these species maintain their thermal and hydric relations go back to the 1940s, though many insights had to wait for more sophisticated equipment to be developed decades later. Studies on both hibernation and aestivation – dormancy during periods of hydric or thermal stress – have also increased as tools to explore the underlying physiological and hormonal processes have become more sophisticated. These studies have broadly focused on homeostasis, or how amphibians (that are generally perceived as particularly water-dependent) and “reptiles” can maintain their internal physiological processes within acceptable limits in the face of hostile environments.

Behavioral components, such as choice of activity time, have long been considered as part of the adaptations brought to bear. In recent decades, studies have shown an increasing sophistication and diversity of mechanisms. Some amphibians found in tropical dry forest lay their eggs on land because standing water may be rare or non-existent. Others, found in extreme deserts, can form “cocoon” that allow them to store sufficient water to remain inactive underground for years at a time. Increasing demonstrations of phenotypic plasticity in morphology related to diet allow tadpoles to become carnivorous in food-limited ponds where speedy development is required because of rapid drying, yet preferentially feed on non-relatives. In “reptiles,” recent work shows that older insights about reproductive plasticity have been too simplistic. For examples, it is true that some species show temperature-dependent sex determination based on conditions the eggs are exposed to during development, but embryos have recently been shown to be able to respond to unfavorable conditions by accelerating hatching, entering diapause, producing protective heat-shock proteins, or producing hatchling phenotype better adapted to the outside conditions that incubation environments indicate.

Despite the variety of strategies and taxa, models predict that ectotherms living in warm areas, and particularly ones with small home ranges and limited genetic variability, may be especially vulnerable to the effects of climate change. However, responses vary among species and may be more closely related to limited water availability than to temperature extremes.

## **Wildlife trafficking, its impacts on global biodiversity, and efforts to reduce harms**

Gad Perry<sup>1,2</sup>, Meredith Gore<sup>3</sup>, Lee Schwartz<sup>1</sup>, Kathleena Mumford<sup>1</sup>, Janet MacLaughlin<sup>1</sup>, and Sara Walker<sup>4</sup>

<sup>1</sup> United States Department of State

<sup>2</sup> Department of Natural Resource Management, Texas Tech University

<sup>3</sup> Department of Fisheries & Wildlife, Michigan State University

<sup>4</sup> Association of Zoos & Aquariums

The 2019 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) summary report documented the current evidence surrounding global biodiversity's extensive declines. Although extinctions *to date* may not warrant the use of "sixth mass extinction" to describe our era, likely near-future outcomes in the absence of major changes do. IPBES estimated around 1 million species already face extinction, many within just a few decades. Illegal exploitation by global criminal supply chains is one important driver of this biodiversity loss.

Motivations for direct exploitation of biodiversity are often economic. Animals are poached in the wild for body parts used to make a variety of products, including food, jewelry, clothing, traditional "medicine," carvings, souvenirs, and household décor. Wild animals and plants are also trafficked around the world and sold into the burgeoning live pet trade. The global criminal economy is actively incorporating wildlife, along with other natural resources, into its activities. The illegal trade of wildlife is estimated by some to be worth somewhere between \$10–20 billion per year, ranking as the fourth most profitable crime. Wildlife trafficking can generate massive profits for professional criminals at great expense to wildlife, the environment, national security; and to local and vulnerable communities and their sustainable livelihoods.

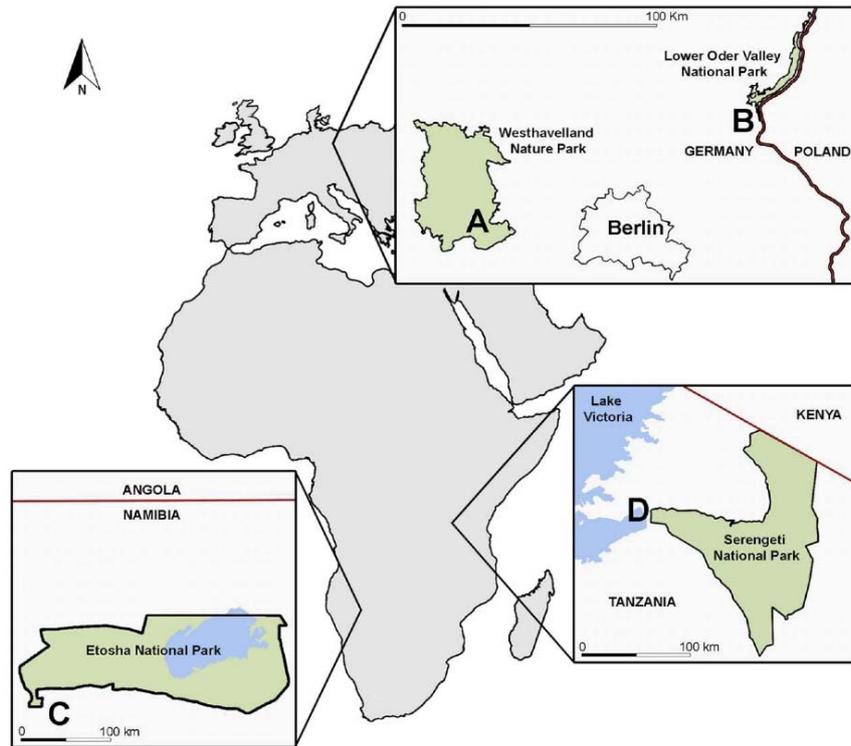
The impacts to biodiversity from wildlife trafficking include, for example, zoonotic disease transmission, biological invasions, altered population dynamics and animal behavior, and even species endangerment or extinction. Data are usually based on seizure records that partially represent effort rather than trade magnitude, are highly taxonomically biased, and likely greatly underestimate actual values. Many of the highest profile seizures of the illegal trade appear to end up Southeast Asia, Europe and North America are also significant import and export and transit stations, especially for taxonomic groups such as iguanas.

We review the current scientific evidence surrounding the impacts of wildlife trafficking on biodiversity, then discuss two efforts designed to reduce harms associated with those impacts. First, we profile a new geospatially-enabled data dictionary and standards designed to support interoperability of data for diverse actors working in source, transit, and destination geographies. We then profile a multisector demand reduction campaign designed to educate and persuade potential wildlife consumers about the harms associated with illegal wildlife consumption and the legal ramifications of trafficking. Although wildlife trafficking is an important concern, other causes of endangerment including land use change (primarily for agriculture and urbanization), climate change, pollution, and invasive species also need to be urgently addressed.

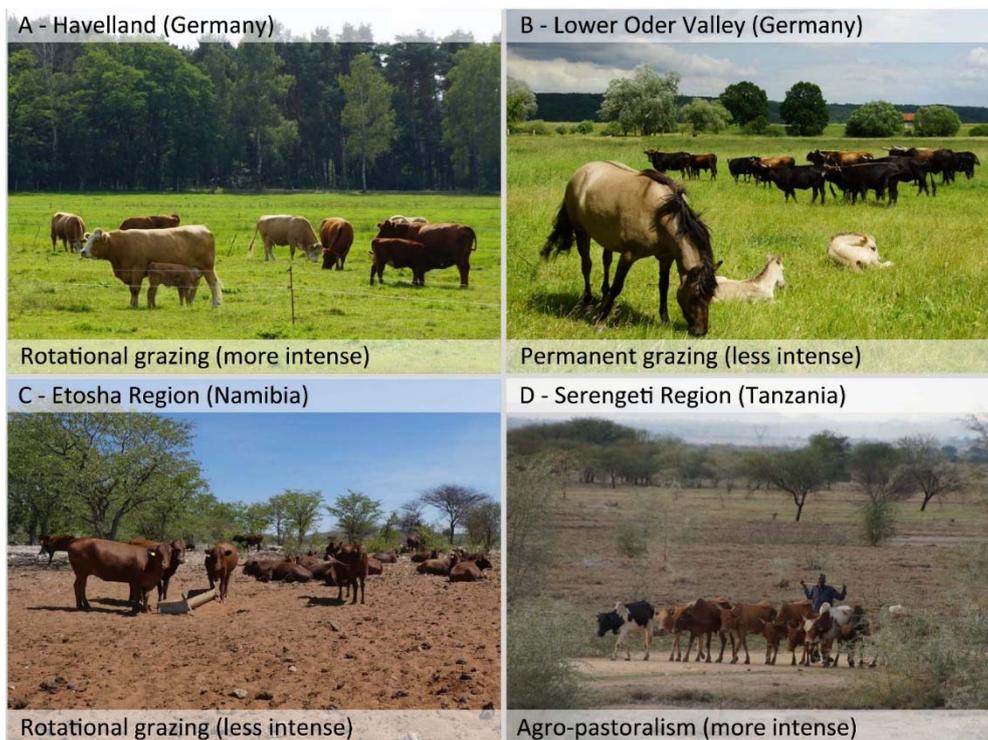
## **Livestock-wildlife interactions: a synthesis of four case studies from central Europe and Sub-Saharan Africa**

*Thomas Rottstock, Thomas Göttert and Ulrich Zeller, Germany*

This study is rooted in an organismic and comparative approach to grassland ecosystems in central Europe and Sub-Saharan Africa. To gain a better understanding of wildlife responses to livestock grazing, we comparatively examined four case studies in three countries (Germany, Namibia and Tanzania; Figure 1). The central question is, whether ecosystems in distinct geographical regions respond in a similar way to disturbances. This poster deals with the results of four camera trap surveys conducted on livestock pastures adjacent to protected areas in the three countries. Despite distinct geographical regions and ecosystems (with distinct medium-sized and large mammal communities), our results reveal a number of common response patterns of wildlife to livestock grazing. We found a significant decrease in total wildlife relative capture frequency (RCF, number of events / 100 camera trap days) (4 areas) and a decrease in species richness (3 areas) in association with the grazing of livestock. Additionally, livestock grazing is associated with a clear shift of the ungulate-carnivore ratio (proportions of events per guild) towards carnivores (3 areas) and a shift of daily activity patterns of observed mammal species towards night hours (3 areas). Wildlife responses towards livestock appear linked with the intensity of livestock grazing within each region, which applies to central Europe and Sub-Saharan Africa in a similar way. Less disturbed African savanna ecosystems provide a valuable reference for more intensively used grazing systems in Africa but also in central Europe. A better understanding of common wildlife responses to livestock grazing can support the development of more sustainable land use strategies and the mitigation of human-wildlife conflict on a transnational scale.



**Figure 1:** Location of the four camera trap surveys in Central Europe and sub-Saharan Africa



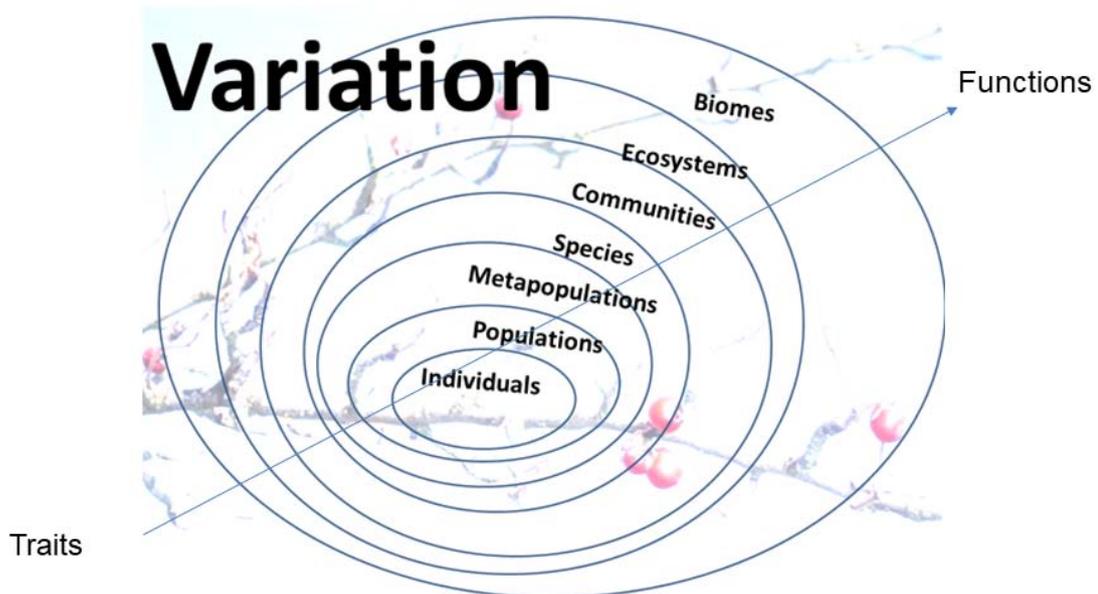
**Figure 2.** The four studied grazing systems (photos: T. Rottstock)

## Relationships between phenotypic traits and fitness

Mar Sobral, Spain

Functional traits are defined such as traits which affect individual fitness. I argue that the use of the term “functional trait” complicates the progress of the field because all traits are potentially linked to fitness. Obviating the potential link of all traits with fitness is related to dismissing (i) the integration of the phenotype, (ii) the spatio-temporal variation of environmental pressures and (iii) the genotype by environment interaction effect on the phenotype. These conceptual gaps could explain the weak predictive power of many functional ecology studies. I develop here some of the reasons why we should consider that all traits are related to fitness -advocating simultaneously for a change in terminology.

## Functional (trait) ecology



## **Phylogenies and Morphologies - on the Evolution of Rarely Considered Organisms**

*Thomas Stach, Germany*

While the taxon Deuterostomia comprises merely 50.000 described animal species, next to Ecdysozoa and Lophotrochozoa, Deuterostomia constitutes one of the three major subdivisions of the animal kingdom. The special interest in the evolution of deuterostomes is on the one hand founded in the tremendous disparity of organisms and their respective life cycles. On the other hand deuterostome evolution is interesting because within this taxon the evolutionary transformation from invertebrates to vertebrates took place. In my talk, I will use the examples of different organ systems, to demonstrate the contribution of precise morphological analyses towards an integrative understanding of evolution. Studies of eye morphology, morphogenesis of the nervous system, detailed cell lineage analyses, and ultrastructural studies of the tunic, exemplify aspects of the complex interdependencies between organism, environment, and evolution. In the talk, I will show existing conflicts in current phylogenetic hypotheses, suggest constructive and productive solutions, and ascertain the indispensable role of morphological studies in scientific analyses of evolution.

## **Organismic responses of insectivorous bats to local land use**

*Nicole Starik, Thomas Göttert and Ulrich Zeller, Germany*

Here, we use insectivorous European bats to assess land use related changes on biodiversity in different agro-ecosystems in Brandenburg (Germany). Assuming that specific organismic traits of temperate bats, such as obligate insectivory, echolocation, reproductive seasonality and roost fidelity determine the distribution and occurrence of the different species, we investigated effects of different land use types on bat occurrence, activity and species composition in two subsequent years (2012 and 2013). We developed a matched-pair design where study sites differed with regard to a complexity index derived from vegetation measurements related to: a) vertical vegetation structure (pine forests), b) tree species composition (mixed forests), c) tree age (deciduous forests), d) crop type (arable land), and e) management intensity (grassland). Mist netting and acoustic monitoring were used as complementary techniques in order to investigate the local bat fauna. In addition, we sampled nocturnal arthropods with light traps and barber traps to assess the abundance of insect prey. A significant increase in bat activity, species richness, and species diversity ( $H'$ ) as well as prey availability was detected on sites associated with management practices leading to an increase in habitat structural complexity (pine forest with understory, mixed forest dominated by deciduous tree species and extensively managed grassland). In addition to this pronounced responsiveness of bats to local land use on the community level, we describe species-specific responses on the organismic level. Our results suggest that specific measures of local woodland and agricultural management, such as natural regeneration of understory vegetation in pine monocultures, careful selection and mixture of tree species in mixed forests and low intensity farming in grasslands, increase habitat quality for bats and may greatly contribute to an environmentally sustainable land management.

## Similar is not the same - Case study on long-eared bats in Brandenburg reveals challenges for their conservation

*Nicole Starik, Thomas Göttert and Ulrich Zeller, Germany*

Here, we present data on the ecology of the long-eared bat species *Plecotus auritus* and *Plecotus austriacus* from Brandenburg (Germany), where the two sibling species occur in sympatry. Between April 2012 and October 2014, data were collected on phenology (seasonal occurrence), habitat use (roosting behavior, foraging behavior), and dietary composition. Different methods were used, including mist netting, acoustic monitoring, identification of roosting sites, microscopic analysis of feces / prey insect remains and radiotracking of each 5 female bats during the maternity season. While *P. auritus* was captured and recorded between mid-April and end of October, the observation period for *P. austriacus* was much shorter (beginning of May until beginning of October). Despite this difference in the seasonal occurrence, we could not detect differences in the nightly activity pattern, e.g. the time of emergence from roost. Roosting sites of *P. austriacus* could only be found in buildings (houses, churches, barns) whereas *P. auritus* used both, buildings (houses, churches) and tree holes in forest stands. We identified also shared roosting sites in churches, where the two species occupied different roosting places (*P. auritus* mainly in crevices of attics and *P. austriacus* mainly open in ridges). Both, mist netting and radiotracking, revealed that *P. auritus* almost exclusively foraged in deciduous and mixed forests in close vicinity to its roosting sites whereas *P. austriacus* foraged up to 6 km from roosting sites mostly in pastures, hedges and tree lines in a grassland-dominated matrix. The provisional analysis of fecal samples (n=67 analyzed samples in total) indicated an overlap in consumed prey categories between the two species and it seems that both species feed mainly on Lepidoptera. Moreover, the lepidopteran families Noctuidae and Arctiidae could be detected most frequently in the samples of both species. However, it seems that the proportion of lepidopteran families in the diet of *P. austriacus* varied seasonally. Our preliminary results suggest both, seasonal and spatial resource partitioning between the two species which could have important implications for the conservation of sympatrically occurring long-eared bats (e.g. legislatives for the protection of trees during the vegetation period, protection of bat species during (re-) construction of buildings etc.).

## **On the biology of the platypus (*Ornithorhynchus anatinus*)**

*Peter Temple-Smith*, United States

Education Program in Reproduction and Development, Department of Obstetrics and Gynaecology,  
Monash University, Clayton Victoria 3168 Australia

The monotremes, represented today by one species of platypus and ~5 echidnas species, evolved more than 160mya. They were part of the Gondwanan fauna with fossils going back over 110Mya. Monotremes are oviparous with meroblastic ova; their reptilian traits are embodied in a distinct mammalian habitus as confirmed by the platypus genome. Platypuses have a discontinuous distribution in water systems along the east coast of Australia and show a strong male sexual dimorphism and a Bergman-like cline in size from Queensland to Tasmania. They are seasonal breeders, with sex hormones reaching maximum levels in August-October, and have some distinctly ornithorhynchid characteristics in their breeding biology. No pouch develops in the platypus; ~two eggs are laid after 21 days gestation in a nesting chamber containing wet vegetation at the end of earthen burrow. Eggs hatch ~11 days later and nestlings are suckled for ~4 months on milk secreted from two large, teat-less mammary glands. Like marsupials, platypus milk changes in protein and lipid composition during lactation. Platypuses have a high metabolic rate, regulate their body temperature at ~31°C, and do not hibernate or enter torpor. They are obligate aquatic feeders on a mostly invertebrate diet and can sustain body temperature for >12 hours in waters <10°C relying on a dense 2-layered pelage.

Monotremes are the only extant mammals to have evolved a novel venom system: a pair of venom glands connected by a duct to a hollow, keratinous spur attached to a male-specific tarsal bone on each hind leg. The venom system is male-specific and only fully functional in the platypus; spur sheaths develop in males and females but the system fails to develop in females. The platypus venom system is used in fights for territory and access females in the breeding season. Other special features of the platypus include its strange gastrointestinal system and the development of monotreme-specific electroreception system for locating prey underwater.

The platypus is the unique survivor in the ornithorhynchid evolutionary line and little is still understood about its social, family and population dynamics. Although relatively common in the wild, particularly in Tasmania, concerns are increasing to reclassify its status because of its reliance on an aquatic environment under stress from climate change and degradation by human activities. Because the platypus has rarely bred in captivity and is the last of a long line of ornithorhynchid monotremes, its continued survival is of critical importance.

## Phylogeny and ecology of the enigmatic microbiotheriid marsupial, the monito del monte *Dromiciops gliroides*

*Peter Temple-Smith*<sup>1</sup> and *Jennifer Hetz Rodriguez*<sup>2</sup>, United States

<sup>1</sup>Education Program in Reproduction and Development, Department of Obstetrics & Gynaecology, School of Clinical Sciences, Monash University, Clayton VIC 3168, Australia.

<sup>2</sup>School of BioSciences, The University of Melbourne, Parkville VIC 3000, Australia.

Extant American marsupials number ~87 species in four distinct families including the Microbiotheriidae, a distinct group of possum-like marsupials. This family contains mostly extinct species with a >40 million years fossil history in South America. It is also one of only two families with fossils in the Antarctic and the only family with a fossil from the Australian continent. This discovery suggests the likely migration of members of this group into Australia during the time of the Gondwanaland connection suggesting that the Microbiotheriidae may have been the original marsupial colonisers of Australia and a base group of the Australian marsupial radiation. The close links between the Microbiotheriidae and the Australidelphia are still evident in the only extant microbiotheriid species, the monito del monte *Dromiciops gliroides*. This ~30-40g species was named by Oldfield Thomas (1894) who named it *Dromiciops* because of its likeness to the Australian pygmy possum *Cercartetus nanas*, previously *Dromicia nana*.

*Dromiciops* is a polyprotodontid scansorial insectivore and frugivore primarily distributed in the pristine Valdivian temperate rain forests of Chile and Argentina; but is also found in secondary quila (bamboo) regrowth and even on agricultural lands. It is nocturnal and a strictly seasonal breeder usually raising a single litter in a pouch containing 4 teats. Individuals store fat in the tail during late summer and fall and hibernate, huddling with conspecifics, in nests constructed in tree and ground hollows under root systems, during the winter and early spring.

Evidence of a close relationship between *Dromiciops* and the Australian marsupial radiation was first provide in a 1982 study of marsupial tarsal bones. This relationship was not widely accepted by marsupial biologists but more recent genetic, paleontological and morphological evidence appears to confirm this view. This presentation will consider this evidence in support of the current phylogenetic relationships of *Dromiciops*.

## **Organisms in nature – evolutionary perspective and ecological significance – an introduction**

*Ulrich Zeller, Germany*

Organisms are living beings in space and time adapted at any stage to their specific environment. Recombination and expression of genetic information, ontogenetic development and adaptive radiation of phenotypes over generations under the influence of natural selection are the driving forces of what we call evolution. This presentation is focused on the historic development of the thought in organismic biology and evolution (Aristoteles, Conrad Gesner, Carl von Linné, Georges de Cuvier, Geoffroy Saint-Hilaire, Alfred Russel Wallace, Charles Darwin and others) underlined with results of own research over the past 40 years. Organismic life on earth is always diverse and the complexity of organisms need to be approached from various and reductionistic viewpoints, namely gene expression, ontogenetic development, structural development and organization and adaptation to ecological conditions, most of which will be considered in the following. Own research is focused on mammals, considering all major groups including monotremes, marsupials and placental mammals with a regional and comparative focus on temperate Europe and Africa. Comparative investigations of crown group members of all major taxa (e.g. *Ornithorhynchus anatinus*, *Monodelphis domestica*, *Tupaia belangeri* and others) made it possible to reconstruct the stem species pattern of the last common ancestor of all living mammals and to develop evolutionary scenarios in which also fossils of Mesozoic mammals could be incorporated. The stem species of recent Mammalia was equipped with the following set of characters which can be regarded as homologous and synapomorphic (evolutive novelties): Yolk-rich eggs with meroblastic-discoidal cleavage, yolk reduction of oocyte induced by lactation, short intrauterine development, immature hatchlings of newborns dependent on the integument of the maternal organism for nourishment (lactation) and capable for survival and development beyond their immaturity (suckling apparatus of head, secondary jaw joint and olfactory organ), ontogeny characterized by the combination of telencephalization, olfactory communication, parental care, yolk reduction and immaturity. Other characters, like the secondary wall of the brain case, were achieved in parallel in monotremes (lamina obturans) and therians (alisphenoid). Compared with monotremes and marsupials (altricial offspring), placental mammals are characterized by a pronounced plasticity of reproductive strategies (altricial and precocial offspring including intermediate stages), enabling niche realization in virtually all existing habitats (aquatic, terrestrial, and aerial) leading to the fact that placental mammals represent approximately 96% of all extant mammalian species. According to biomass, however, wild mammalian and other species are dominated by their domesticated forms with wide overlap between both in organismic abilities and limitations. This is leading to competition and ecological disturbance – an imbalance which is highly influential for the current global biodiversity crisis.

## List of participants

**Asher, Robert J., Dr.**

Mammal Evolution and Morphology Group  
Department of Zoology  
University of Cambridge

**Eiseb, Seth J., Dr.**

Department of Biological Sciences  
University of Namibia  
Private Bag 13301  
Windhoek, Namibia

**Göttert, Thomas, Dr.**

FG Spezielle Zoologie  
Lebenswissenschaftliche Fakultät  
Humboldt-Universität zu Berlin  
Unter den Linden 6  
D-10099 Berlin, Germany

**Gutmann, Mathias, Prof. Dr. Dr.**

Karlsruher Institut für Technologie  
Institut für Philosophie  
Douglasstr. 24  
D-76133 Karlsruhe

**Homberger, Dominique G., Alumni Prof. Dr.**

Dept. of Biological Sciences  
202 Life Sciences Building  
Louisiana State University  
Baton Rouge, LA 70803-1715

**Kuznetsov, Alexander, Dr.**

Borissiak Paleontological Institute of the Russian Academy of Sciences  
Profsoyuznaya Ulitsa, 123  
Moskva, 117997  
Russia

**Langgemach, Torsten, Dr.**

Landesamt für Umwelt, Ref. N4  
Staatliche Vogelschutzwarte  
Brandenburg State Bird Conservation Centre  
Buckower Dorfstr. 34  
D-14715 Nennhausen / Ortsteil Buckow

**Luo, Zhe-Xi, Prof. Dr.**

Department of Organismal Biology and Anatomy  
University of Chicago  
1027 E. 57th St.  
Chicago, IL 60637

**Macandza, Valério, Prof. Dr.**

Department of Forestry Engineering  
Faculty of Agronomy and Forestry Engineering  
Universidade Eduardo Mondlane  
C.P. 257 Maputo  
Mozambique

**Maier, Wolfgang, Prof. Dr.**

Universität Tübingen  
Fachbereich Biologie  
Auf der Morgenstelle 28  
D-72076 Tübingen

**Panyutina, Aleksandra A., Dr.**

Russian Academy of Sciences  
Department of Morphological Adaptations of Vertebrates  
A. N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences  
Moscow, 119334  
Russia

**Perry, Gad, Prof. Dr.**

Department of Natural Resource Management  
Division of International Research and Development  
International Center for Arid and Semiarid Land Studies  
Texas Tech University  
2500 Broadway, Lubbock, TX 79409, USA

**Rottstock, Thomas, MSc**  
FG Spezielle Zoologie  
Lebenswissenschaftliche Fakultät  
Humboldt-Universität zu Berlin  
Unter den Linden 6  
D-10099 Berlin, Germany

**Sobral, Mar, Dr.**  
Departamento de Biología Celular e Ecoloxía  
Facultade de Biología  
Universidade de Santiago de Compostela  
Campus Vida, Rúa Lope Gómez de Marzoa  
15782 Santiago de Compostela  
La Coruña  
Spain

**Stach, Thomas, PD Dr.**  
Molekulare Parasitologie  
Institut für Biologie  
Lebenswissenschaftliche Fakultät  
Humboldt-Universität zu Berlin  
Unter den Linden 6  
D-10099 Berlin, Germany

**Starik, Nicole, Dr.**  
FG Spezielle Zoologie  
Lebenswissenschaftliche Fakultät  
Humboldt-Universität zu Berlin  
Unter den Linden 6  
D-10099 Berlin, Germany

**Temple-Smith, Peter, Prof. Dr.**  
Faculty of Medicine, Nursing and Health Sciences  
School of Clinical Sciences at Monash University Health  
Monash University  
Victoria 3800  
Australia

**Zeller, Ulrich, Prof. Dr.**  
FG Spezielle Zoologie  
Lebenswissenschaftliche Fakultät  
Humboldt-Universität zu Berlin  
Unter den Linden 6  
D-10099 Berlin, Germany