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Evolutionary biology today – a contribution to the Darwin Year 2009: 150 years since the publication of *On the Origin of Species*

Wolfgang Schad

The discovery of mutualism and symbiosis

It was a key moment for the later discipline of ecology when in 1779, in his capacity as court physician to Empress Maria Theresia in Vienna, the Dutch doctor and botanist Jan Ingenhousz (1730-1799) discovered experimentally that the green organs of plants emit oxygen (he called it 'purified air') during the day under the influence of light, but during the hours of darkness transpire carbon dioxide. However, those organs which receive no light – such as the roots, for example – emit only CO₂, which is not suitable to be breathed by either humans or animals and which, for that reason, he named 'injured air'.

The discovery of oxygen (the 'fire gas') by the English theologian Joseph Priestley (1733-1804) and the German-Swedish apothecary Carl William Scheele (1742-1786), simultaneously and independently of each other, had come only five years before in 1774. These chemical investigations of the gases of the air had become possible through the writings of the Flemish doctor and philosopher Johann Baptista van Helmont (1579-1644), who created the bridge between the teachings on the elements – deriving from Ancient Greece and Rome, the Middle Ages and the medical writings of Paracelsus – and the emerging chemistry of the modern age. He rejected the old idea of air as a uniform substance, recognised that it comprised several different components, invented the new word 'gas' (from the Greek chaos), and was thus the first to discover carbon dioxide, which he called 'gas sylvestre'. It was these earlier discoveries which paved the way for Jan Ingenhousz' identification of assimilation via photosynthesis and dissimilation via respiration.

It was not long before the cycle of matter in the entire organic realm had become clear: what green plants constitute as organic matter and also release as oxygen in and through the sunlight, they break down again during the hours of darkness (as do all bacteria, fungi, animals and humans also during the day) in a kind of internal combustion process using the oxygen they have absorbed, exhaling the carbon dioxide which is so important for those same green plants. All organisms depend on each other as either (or both) producers and destroyers of living substance – creating an obligatory symbiosis in the Earth's biosphere, which is a major determining factor in the processes within the other 'layers' of the Earth: the atmosphere, the hydrosphere and the lithosphere.

Recent research has shown that the biosphere – the zone of life of the Earth – is very much larger than was believed to be the case only a century ago. Studies of the Archaeobacteria in particular (now commonly referred to as the Archaea), which despite their name are not in fact older than the Eubacteria, revealed that they can survive in the coldest waters of the polar regions and the deepest ocean depths, on smouldering coal tips and in hot springs where the temperature can be as high as 113°C, within environ-

ments rich in hydrogen sulphide which are lethal to higher organisms, and in supersaturated salt solutions and salt domes of geological age as so-called 'extremophiles' (Simon 2008; <http://www.astrobiology.com/extreme.html>). Geobiological studies of the lithosphere have also shown the presence of eubacteria and archaebacteria with active metabolisms at depths of up to at least 1.5 kilometres in the Earth's crust, both below the ocean floor and deep within the continental land masses (Parkes et al. 2000). The pollen from the Earth's flowering plants is blown far up into the atmosphere – even as far as the lower stratosphere – and bacteria have been found in dust particles at heights of up to 6000 metres. Both of these are spread around the entire globe. The whole biosphere of the Earth, together with its cycles of matter, thus forms a real superorganism.

That organism possesses considerable regulatory capabilities – for example, in relation to the thermal balance of the Earth's crust. It turns out – contrary to the simplistic idea that the Earth cooled at a uniform rate throughout identifiable geological time – that the uppermost rock layer of the Earth has remained astonishingly stable in terms of temperature since it first hardened (some 3.8 billion years ago): remaining largely, if not always, within the range 0-90°C (Wunderlich 1974:72). The large scale icing over of the Earth in the late Precambrian did not at all create a 'snowball Earth' (Kirschvink 1992), but left the tropical zone ice-free (Micheels & Montenari 2008). The thermal balance of the upper surface of the Earth results from a combination of the warmth coming from the Earth's interior and the absorbed heat from the sun. Yet it is specifically the troposphere, with its rich water vapour and especially its carbon dioxide content, which actively creates the thermal balance. An increase in CO₂ or water vapour creates the 'greenhouse effect', which could theoretically (in an extreme scenario) cause the Earth's surface to become so hot that the rocks would melt – as is the case on Venus. Countering this effect is the increased photosynthesis of the Earth's vegetation, which binds the CO₂ into such organic substances as coal, oil and natural gas; and also into the carbonates – more than one hundred and sixty different rock types, including what are commonly referred to as limestones, chalks, dolomites etc. If the cooling effect were too great, the layer of molten rocks beneath the Earth's surface – known as magma and extruded as lava – could solidify, as on the Moon and Mars. But with increasing levels of oxygen, the biochemically destructive organisms can produce more free carbon dioxide and the thermal balance is enhanced (Kull 1985). Evidence is now available for the presence of forms of life at the time when the earliest rocks were being formed (Pflug 1984). Since then, the Earth's biosphere has been maintaining the planet as a relatively homeothermic (= equal temperature) superorganism, which is not too cold and not too hot – supporting both a solid upper crust (the sial: consisting mainly of silica and aluminium) and also a viscous molten lower layer (sima: main elements silica and magnesium).

The Earth is thus the only planet in our solar system which, throughout its entire geological history, possessed (and still possesses) the dynamics of plate tectonics i.e. the 'drifting' of the sial continental blocks over the semi-fluid sima. At least three cycles of separation and rejoining of the continents have been reconstructed. We are currently in a phase of renewed separation, of which Africa is the relatively stable centre. The expression on the 'face' of the Earth, reflected in the distribution of its oceans and continents,

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Bovine spongiform encephalopathy and uric acid, *Judyth Sassoon*

Table of bird names

bearded tit	<i>Panurus biarmicus</i>	linnet	<i>Carduelis cannabina</i>
bittern	<i>Botaurus stellaris</i>	marsh tit	<i>Parus palustris</i>
blackbird	<i>Turdus merula</i>	marsh warbler	<i>Acrocephalus palustris</i>
blackcap	<i>Sylvia atricapilla</i>	mistle thrush	<i>Turdus viscivorus</i>
blue rock thrush	<i>Monticola solitarius</i>	nightingale	<i>Luscinia megarhynchos</i>
blue tit	<i>Parus ceruleus</i>	nuthatch	<i>Sitta europaea</i>
bluetroat	<i>Luscinia svecica</i>	ortolan bunting	<i>Emberiza hortulana</i>
canary	<i>Serinus canaria</i>	pheasant	<i>Phasianus colchicus</i>
chaffinch	<i>Fringilla coelebs</i>	pied flycatcher	<i>Ficedula hypoleuca</i>
chiffchaff	<i>Phylloscopus collybita</i>	red-backed shrike	<i>Lanius collurio</i>
cirl bunting	<i>Emberiza cirlus</i>	redstart	<i>Phoenicurus phoenicurus</i>
coal tit	<i>Parus ater</i>	redwing	<i>Turdus iliacus</i>
collared flycatcher	<i>Ficedula albicollis</i>	reed bunting	<i>Emberiza schoeniclus</i>
corn bunting	<i>Emberiza calandra</i>	reed warbler	<i>Acrocephalus scirpaceus</i>
crested tit	<i>Parus cristatus</i>	ring ouzel	<i>Turdus torquatus</i>
cuckoo	<i>Cuculus canorus</i>	robin	<i>Erithacus rubecula</i>
duncock	<i>Prunella modularis</i>	rock bunting	<i>Emberiza cia</i>
fieldfare	<i>Turdus pilaris</i>	scarlet rosefinch	<i>Carpodacus erythrinus</i>
garden warbler	<i>Sylvia borin</i>	shama thrush	<i>Copsychus malabaricus</i>
goldcrest	<i>Regulus regulus</i>	siskin	<i>Carduelis spinus</i>
golden oriole	<i>Oriolus oriolus</i>	skylark	<i>Alauda arvensis</i>
goldfinch	<i>Carduelis carduelis</i>	song thrush	<i>Turdus philomelos</i>
grasshopper warbler	<i>Locustella naevia</i>	tree pipit	<i>Anthus trivialis</i>
great tit	<i>Parus major</i>	whitethroat	<i>Sylvia communis</i>
greenfinch	<i>Carduelis chloris</i>	willow warbler	<i>Phylloscopus trochilus</i>
greenish warbler	<i>Phylloscopus trochiloides</i>	wood warbler	<i>Phylloscopus sibilatrix</i>
grey catbird	<i>Dumetella carolinensis</i>	wren	<i>Troglodytes troglodytes</i>
house martin	<i>Delichon urbica</i>	yellowhammer	<i>Emberiza citrinella</i>
house sparrow	<i>Passer domesticus</i>	zebra finch	<i>Taeniopygia guttata</i>
lesser whitethroat	<i>Sylvia curruca</i>		

has thus predominantly been a changing one – thanks to the presence of life. Since the very first deposition of solid matter in the rocks, the biosphere has actively shaped its own environment. The idea – still current in biology – that life forms are passively dependent on finding suitable, pre-existing ‘niches’, is simply false; they themselves help to create and transform their habitats (Lewontin 1979).

Looking at an organism as a whole (i.e. using a synthetic rather than analytical approach) is certainly worthwhile, but the approach needs to be complemented by the fact that each organism is not a *simple* whole, but is always a thoroughly *differentiated* whole. Thus, in looking at the Earth, it is also necessary to examine the functionally smaller cycles – such as the numerous circulating ocean currents, oceanic basins, the Amazon river basin of South America, the Congo river basin of Central Africa, etc. August Friedrich Thienemann (1882-1960) made a classic study of the inland lake as one such symbiotic community (also known as a ‘biocoenosis’) which has all the characteristics of an organism. In doing so, he became the founder of the new discipline of limnology, which for the first time enabled a detailed examination and differentiated description of such an ‘eco-organism’ to be made. The thousands of microscopic and macroscopic species form a mutually supporting symbiotic community – the biocoenosis. In a classic study of Lake Plön in Schleswig-Holstein, Thienemann pointed to the symbioses which exist between many species sharing the same living space (Thienemann 1925, 1956).

The term ‘symbiosis’ has been in use in biology since 1866, introduced by the Basle botanist Heinrich Anton de Bary (1831-1888). He was the first to make the revolutionary discovery that a simple-looking organism might turn out to be far from simple; that it might, for example, be made up of two very different forms of life. He had made the discovery in the course of his microscopic studies of lichens, which turned out to be a symbiotic composite of photosynthesising (assimilating) single-celled algae, and types of fungi which decompose organic substance. In 1869 the Swiss botanist Simon Schwendener (1829-1919) had demonstrated experimentally just how close was the co-existence of these two types of lower plant. The question arose as to which class the lichens should be assigned: to the algae or to the fungi. But the symbiosis is so close – despite the two partners always maintaining separate cellular structures (even if one cell penetrates into a cell belonging to the other partner) – that it is only by virtue of their co-operation that the partners can colonise, and flourish in, such barren and inhospitable environments as deserts, high mountains, polar tundra etc., which individually they could not tolerate. The algae’s photosynthesis provides the fungus with sugar, starch and oxygen; the fungus gives the algae water, mineral salts, and carbon dioxide. Their interaction also produces new organic substances – the lichen acids – which often give the lichens their colour and which neither of the two component parts can produce by themselves.

De Bary distinguished two different forms of symbiosis. If both partners offer each other more or less equal levels of support, he named this ‘mutualism’; if the balance is not equal, but one partner ‘exploits’ the other to a greater extent, he labelled it ‘parasitism’. There are also all kinds of intermediate states between these two – as is also true of any symbiotic relationship within a biocoenosis, whether in a pond or a forest.

Later on, the surprising discovery was made that the majority of higher plants – the classic terrestrial plants – also exist in symbiotic relationships with fungi: in the root

zone. Some 90% of land plants possess this fungus-root (mycorrhizal) symbiosis, with the remaining 10% having a bacteria-root symbiosis in the mucigel which surrounds the roots. These root symbioses were first discovered on trees, in 1885, by the Berlin botanist Bernhard Albert Frank, who also introduced the term 'mycorrhiza'. It is typical for most trees that the hyphae (threads of fungal mycelium) of the underground fungal network penetrate the outer 'skin' or bark of the roots, but not the cells (the mycorrhizae are then defined as ectomycorrhizae). Nonetheless, a dynamic exchange of materials takes place: of assimilated products of photosynthesis from the tree, and of water and soluble salts from the fungus. The mycorrhizae increase the effective (functional) surface area of the roots – and thus their growth potential – a thousandfold. When the roots of different individuals of the same tree species – or sometimes even of different species – become entangled, and also through the hyphae, which can act as intermediaries, one tree can help another to grow by transmitting nutrients to it. A number of trees growing near to one another thus forms – either directly, or via the symbiosis of their root fungi – a cooperative system of mutual exchange of substance. In the root zone, a forest or wood does not consist of separate, autonomous individual trees, but – if it is healthy – forms a common, biocoenotic eco-organism.

The 'dying forest' phenomenon which is affecting upland areas, in some cases on a large scale, literally has its roots in the destruction of the mycorrhizal symbiosis by acid rain. The health or sickness of a forest is determined not so much at the level of the trees' crown of foliage (the phyllosphere), but in the root zone (the rhizosphere) and its symbioses (Meyer 1987). Woods and forests have always been able to deal with massive attacks on their foliage from armies of caterpillars or cockchafers: the trees simply produce new leaves the following year. But the mycorrhizae in the ground are much more sensitive and vulnerable.

The root-fungi symbiosis can be a much closer one than that seen in trees. In many herbs and especially in all orchids, the hyphae are taken into the core of the living root bark cells and are actively digested there, being then known as endomycorrhizae. In this case the symbiosis is an intracellular one, looking almost like parasitism; but it is not, as the root fungus as such is nurtured and nourished, and only the excess is consumed.

There are numerous intermediate states between those of the ectomycorrhizae and the endomycorrhizae in the form of so-called vesicular-arbuscular mycorrhizae (VAM), which can be found between the two other modes in the root bark cells of the host plant i.e. in both inter-cellular and intra-cellular forms. Within the cells the hyphae form themselves into many-branched 'dwarf trees' – the 'arbuscles' – which play a role in the exchange of substance. The 'vesicles', on the other hand, are like tiny sacs or bladders of hyphae, which are formed primarily between the cells and which provide more stable storage organs for nutrients than the arbuscles (Knöbel 1987).

This third, 'ambidextrous', type of mycorrhizae is probably the oldest. It has been found in the rhizomes of the first land plants of the Lower Devonian (part of the Palaeozoic era) (Pirozynski & Malloch 1975). It makes sense, therefore, to connect the historical emergence of the root organ in the evolution of the higher plants with the proven presence at a very early stage of root-fungus symbiosis. It is a good example for the supposition that the macro-evolutionary creation of innovative body plans – in this case the transition

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sing in chorus, or when, during matching dialogue song, the singers listen even more intently to one another, starting to match their song phrases or motifs to make them increasingly alike.

Similar stages can be demonstrated for juvenile and subsong, flight song, choral song and, with even more differentiation, for the imitative song where each of the upper levels often exhibits an astonishing increase in singing ability and corresponding degree of freedom. Just as in the matching dialogue song when neighbouring songbirds listen to one another increasingly intently, starting to match each other in order to make their songs alike, we for our part require to make our sense perception more sensitive, to refine our listening to the level of the spherical song so that we can experience the songbirds more consciously. We will then increasingly be able to hear the surprising individual variety in what at first sound like simple songs. This is where we can discover something for the future: to let hearing increasingly become listening.

Is not the fact that songbirds – in comparison with other vertebrates – resolve most of their territorial disputes through song significant evidence for an increase in autonomy? This *musical defence method* is unusual in animal evolution. Both the degree of freedom and the musical dimension of this phenomenon should be accorded greater importance within behavioural biology.

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from the Thallophyta (relatively simple 'lower' plants with undifferentiated bodies) to the Cormophyta ('higher' plants with roots, axis and foliage) – was accompanied by symbioses; that one can therefore speak of the evolutionary steps as 'symbiogeneses'.

Intracellular symbioses with single-celled algae are also numerous in the lower animal kingdom (Buchner 1921). Light-metabolising algae exist not only in protozoa (*Amoeba viridis*, *Paramecium bursaria* etc.), but also in sponges (*Spongilla lacustris*), polyps (*Hydra viridis*), flatworms (*Convoluta roscoffensis*), sea snails and sea-slugs (Sacoglossa), clams (*Tridacna*) and most corals; these animals, which live in the light-filled upper zones of the seas, receive a distinct nutritional boost from the products of photosynthesis generated by the algae. In the shallow tropical seas, where the water temperature does not fall below 20°C, vast coral reefs covering a total of more than 600,000 km² have been formed. The corals (animals which secrete an exoskeleton of calcium carbonate which gradually forms the 'stone' of the reefs) have an intracellular symbiotic relationship with the single-celled alga *Symbiodinium microadriaticum*, which enables them to grow from three to ten times faster than they would in the dark. That is why the living coral reefs based on this animal-plant symbiosis are mainly to be found in the light-filled coastal areas of the tropics – a massive ecosystem primarily based on symbiosis.

There are many protozoa and animals in which eubacteria and archaeobacteria live as endosymbionts, enabling the host organisms to survive in otherwise uninhabitable environments – such as ciliates with methane bacteria in anaerobic watery environments (Görtz 2001), hydrogen sulphide oxidising eubacteria in shells (*Calyptogena*), and tube worms (*Riftia*) in hot deep-sea vents (Matthes 1987, Moya et al. 2008).

Other, even closer, symbiotic relationships have now been revealed. In recent decades, molecular biology discovered that the presumption of rigid genetic barriers between species was false. The nineteenth century formulated the 'General Cell Theory', with the assertion that all living things are composed of cells and that the cell is – as stated in 1861 in Vienna by Ernst von Brücke – the 'elementary organism': the smallest functional component of all organisms. But by 1883 the claim was already being questioned by Andreas Schimper in Bonn, who suspected that the chlorophyll-containing chloroplasts in plant cells could be 'immigrant' symbionts, since they always descend from others of their own type. In 1905, the Russian Konstantin Sergeyovich Mereshkovsky repeated Schimper's suspicions, backing them up with further arguments. Nonetheless, a symbiotic theory valid for all plants seemed for a long time to be incredible – until molecular genetics found that the chlorophyll grains had their own distinctive DNA, which – as in bacteria – is arranged in rings (plasmids); and that large parts of its sequence of bases are similar to that of the cyanobacteria: the blue-green algae. This means that such photosynthesising bacteria must have migrated into higher cells at an early stage of life on Earth, making them into genuine plants (Fig. 1). The migration of cells into cells can even lead to multiple 'boxes within boxes' (Fig. 2), which can all be conceived of as the result of a multiplication of intracellular symbioses (Sitte 1991). Dinoflagellates can consist of up to six 'nested' cells within a cell – and also themselves be symbionts within giant radiolaria, which as plasmodia with multiple nuclei, are themselves more than simple cells.

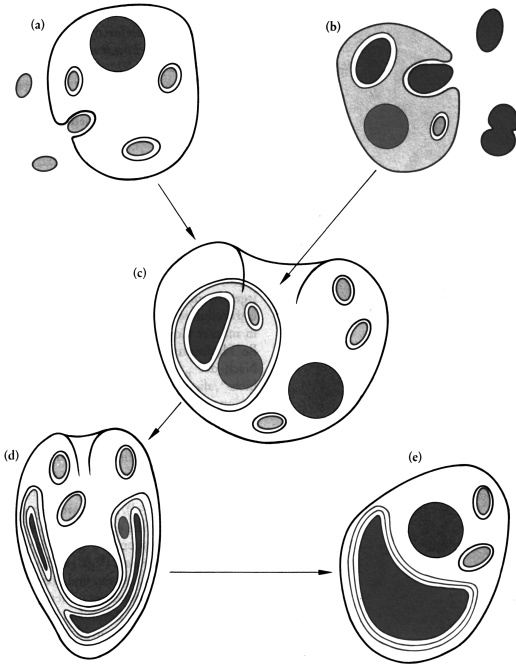


Fig. 1. Evolution of eukaryotic cells (cells having a nucleus) via endocytobiosis:

- integration of proteobacteria (performing respiratory breakdown of substance), which thus became endosymbionts with twin membranes (mitochondria).
- integration of photosynthesising cyanobacteria, which likewise became endosymbionts with twin membranes (plastids).
- integration of cell (b) containing plastids and mitochondria into cell (a).
- as a symbiont, cell (b) loses its mitochondria, its nucleus becoming a nucleomorph with relatively few functions, as with the *Cryptomonads*.
- in its final state the protozoan contains a large plastid with three membranes, only the innermost of which is a bacterial membrane – as with the dinoflagellates and *Euglena* (from Sitte 1991).

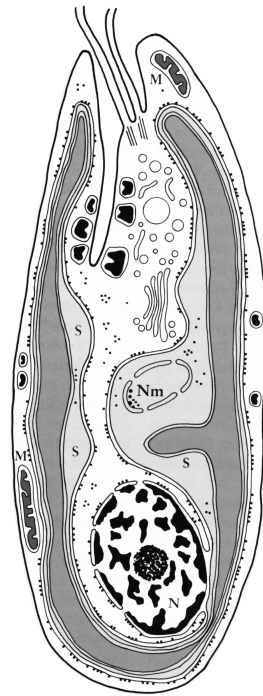


Fig. 2. Schematic longitudinal cross-section of a *Cryptomonas* with twin flagellae and a large nucleus (N). The anterior slit (upper left) points to the original protozoa-like character of this single-celled organism, already equipped with mitochondria (M). *Cryptomonas* became a vegetable protozoan through the integration of a second protozoon containing plastids, which then lost its mitochondria and reduced its nucleus to a nucleomorph (Nm). The U-shaped plastid is shown in dark shading (from Sitte 1991).

constraints of an inherited range of vocalisations. It can be assumed that the process of becoming increasingly emancipated from predefined vocal characteristics and development towards individual learning were mutually dependent in the course of evolution and, with the changing circumstances of having (and being able) to learn the species-specific song, the possibility for individual variations in song phrases first arose. Looking at the development of song as a whole, it then appears that, later on, greater opportunities arose for types of song which are less strongly determined by biological factors. The emotional changes accompanying this development can be divined and understood if we look at the metamorphosis of song phrases more closely.

Just as it is important to pay attention to the performance differences in song phrases and the changing rhythms, it is also important and instructive to listen to the acoustic transitions from one song level to another. These transitions can be noticed when a male is still singing his varied motifs in a relaxed way, but then begins to sing more aggressively and louder when a singing territorial neighbour approaches. Accompanying the inner emotional mood or level of excitement, the phrases are now performed more aggressively and frequently shortened. It is like a short-term relapse from relaxed motif singing into the excited conflict song. Later the opponents calm down and start to sing more softly and relaxed in alternating mode. The conscious awareness of the transitions shows us that the singing males do not simply change their type of song but that a bird's emotional level is reflected in its song performance.

When scientific papers report that aggressive males adopt overlapping song when countersinging or that an excited golden oriole sings double phrases, this is correct. But this scarcely reveals that the singer 'interrupts' or that the voice of the golden oriole 'cracks' with excitement. The birds do not adopt the various song patterns *on demand*, but changing the type of song accompanies the change of mood, something clearly demonstrated by the fact that, for example, the song does not undergo an abrupt change from the excited phase to the relaxed phase but an audible musical transition takes place. The transformation from the relaxed phase to the excited one is shorter by nature.

In every aggressive singing duel, two male nightingales, bluethroats, song thrushes or wood warblers display something of an earlier developmental stage when they revert to old response patterns which have been overcome in the course of evolution or even lapse into partly innate song structures. At the same time this reveals the degree of freedom attained towards a playful use of the voice right up to the present day varied relaxed motif song.

The musical transformation from the excited song to the relaxed one in particular can provide a direct experience of being able to participate a little in the songbirds' long musical developmental path within the space of a few minutes. The calming down phase is something like the extremely shortened developmental history of the song.

On the lower level of territorial singing, the past becomes audible in the excited conflict song and also in the excited counter song. In the relaxed motif song, in joint singing we can experience the present day musical level of songbirds. Lastly, at the upper level of territorial singing – the spherical song – there is a hint of the future, for example when a blackbird, removed from territorial events, creatively pours out its motifs in the late evening or when territorial birds (nightingale, reed warbler) rise above themselves as it were and

rial song does not only function to defend the territory and keep rivals at a distance but also serves to attract females. The attracting effect of the song is, however, not limited to females alone as might be thought. Naturally it at first appears strange to suppose that male songbirds could have an interest in attracting potential rivals. But this only sounds odd under the premise that songbirds are fundamentally *rivals*. If we become aware that it is primarily a question of *singing neighbours*, then they might clearly have a wish to attract male members of the same species so that these nest and sing in their vicinity. In any case, males which arrive later react immediately to singing members of the same species and attempt to settle in the audible range, on the one hand because of similar requirements from the habitat but on the other due to vocal stimulation.

The attraction of song for male members of the same species has now been established for several species (whitethroat, red-backed shrike, linnet, pied flycatcher, reed warbler, reed bunting). Over the past four decades I have increasingly had the impression that the males of most talented songbird species react in a very similar way.

Picture a river channel with adjoining natural alluvial woodland which is large enough to provide around 100 pairs of nightingales with favourable nesting habitat. In years of higher population density the singing activity also increases. It is assumed that this is connected to the reciprocal stimulation of the males (Horstkotte 1965). Territorial size in a particular area varies from year to year depending on the number of nesting pairs. If, however, in a particular year only 20 pairs of nightingales were to breed so that the density were significantly lower, the territories would not become five times larger. The few birds almost always nest in a loose population – it might also be two smaller populations separated from each other. However I have never made the observation that, given equally good habitat quality, the males use a situation like this to claim enormous territories. The territories may be somewhat larger under these conditions, but the expansion does not take place to the detriment of communication through song. At higher densities it can be observed, however, that the males of nightingales, for example, more frequently try to expand their territories which were reduced in size at the beginning of the nesting season. During nesting and singing periods, the priority is to live in *audible* range of others of the same species. Conflict over the most favourable nesting opportunities, within or at the edge of a population is of secondary consideration. In comparison, occupying an equally good or even better nesting area far away, without singing neighbours and without any conflict, is less attractive for most songbirds.¹²

Development of the voice – emotional change of mood

Nowadays a very large proportion of songbirds are not (or no longer) subject to the

¹² In the case of hole-nesting birds (e.g. blue tit, pied flycatcher and nuthatch) which, in comparison to songbird species that nest in the open, can only choose a nesting place depending on a mostly limited supply of available holes in trees or nest boxes, the nesting area seems to have greater importance in relation to territorial behaviour and song than in species nesting in the open. It appears that the frequent display flights of the nuthatch are connected to competition for nesting holes (Löhr 1958). However, in the case of blue tit, great tit and pied flycatcher, male members of the same species in another bird's territory are tolerated as long as they do not sing, in other words do not show any territorial demands.

The same was found to be true also for the systems which represent the complementary opposite to photosynthesis – the respiratory organelles of all higher cells. They were discovered in 1894 by Richard Altmann in Leipzig at the very limit of detection by a conventional light microscope, and named 'mitochondria' by Carl Benda. They carry out the respiratory breakdown (= dissimilation) of organic substances into carbon dioxide and water. The American Ivan Wallin suspected as early as 1927 that the mitochondria in the eukaryotic cell were 'immigrant' symbionts. DNA sequence analyses later showed that they are related to Proteobacteria. They too have become obligatory procyclic endosymbionts in all modern plants and animals.

The building up and breaking down, production and destruction, of living substance in all single-celled protists, as well as in all metazoa such as plants, animals and humans, is thus carried out not by the organism's original cells themselves, but in the final analysis by the plastids and mitochondria which once 'immigrated' into them as symbionts. Every higher cell (= 'eucyte' of the eukaryotes) is thus a mini-biocoenosis: a symbiosis of 'procytes' of the prokaryotes (cells without a nucleus: such as bacteria, viruses, proviruses, prochloroplasts etc.). The first fossils in the oldest rocks are the stromatolites dating from around 3.8 billion years ago (banded haematites, calcium carbonate or dolomite precipitates etc.) excreted by prokaryotes. From around 1.5 billion years ago, cellular organisms which are ten times the size are found: the first higher cells, the eucytes, are formed – the beginning of all higher life on Earth. This immensely important process in the macroevolution of early life was a genuine *syntrophogenesis* – not a symbiosis between procytes which were still spatially separated, but a 'spatially internalised' symbiosis. The term 'syntrophogenesis' was first coined by Merezchkovsky in 1909; Margulis (1981, 1999), and Margulis & Sagan (1999, 2000) took it up and applied it to modern biology.

The cell as a miniature landscape soon became even more tightly constituted than a mere spatial collection of elements within a shared cell plasma. In the course of evolution, a partial exchange of genes took place between the cell nucleus, the mitochondria and the plastids; the two latter were no longer able to manufacture for themselves all the proteins they needed (Gellisen 1987). So we are dealing not only with an intra-cellular symbiosis, but also with the breaking down of earlier genetic barriers to form a direct *genetic symbiosis* (Fig. 3). There are many examples of this in the living world of today,

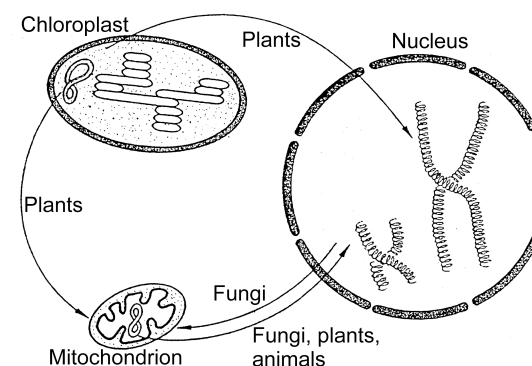


Fig. 3. Evolutionary gene transfer between cellular organelles containing DNA. The DNA of the mitochondrion and the plastid is contained in a ring-shaped structure; that of the cell nucleus as a double helix. The direction of the arrows indicates the path of the intracellular exchange of DNA in the large phyla of plants, fungi and animals. (from Gellisen 1987).

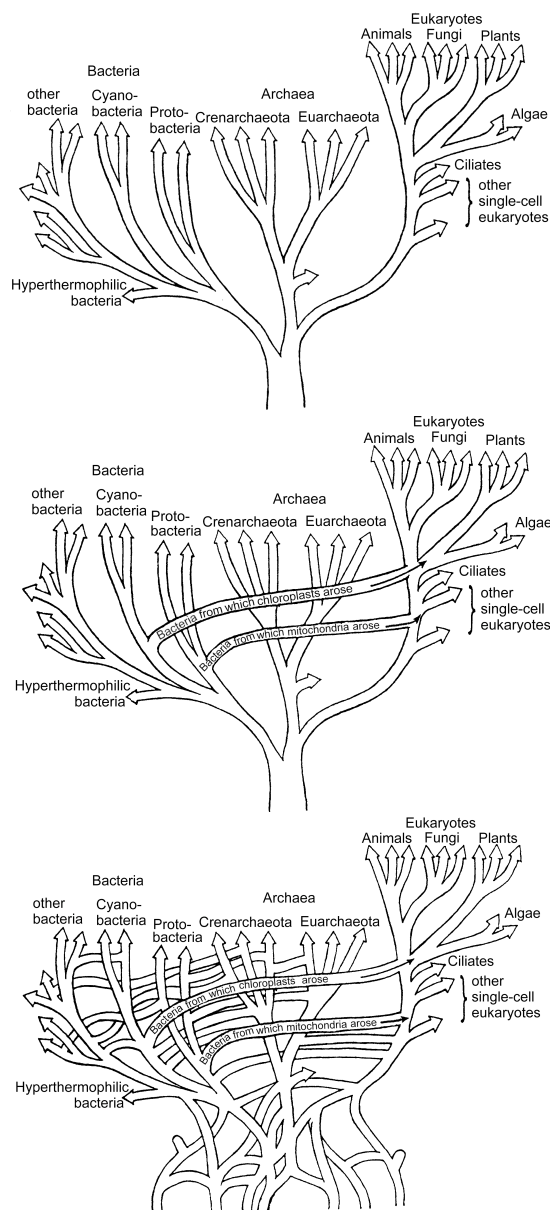
especially within the world of contemporary bacteria. It is thus not only the General Cell Theory – of the eukaryotic cell as the fundamental constitutive organ of all forms of life – which has been set aside, but also another long-held fundamental law of biology: namely the claim that all procreation proceeds from the parent organisms, i.e. that the genetic constitution of the offspring derives exclusively from its parents. Where that is the case, one speaks (from a temporal perspective) of a ‘vertical’ transmission of hereditary char-

Fig. 4. Changes in the modelling of the genealogical ‘tree’ in the last 50 years:

A. Based on Darwin’s principle of divergence: at the base of the trunk is a single, original, universal ancestor, referred to nowadays as the ‘progenote’.

B. After the introduction of the symbiont theory of the eukaryotic cell after 1970: cyano- and proteobacteria become the chloroplasts and mitochondria of the higher cells.

C. Recently modified genealogical tree showing predominantly convergent genetic pathways of the prokaryotes and predominantly divergent ones for the eukaryotes.
(from Schad 2001, after Doolittle 2000)



longer (e.g. great tit or marsh tit). Something of the social behaviour of a species is evident even early on. Some songbirds such as house martin, bearded tit and house sparrow are also sociable throughout the year as adults. Other songbirds, even if they nest more or less singly, become sociable after the breeding period and during migration the territorial behaviour of many species disappears completely. There is a great deal in favour of communal living as many eyes see more, whether it be sources of food or enemies, it is safer in a flock, birds are in vocal contact and can look for communal roosting places. Behaviour biologists repeatedly emphasise the benefit of this way of living, particularly during migration. But it requires being able to tolerate others and this poses a problem for the *master singers*.

I should like to present for discussion the following possible developmental process for songbirds and birdsong: in accordance with the higher development of musical faculties in which sound increasingly gains in importance, there is an increase – consistent with the further development of the organ of hearing and the vocal organ (syrinx) – in the urge to lay claim to an ever larger acoustic territory. The distance of talented singers to others of the same species becomes larger and this may last throughout life.

The gradually increasing emancipation from biological necessities and the vocal development connected to this, right up to soloistic individualism, is linked to the loss of sociable living. This significant increase in autonomy makes the master singers *lonely* to a certain degree¹¹ because they can no longer bear to have their own sort singing too near. They now fill in the resulting social gulf on an appropriate level for them, the musical one. In my opinion this is where the deep longing for communal singing lies, even in territorial songbirds. It can be seen for example in the fact that

1. the relaxed motif song which is produced in an undisturbed peaceful atmosphere comprises by far the larger part of territorial singing;
2. even territorial birds almost always attempt to breed within hearing distance of one or more members of the same species; and
3. territorial singing neighbours in dialogue song approximate each other musically in such a way that their song phrases almost match, as though they could overcome the old separation which took place with the development of song and the associated territoriality by singing similar songs.

In any case, as a musical intensification beyond the relaxed motif song, this shows the desire for similarity very well. In effect, the territorial behaviour of songbirds can only be properly understood if the musical element is taken into account.

Something should be added to the second point given above, which is rarely paid any attention, this being that even territorial songbirds prefer to have their nesting and singing places in the vicinity of a member of the same species. As already mentioned, the territo-

¹¹ Over a hundred years ago the ornithologist and theologian Bernard Altum (1824-1900) pointed out this phenomenon in his book *Der Vogel und sein Leben* (The bird and its habits): ‘The degree of perfection of the song is in inverse relationship to the degree of sociability of the bird. Only birds which live separately in nesting territories during the nesting and singing period are good singers. What a confused impression it would make if for example half a dozen nightingales wanted to perform their wonderful song together in one bush or in several neighbouring bushes! All good singers live alone ...’ (Altum 1898).

ring phrases adapt to one another: ‘singers only a few meters from each other sometimes sing so synchronously (same length of phrases) and at a very similar pitch, especially soon after their arrival, that they can only be distinguished at close hand’ (Glutz & Bauer 12/I). Territorial neighbouring nuthatches can also match their motifs: when one calls downwards, the other also usually chooses this pitch sequence (Schmidt 1979).

In order to recognise individual male blackbirds, the beginning of the song phrase which differs between individuals is important. In the matching dialogue song, where territorial males respond to the song of a neighbour with the most similar phrase of their own in the same phrase class, the initial element plays a key role. A similarly important part is played by the artistic and complex development of the appendix to the song (Glutz & Bauer 11/II).

In the matching process, which can also extend to the rhythm and tone quality, the desire for similarity is evident.

A disharmonious development in the matching dialogue song likewise emphasises this tendency towards similarity. If, for example, two males (chaffinches, nightingales or blackbirds) are communicating in relaxed or matching dialogue song and a particular motif from one male is not picked up and used by the territory neighbour, then the male affected will only sing this motif relatively rarely or even not at all. Songbirds are therefore not only acoustically connected to one another through harmonious dialogue song, but the response obtained from the singing neighbour determines which motifs will remain or be dropped from the individual’s song repertoire.

If we are able to hear the individual differences in song within a songbird species, then it is easy to appreciate that, as already mentioned, birds can recognise their singing neighbours individually by the smallest variations in song. Closely connected to this is the fact that at the beginning of the breeding period, as soon as territory division is complete, the excitement of the males eases off and they fall back to the level of excited conflict song less and less often. This must play a decisive role in songbirds being able to sing in such a relaxed way together. Looking at the levels of freedom in the summary of song levels (see Table 2, page 43) we can say that conflict dominates on the level of excited aggressive song. Reflecting this, in the excited dialogue song or countersinging the harmonious singing rhythm is disrupted.

The relaxed motif song displays free playful song development. Harmonious rhythm characterises the relaxed dialogue song and neighbours sing with one another. On the level of the spherical song we can experience almost *autonomous* singers, for example ‘the complete freedom from biological necessity in the *composing* of the nightingale’ (Hassenstein 1969).

In the matching dialogue song territorial neighbours adapt even more to one another and attempt to bring their song phrases and motifs increasingly into line with one another in an active vocal matching.

Development of the voice – loss of sociability

In some species of songbirds, young birds scatter in all directions as soon as they are fledged (for example, nuthatch) while others remain together in a family group for much

acters (*vertical gene transfer*).

However, it was discovered that, among the bacteria, hereditary material can also be taken in directly from a neighbour and subsequently passed on to the descendants. This is what is known as ‘horizontal or lateral gene transfer’. In the early epochs of life this was the predominant form (Doolittle 2000, Martin & Embley 2004; cf. Fig. 4). What significance does this have for the process of evolution? The concept of the ‘species’ is fundamental to the understanding of evolution, as the title of Darwin’s famous book makes clear: *On the Origin of Species*. As is known, the common definition of a species is a group of organisms whose members can successfully interbreed and produce fertile offspring. A species is thus a potential reproductive community with a shared ‘gene pool’ transmitted by vertical gene transfer. Lateral gene transfer extends the gene pool to include all those organisms which interact. Comparisons of the gene sequences in the DNA of modern prokaryotes indicates that lateral gene transfer was widespread in early evolutionary epochs: meaning that all the organisms involved were part of a common gene pool – and were thus members of one species (Margulis et al. 1999:73). Thus Rivera & Lake (2004) suggested replacing the primitive genealogical tree with a ‘ring of life’ (Fig. 5), from which the increasingly branching lines of descent of the various types were separated out as a result of the growth of stronger and stronger genetic barriers between them. As a result, the vertical mode of gene transfer progressively took over from the lateral mode – but without the latter ever disappearing entirely.

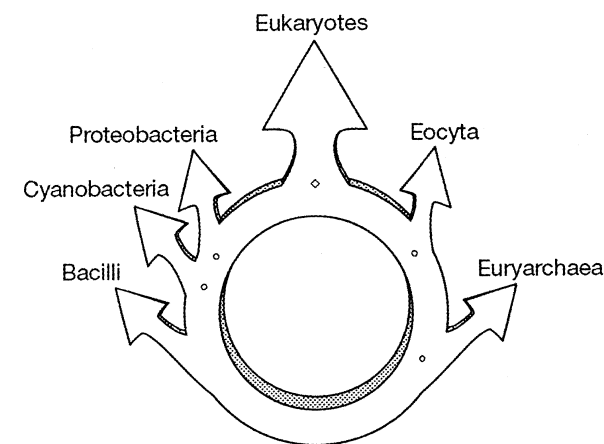


Fig. 5. Diagram of the proposed original genetic ‘ring pool’, out of which the various groups of prokaryotes and the eukaryotic branch emerged.

It was recently discovered that lateral gene transfer can also occur in higher, multi-cellular organisms, meaning that evolution does not depend solely on the small steps of individual mutations of the DNA received from the parents (the gradualistic model of microevolution of classical Darwinism). In 1970, and independently of each other, American scientists Howard Temin and David Baltimore discovered a particular enzyme in viruses which can reshape single-stranded ribonucleic acid (RNA) into double-stranded deoxyribonucleic acid (DNA); the enzyme is known as ‘reverse transcriptase’. The discovery signalled (not for the first time) the collapse of one of biological science’s general

laws: the so-called ‘central dogma of molecular biology’, which had been established soon after the discovery of the molecular structure of DNA by Crick, Watson & Wilkins (1953). It stated that DNA can be ‘transcribed’ into RNA for the specific synthesis of proteins, but that the reverse process is impossible – as that would be the beginning of the acquisition (inheritance) of ‘externally’ derived characters. But the reverse process is precisely what was discovered in 1970 (cf. Varmus 1987). The insertion of the RNA of the AIDS virus into the DNA complement of certain human immune cells (T4 cells) is the best known contemporary example. The DNA dogma holds good for the most part – but not entirely. There are, for example, base sequences in the DNA of higher organisms which can be traced to formerly ‘immigrant’ viruses, which then lost their viral characteristics. Many of the repetitive sequences are probably the result of ‘viral infections’ which subsequently became transposons and the like.

Further unexpected discoveries were added in 1989 by the O. Berg and his colleagues. They discovered that 1 ml of sea water contains 250 million viruses which are so small that they had never previously been detected even with the finest filter. In proliferating, they ‘lyse’ i.e. break down the cell membrane of a third of the population of bacteria in their environment every day, thus regulating them. The free nucleic acids probably derive from this breakdown of the microbial ocean plankton, i.e. the oceans hold large quantities of extra-cellular freely available nucleic acids. Why should they not also have been available for evolution in the organic world? In terms of pure quantity, by far the largest proportion of conversion of organic substance (biomass) on the Earth takes place in the microbial world of the protists (single-celled organisms), and especially in the bacteria (prokaryotes). Their metabolic processes occur more in the ‘intermediate’ zone of the environment than within the bacteria themselves, even if they are regulated by the latter. Microbial life is characterised by a vastly greater total surface area compared to its volume than is the case with macroscopic forms of life. This ‘extended organism’ (Turner 2000) is thus ecologically the most effective – as it has also always been in the geological dimension (Pflug 1984). Thus the evolutionary process can be described as a process in which mutual genetic isolation – the creation of genetic barriers – became more and more predominant, with the gradual formation, firstly, of the eukaryotes, then of the prokaryotes; of the higher plants as against the more primitive forms; and of the higher animals compared with the lower ones. Vertical gene transfer progressively took over from lateral gene transfer; the physiological homeostases also increased somatically, with the result that the individual organism separated itself out more and more distinctly, both morphologically and functionally, from its embedding in its environment. In our opinion, a critical review of all the criteria of biological progress which rejects any and all anthropomorphic value-judgements leaves the increase in physiological autonomy as the sole valid criterion (Rosslenbroich 2007).

Yet it is never a question of the total predominance either of the ecosystem (extrinsic factors) on the one hand, or of the individual organism (intrinsic factors) on the other; but rather of the shift of the mutual functional relationship towards the relative autonomy of the latter. This process can be clearly seen in the strengthening of the immune system in the course of evolution. Plants, including higher plants, demonstrate a high degree of

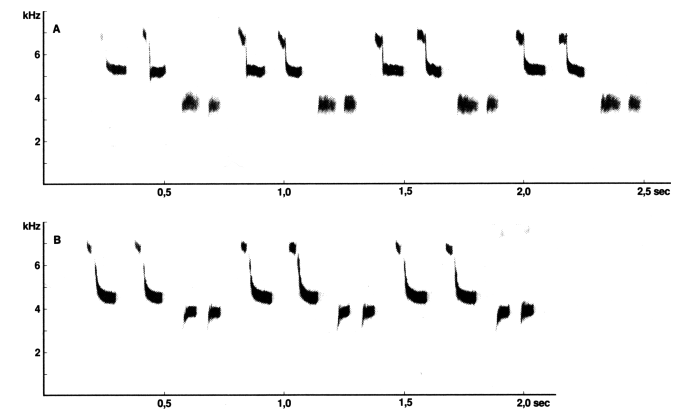


Fig. 5. Motif matching in dialogue song of two male great tits (*Parus major*) (A, B). (Sonogram: E. Tretzel, in Glutz & Bauer).

to become aware of the matching dialogue song:

The territorial song phrases of the great tit are varied in many ways by changing the rhythm, whereas in the dialogue song the motifs resemble each other. The songs normally differ but in the matching dialogue song of two neighbouring males often the same motifs are to be heard (Glutz & Bauer 13/I). The sonogram of two male great tits (Fig. 5) clearly shows the consistency of the motifs and pitch.

During around ten to thirty-five minutes of constant dialogue song in the marsh tit, the singing locations are arranged in such a way that the largest possible number of territory owning males can hear each other at the same time. No two marsh tits appear to have an identical repertoire. However, neighbouring males often use the same type of phrase during dialogue song. After several repetitions of one type of phrase, the marsh tit changes to another which is itself then repeated several times (Glutz & Bauer 13/I).

Neighbouring male scarlet rosefinches adapt their song to one another so that small groups are formed of up to 6 males with the same type of phrase (Höhnchen 1991).

Males in local populations of the greenish warbler can match their repertoire to such a degree that almost all their phrase types can be directly compared in structure and sequence in the sonogram (Glutz & Bauer 12/III). In the chaffinch, motif matching in dialogue song leads to striking local similarities in the preferred types of phrase, affecting the very varied final phrase in particular.

The alternating singing of the nightingale likewise leads to matching dialogue song, shown in the fact that the repertoires of nightingales which settle adjacent to one another have a proportion of matched phrase types. In what is known as the ‘performance role concept’, which is concerned with temporal interaction of singing nightingales, a male which does not interrupt another male, in other words sings ‘without identifiable temporal reference to the phrase arrangement’, is designated as an *autonomous* singer (Glutz & Bauer 12.II).

In the case of the extremely talented marsh warbler males ‘singing in canon often occurs, where the singer repeats the motif which his opponent performed a short time before’ (Glutz & Bauer 12/I). Grasshopper warblers with their very simply structured whir-

an average body temperature of around 41 to 44°C, depending on activity. Particularly when we wish to observe songbirds in matching dialogue song we should be aware that these creatures live at a different tempo which is also expressed in more rapid singing.

In matching dialogue song (or vocal matching) which usually sounds relaxed but can also be performed with vigour, two males of the same species try to respond to the singing phrases of the other with phrases which are as similar as possible until the motifs resemble one another. As soon as we hear this we have the impression that here the birds are not singing against each other but with each other in a special way. The reciprocal matching of songs occurs in many songbird species and is even present in juvenile birds (Wickler 1986).

In general, matching dialogue song is not connected to conflict song, as is often stated, but to a musical expansion of the alternating song. In the view of some ornithologists, however, matching of motifs up to the point of synchronisation can also occur in an aggressive mood. However, a study would need to be made of how the singing dispute of the two opponents continues, whether fighting follows or whether it tends to progress to fluid transitions from initial countersinging to relaxed and matching dialogue song. Does increased singing activity signal an aggressive mood in itself? Does the description 'matching counter song of competing (or rivalling) males' which is sometimes used in scientific publications necessarily imply an aggressive level? Why is it automatically implied that two vigorously singing males are in conflict? According to the prevailing scientific opinion that songbirds in fact *only* sing against each other, this is indeed logical, but it also means that without any clear classification of territorial song, general formulations such as 'competing' or 'rivalling' no longer have any specific informative value. They are a reflection of old Darwinistic thinking and therefore the interpretation of all written records on matching dialogue song actually need to be examined case by case. My experiences clearly support the opinion that matching dialogue song (or convergent counter song) goes beyond the relaxed dialogue song.

If it were to be accepted that territorial song should also be described from a musical viewpoint, then a *competitive* interpretation on the upper level could be endorsed, but one in which the singers in the matching dialogue song vigorously and jointly compete as to who is the better singer.¹⁰

It is possible that there is a kind of transfer of mood between territorial neighbours, but in any case an active musical convergence takes place which goes beyond the relaxed joint singing and requires that increased attention is paid to the singing neighbour, something which is revealed in the increasing similarity of the motifs. Naturally this musical matching process requires a certain talent for imitation. On account of the noteworthiness of this type of song and this singing level, several examples will be given to make it easier

¹⁰ The ortolan bunting is described as frequently producing dialogue song usually with strictly alternating singing when setting up its territory. Overlapping and even congruity of phrases is said to occur in a very aggressive mood (at close quarters) among competing males. Whether this latter should actually be evaluated as an increase in aggressiveness would need to be investigated in more detail. – Neighbouring yellowhammer males 'when countersinging can insert their phrases into the intervals of the rival in such a way that a high level of synchronisation arises between the two singers' (Glutz & Bauer 14/III).

compatibility (protein tolerance); not only, as would be expected, in endotrophic mycorrhizae symbiosis, but also in organ transplants – which is what all forms of grafting in arboriculture really are. Now there are no difficulties in understanding the gradual spatial incorporation of the haploid gametophyte into the ovule of all seed-bearing plants, or the long presence – in the seed coat and in the fruiting body formed from maternal tissue – of the plant embryo (genetically heterologous as a result of fertilisation) and its endosperm. With cacti, genetically 'foreign' chimaeras can be easily created; they are for sale in just about any flower shop.

Among the lower animals intracellular symbioses are frequently surprisingly well tolerated, as we have already noted above in the example of the photosynthesizing symbionts. As the evolutionary process moved from the first primitive fish-like animals in the Cambrian to the genuine fishes, then on to the amphibians, reptiles and birds, and finally to the mammals, the strengthening immune systems came more and more strongly to reject all foreign protein. Protein-specific autonomy was clearly preferred to the algal symbiosis, despite its being so successful in many lower animals.

All the more puzzling, then, is the still unresolved question as to how in the most highly evolved vertebrates – the mammals – there could have been the parallel evolution of both an increasing autonomy from the environment in animal gestation (through the internalisation of the embryo's developmental milieu within the uterus) and the development of a high degree of immunological tolerance on the part of the maternal organism towards an embryo which embeds itself in the maternal tissue. As we now know, the early development of the embryonic sheaths – especially of the trophoblast – is predominantly controlled by the paternal component of the embryonic DNA (thus 'foreign' to the mother), whereas the subsequent embryonic body is at first determined only by the embryo's maternal genes (Petzoldt 1988). There are, to be sure, rare instances – in humans, for example – of immunologically conditioned sterility, when the mother's immune system rejects implantation.

Recent research (Stoye & Coffin 2000) shows that, during pregnancy, specific genes which trigger the immune tolerance of the adjacent maternal tissue are activated solely in the outermost layer of the mammalian embryo (in the so-called syncytiotrophoblast). Detailed genetic analysis revealed base sequences which point to their origin in former retroviruses which became endogenous (ERVs = endogenous retroviruses) – suggesting that the evolution of uterine gestation in mammals was dependent on the incorporation of the appropriate retroviruses in the course of a lateral gene transfer. We are faced here, once again, with the fact of a massive macroevolutionary process by means of a genetic symbiosis with viral material from the surrounding biosphere. Stoye and Coffin report that we are not dealing here with a rare and exceptional evolutionary event, but that over long periods of evolution thousands of proviruses have been genetically incorporated by lateral transfer, including into the human genome, i.e. not from the parental line of descent, but from the environmental gene pool.

Summarising, we can arrange the various types of symbiosis on a ladder of increasingly complex integration:

global symbiosis, in particular of all prokaryotes;
 symbiotic systems of relatively separable biocoenoses;
 mutualistic symbioses between macro-organisms;
 extra-cellular symbioses in a tissue complex (mosses, ectotrophic mycorrhizae);
 intra-cellular symbioses (eucytes, endotrophic mycorrhizae);
 genetic symbioses in the plasma of eucytes (plastids, mitochondria);
 genetic symbioses in the nucleus of eucytes (horizontal=lateral gene transfer).

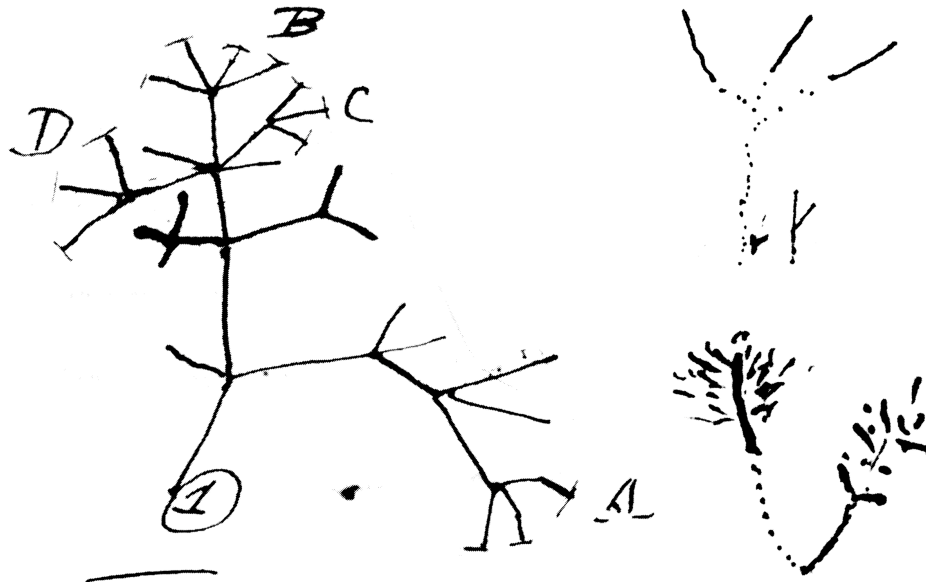


Fig. 6. Three sketches by Darwin (from his 1837 notebook) to illustrate the possible process of the divergent separation of new types from old ones. Dotted lines: extinct species. Darwin used the model of the coral, whose lower parts 'die away'. (from Bredekamp 2005).

Symbiogenesis as a complementary process of evolution

The last four, and more especially the last two, of the forms of symbiosis listed above challenge an interpretation introduced into evolutionary biology since Darwin: his principle of divergence. His basic concept of the development of new species was that some of the members of the original species population evolved through mutation and selection, while others continued to exist unchanged. After each new step in evolution, therefore, there were now two species instead of only one i.e. there is always a 'branching' or divergence, which Darwin initially sketched out (Fig. 6) on the model of the way coral grows, and which he later (in the *Origin*) represented as a tree. Ernst Haeckel spoke of 'Stammesentwicklung', i.e. *phylogenesis* (Figs. 7 & 8), and established his 'Phyletic Museum' in Jena. But with the discovery of the coalescence of genetic streams, the principle

to notice a musical intensification taking place in the dialogue song. As singing neighbours, males of the same species do not just perform their songs alternately but begin to adapt their motifs gradually to one another, as can be observed for example in the redstart, nightingale, whitethroat, yellowhammer, chaffinch, great tit, nuthatch, linnet or greenfinch.

Most people find that simple songs, for example from a chaffinch or yellowhammer, sound rather similar at first, perhaps even monotonous. This is partly due to the fact that we do not listen so carefully to songs that we are familiar with and thus miss the subtle differences. But it is also due to the fact that the human ear cannot distinguish everything that a songbird produces in a few seconds. In relation to their musicality and their singing performance, songbirds apparently live in a different stream of 'inner' time. They live:

at a faster tempo than us, so that for them *short* does not have the same meaning it does for us ... In addition to the tendency for high notes compared to human musicians, birds tend to hold notes for a very short time ... The upper limit of hearing for small songbirds appears to lie somewhat above that of human beings and as a result, what to us sounds extremely shrill is probably something normal or moderate, a *soft* note for birds. (Hartshorne 1958).

Birds do not only see things more quickly, but also hear more comprehensively, and so appear to have a considerably greater *perceptive precision* than human beings. At least 'the time resolution is better than human hearing so that birds hear many details of calls which merge for us' (Westheide & Rieger 2004). In studies on the structure and composition of birdsong, some of the songs:

were processed using sound microscopy techniques ... The increased recording precision and separation accuracy achieved using artificial means corresponds to the *standard performance* of the bird's ear. The significant agreement between what is taught and what is learned proves that the bird not only perceives the main structure of the given note pattern and develops this into a song, but recognises and reproduces all the details of what is heard. This means that the fine details which emerge when playing back notes at a reduced speed represent a reality of the environment and world of perception of the bird which is *hidden from us*, inaccessible due to the speed. An unexpectedly detailed structure was discovered in birdsong which suggests a far greater speed and accuracy of perception. Where we human beings hear only an undifferentiated twittering because of the high speed, birds are well able to perceive the actual form of the song of members of the same species. (Bornemisza 1999).

This may also be connected to the fact that, with few exceptions (e.g. skylark, garden warbler, wren), most songbird songs are relatively short. In a different context, Andreas Suchantke has discussed the temperament of the humming birds which visit flowers and their unusually fast wing beat:

A life of this kind at full speed is only possible through incredible alertness and sensory awareness ... This constitutes an unfamiliar and incomprehensible ultra-alertness of the senses which means that in an extremely short space of time which appears completely uneventful to us, other creatures experience an unbelievable amount due to a resolution capacity for time of which we are unaware. (Suchantke 2002).

This applies to numerous songbirds to a lesser degree. The excitable temperament must also be connected to the increased temperature of these animals, because songbirds have

tit and blue tit⁸. It usually remains a fierce musical struggle, however the gradually emerging short pauses indicate that the birds have begun to calm down somewhat: the transitions from excited to stimulating (and vice versa) are always fluid.

Visually it can be recognised that the excited dialogue song is directed straight at the rival, as in countersinging the two competing males stare at one another. Each sings – irrespective of the distance – straight in the direction of the opponent, sometimes accompanied by threat or display postures. This clear signalling effect generally achieves the desired result with intrusive territorial neighbours. In this situation the males sing fiercely and straight towards each other.

A comparison in the realm of human communication may help us understand this better. Everyone knows that an amicable and fruitful conversation between husband and wife, friends or neighbours can descend to the level of an opinionated insulting argument (or even violence). The opponents in general become louder, speak faster and often reduce their sentences to snatches. And because at this level it is an effort to let the other finish speaking in peace, not to interrupt his flow of words, there is the risk of butting in unthinkingly and impetuously.⁹ But this does not mean that we ascribe a distance regulating effect to human communication or hold the opinion that human speech is composed only of dispute, threat and attack.

When interpreting territorial singing, would it not also be better to proceed more methodically and cautiously? It is important to point out that territorial song does not merely support conflict but represents a much more comprehensive phenomenon than is generally accepted. I believe this problem to have arisen due to the fact that territorial song in its function as territorial defence has rarely been investigated from a musical point of view, just as it seems strange to some people that it is primarily an acoustic territory that is defended by excited conflict song.

Matching dialogue song

Within a species the males get to know each other very well through alternating singing. Due to their acute and highly developed sense of hearing, they can distinguish singing neighbours individually from their phrases. It is not only exciting and amazing to listen to the differences in the song phrases of neighbouring males of the same species, to the variety in the motifs, the pitch and loudness for yourself, it is also a prerequisite in order

⁸ The corn bunting reacts completely differently. Normally territorial neighbours sing their phrases alternately within hearing distance. If a neighbour inserts his phrase at almost the same time, so disrupting the pause rhythm, then the first bird will usually break off his own phrase (Glutz & Bauer 14/III). The harmonious rhythm, the cooperation, is interrupted here as well.

⁹ It would be a complete misunderstanding to label this comparison of the animal singing level with the human speaking level, and also the comparison of choir singing and soloists with simple and accomplished songbird species (see footnote 4 on p. 30) as anthropomorphism. The opposite is true. No human characteristics and behaviours are being transferred to birds. Rather, the clearly perceived phenomena in nature described – through concentrated participation – evoke related emotions in us. The beautiful wording by Konrad Lorenz, that we are able to hear the most exquisite song of a blackbird or bluethroat, ‘when they compose their song in a quite ordinary state of excitement’ should be viewed in the same vein (see page 33).

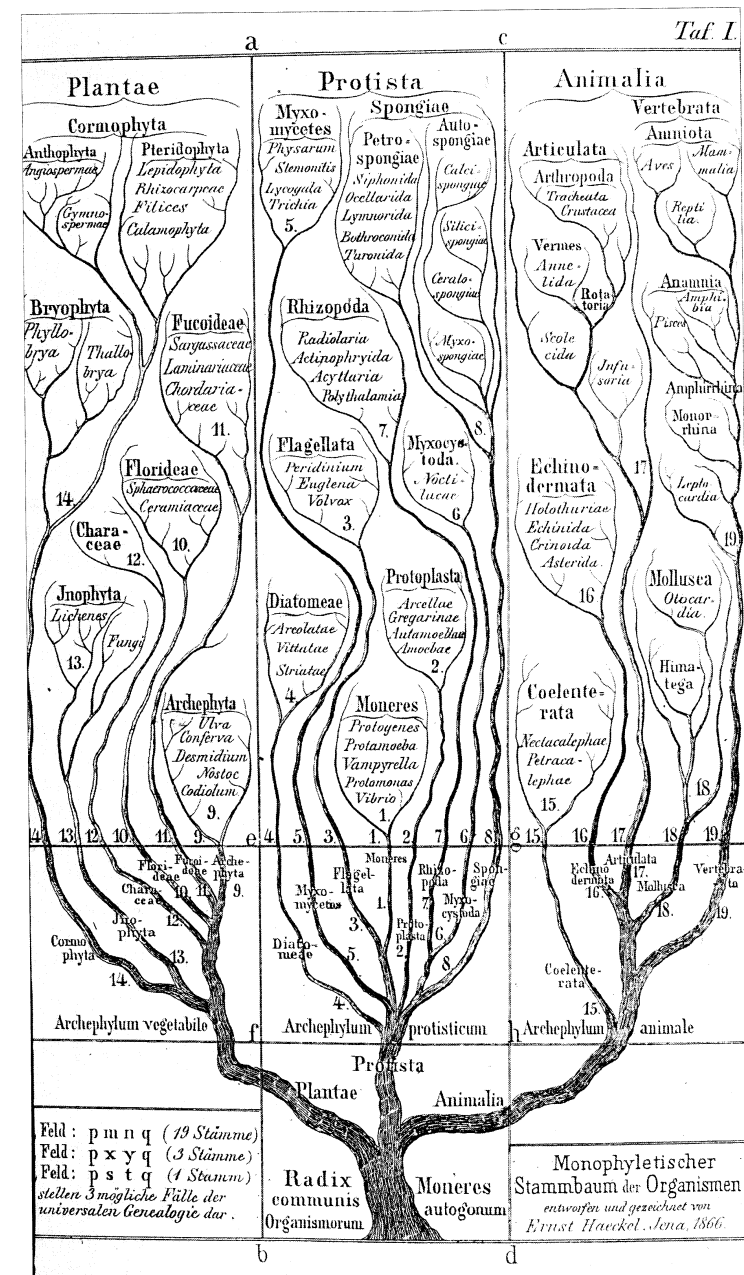


Fig. 7. Haeckel's model for the evolution of all organisms is first a bush with a short trunk. (from Haeckel 1866). (Legend: 'Monophyletic genealogical tree of all organisms conceived and sketched by Ernst Haeckel, Jena 1866').

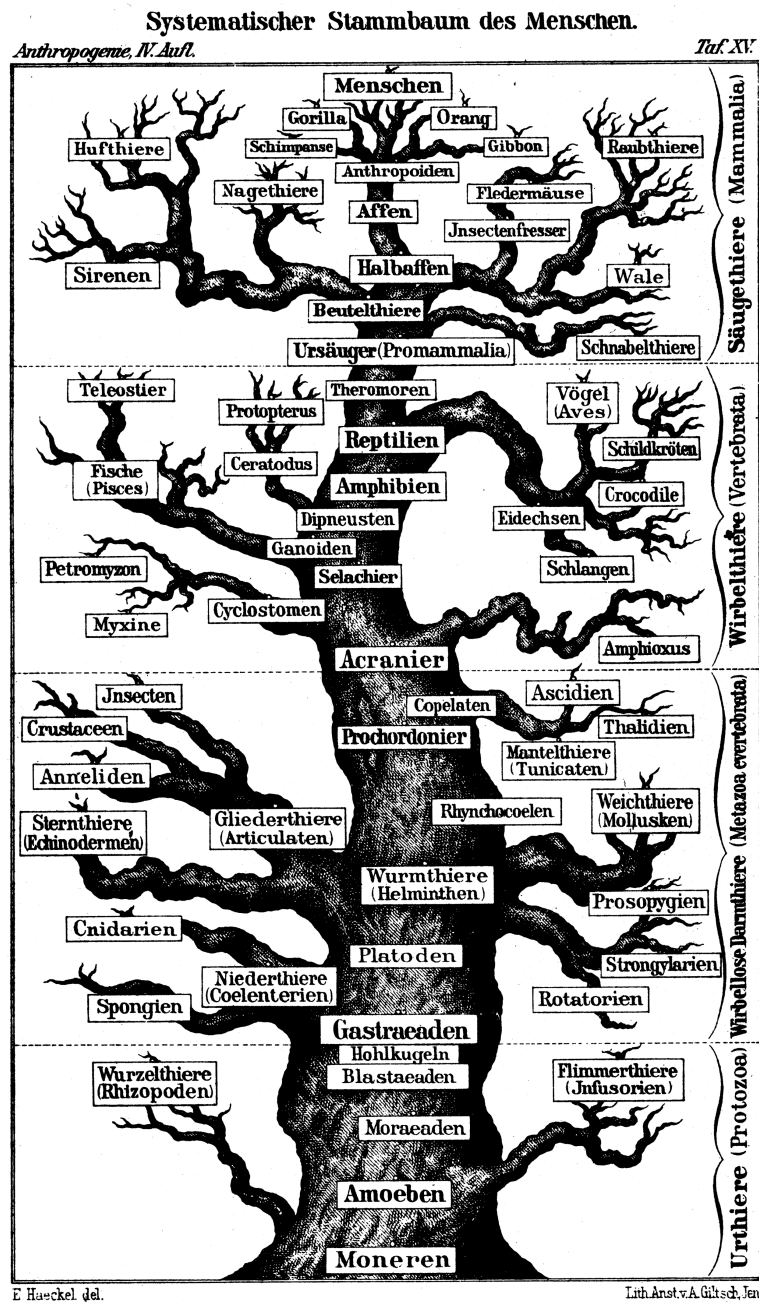


Fig. 8. By 1874, Haeckel's genealogical model has become an oak with a tall trunk and many branches. Legend: 'Systematic genealogy of the human being'.

MUSICAL INTENSIFICATION IN TERRITORIAL SINGING	
Comparison of song development and variety of motifs in songbird singing performance	Comparison of communicative rhythm in behaviour of neighbouring songbird males
Spherical song 'Going beyond the species'	→ Matching dialogue song 'Active musical approach'
Musical intensification	↑ Need for harmony
Relaxed motif song (Full song) <i>Males sing with one another</i> Song with many motifs, varied, differentiated; playful free use of the voice	→ Relaxed dialogue song <i>Harmonious rhythm</i> Quiet alternating song of neighbouring males of same species
Musical reduction: Frequently disharmonious changes	↓ Harmonious rhythm is disrupted
Excited conflict song (Excited or aggressive song) <i>Males sing against each other</i> Song aggressively harsh, usually louder and more monotonous than the relaxed motif song; song phrases are often shortened	→ Excited dialogue song (Countersinging) <i>Conflicts (with readiness to fight)</i> The opponents interrupt each other (what is known as overlapping song); in some species the voice cracks with excitement (what are known as double phrases).

Table 2: Three-stage territorial song

Excited dialogue song (countersinging)

As already mentioned, the designation 'countersinging' is only suitable for the lower (conflict) level of excited conflict song, if a male sings too close to the border or even in the neighbouring territory. This is accompanied by clear signals of both an acoustic and optical nature.

Acoustically, on this level it can be perceived that the otherwise harmonious exchange in the performance is disrupted. The opponents are too excited to sing their phrases in a rhythmical sequence in the usual way. The song phrases suddenly sound loud and aggressive and at times overlap each another. Neither male waits until the other has finished singing, so the usually short (or longer) pauses after each singing performance disappear. The lower aggressive level is thus evident from an acoustic angle. The alternating performance of phrases begins to overlap. From that point of view the scientific designation of 'overlapping song' for this situation is not wrong, but disguises the emotional state of the singers which 'interrupt each other' through excitement.

Genuine fighting can then ensue, but usually the intruding male flies back into his own territory. Countersinging frequently intensifies to lengthy singing duals in which the territorial neighbours often sing to each other in strict alternation from song posts close to the territory edge, as can be observed in species such as the whitethroat, coal tit, crested

Relaxed dialogue song

The three levels of territorial song⁷ differ in both their musical quality and also the behaviour of the singers. These differences can be appreciated even more clearly if we include the alternating singing of neighbouring males of the same species in our observations. As soon as we notice the alternating phrases performed in a communicative rhythm between two males, we can gain an even deeper understanding of the types of song described previously.

Countersinging is the name given to the competitive singing of two (or several) males of the same species whose phrases are performed in predominantly regular alternation. Countersinging is ascribed a distance regulating function between the territorial neighbours. Irrespective of whether greater emphasis is placed on the aggressive level or the co-operative level, the songs have a rhythmical relationship to one another.

Let us listen more carefully to the phrases of neighbouring members of the same species in spring, for example robin, chaffinch, great tit, blue tit, nightingale, song thrush or redstart.

We soon see that the alternating songs of the territory neighbours, like the peaceful sphere in relaxed territorial song, do not overlap but that a certain rhythm is adhered to. As soon as the first singer has finished his phrase, the second bird's phrase follows, usually a short time later and so on. Each bird answers the song of the other, indeed appears to wait for its phrase in order to add its own sounds again. The dialogue song of two neighbouring blue tits can last for over an hour. Each male encourages the other to sing and at the same time announces that the territory from which the song emerges is already occupied. On rare occasions dialogue song also occurs between different species, for example between chaffinch and tree pipit or chaffinch and lesser whitethroat. The song of the rock bunting at times has such a stimulating effect on the dunnoek (or vice versa) that enthusiastic alternating song can result. Countersinging is often interpreted as territorial singing or used in this context. However, on the relaxed level no aggressive exchange takes place but a lively response to each of the phrases produced by the singing neighbour. For this reason the term 'dialogue song' seems more appropriate to me, particularly on the relaxed level. If the communicative rhythm of the performance is noted, the dialogue song displays a good reflection of the three-tiered territorial song.

During the breeding season, particularly early in the morning, the males of many species of songbirds perform their songs from particular song posts. The dialogue song is usually harmonious and it can be noticed how the males often deliver their song phrases in a non-directional manner. On this relaxed level the birds sing with one another. The concept of a rival could be replaced on this level by territorial or singing neighbour, because the singers actually only behave like rivals briefly. We should therefore not refer to a conflict song on this middle relaxed level of countersinging, but to a song contest (Table 2).

of divergence no longer provides the full picture. There are also new combinations, i.e. *evolutionary anastomoses*. Sitte (2002, 2007) calls them 'intertaxonic combinations'. The Darwinian principle of divergence has to be supplemented by the complementary polar opposite principle of convergence (not to be confused with the 'convergence' which refers to the 'analogy' of similar functions appearing in different structures). Once again it becomes clear that biological processes can never be fully comprehended by a single paradigm, but always require several different ones at the same time. Only with this understanding does it make sense to ask where in the evolutionary process divergence predominates, and where convergence. The answer which the biological facts offer us today is that the principle of divergence primarily operates in gradualistic microevolution – in the process of evolutionary changes within a species, i.e. in the intraspecific evolution of subspecies, races and morphs. We see the principle of convergence, on the other hand, in the more saltatory macroevolutionary processes of the incorporation of other genomes, either in whole or in part, i.e. in the formation of new designs and body plans in the trans-specific evolution of genera, families, orders, classes and even phyla and kingdoms.

The complex of a species itself is the interface field where micro- and macroevolutionary processes meet. However, in relation to the fossil remains of extinct organisms, we have no reliable way of assessing what a species is, because no cross-breeding experiments are possible – and thus there is no means of determining characters in the sense of a biospecies. All species definitions in palaeontology are unreliable, because imprecise. There is no possibility of distinguishing one species from another experimentally. The same is true for all current life forms which have asexual reproduction, precisely because they cannot be cross-bred, but only produce clones of themselves. We have to content ourselves here with what is available to us as evidence: indications of pure *morphospecies*. This in no way undermines the fundamental idea of evolution, either in the fossil record or in the living world of the present. It is only that we can never say precisely where microevolution passes over into macroevolution, divergence into convergence.

Let us return to the question of genetic symbiosis in the biology of the cell nucleus. Symbiosis is, of course, always present in any form of sexual reproduction – where the haploid parental genomes fuse to form the diploid genome of the offspring. This classic instance of the genetic 'anastomosis' of genealogies, i.e. the genetic convergence principle, has long been known – though, to be sure, only *intraspecifically*, i.e. within the boundaries of individual species. Each offspring is thus a hybrid of its parents, and (as is well-known) this re-combination – together with the effect of any mutation – offers considerable evolutionary potential. In the 'crossing-over' in the prophase of meiosis I; followed by the recombination of the grandparents' genetic material in the arrangement of the pairs of chromosomes into the metaphase level; and finally in the further recombination which occurs in fertilisation, three degrees of biological freedom are presented which permit the offspring always to be somewhat different from its parents. Sexuality thus shatters the rigid determinism of identical clones. Because in sexual reproduction the offspring always has two parents – and thus has two genes to choose from for each trait – there is a further indeterminism in relation to the expression of genetic characteristics in the 'decision' as to which gene to use. In 2007, Alexander Gimelbrandt and his colleagues discovered that in human DNA there are some 4,000 genes which come solely

⁷ A summary of the varied territorial song is given in Table 2 on page 43.

from either the paternal or maternal side, for more than 300 of which the derivation cannot be predicted in advance i.e. is indeterministic. This further degree of freedom supports the increase of individualisation at the biological level, with the result that even monozygotic twins can differ far more in their DNA than had previously been assumed from the theory of inheritance. This certainly applies to mammals, and perhaps also to all amniotes (reptiles, birds and mammals). In addition, mitochondrial DNA is never identical, even in so-called 'identical' (i.e. monozygotic) twins, since this DNA is never distributed in exactly the same way in any mitosis.

When, with the creation of the eucyte as a result of intracellular symbioses, sexuality also arose, higher degrees of freedom – and thus an acceleration of evolution – also became available. But the increasing unpredictability of the individual offspring is inconvenient for breeding purposes (breeders would like to know exactly what the outcome will be) – which is why artificial cloning has been introduced into plant and animal breeding. But this is effectively to eliminate and invalidate the most important evolutionary processes, i.e. the emergence of sexuality and meiosis around 1.5 billion years ago; lateral gene insertion and/or cloning wind back the evolutionary clock to the stage of the pure prokaryotes typical of the first half of the evolution of life on Earth, thus undermining and nullifying the developments of the subsequent second half.

On semantics

As with much else in the life sciences, the term 'sexuality' is very unfortunate. It derives from the Latin word 'secare' = 'to cut or divide' and thus has a connection to Plato's *Symposium* dialogue, in which Aristophanes presents the mythical picture of an earlier hermaphroditic human being which was cut by Zeus into two unisexual halves – one male, one female – which have since sought to reunite with each other. But sexual union is the very opposite of 'sexuality = division'. The hereditary material that is passed on there does not diverge – but rather converges in a genetic symbiosis.

'Evolution' is an equally clumsy term. Biological science of the baroque era understood it literally as a 'rolling out' of what was already fully present in miniature in the germ. There could be nothing new under the sun because that would have meant that God's creation was imperfect – an idea which was considered blasphemous. Evolution was not viewed dynamically, but statically. Both Goethe and Darwin consciously avoided the word in their scientific writings, the former preferring the term 'metamorphosis' i.e. transformation/change of shape; the latter speaking simply of 'descent with variation'. It would be a good idea sometime to launch a competition to see who could come up with a better choice of words for this and many other misleading terms in modern biology.

The unthinking use of the expression 'struggle for existence' belongs in that category. Immediately after the publication of *The Origin of Species* in 1859, some of Darwin's closest friends raised the objection that the use of such an expression implied a conscious subject, which did not belong in a science based purely on natural causes. Physics and chemistry managed without a 'war of the molecules'. And who is doing the selecting in 'natural selection'? A year later Darwin had also accepted that such anthropomorphisms were linguistic errors. On 28th September 1860 he wrote to Charles Lyell: 'Talking of

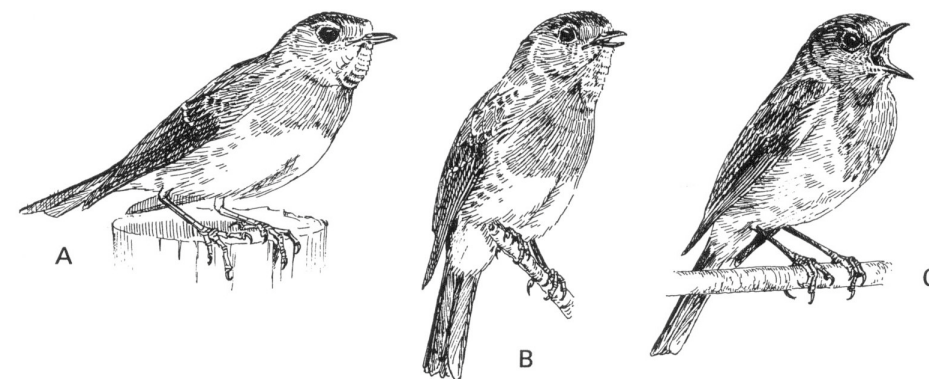


Fig. 4. Robin in subdued winter song (A) and in subdued and full territorial song (B, C). (Drawings: F. WEICK, in Glutz & Bauer).

Rhine, and join the nocturnal world of these master singers to listen to the almost heavenly chorus. These varied motifs performed more softly than through the day reach far beyond the level of relaxed singing⁶. In these conditions the birds belong to another sphere as it were. Everyone should have absorbed this with all their senses at least once in their lives. It would definitely then be easier to convince people that birdsong is more than just a biological function for the purpose of territorial defence.

Rainer Maria Rilke had this experience once and described it in a letter to Clara Rilke:

...but sometimes in the night I waken with the calling, a calling somewhere below in the valley, calling out of a full heart. That sweet ascending voice that does not cease to mount, that is like an entire being transformed into voice, ... And yesterday I found them all, the nightingales, and in a mild, curtained night wind walked past them, no, right through the midst of them, as through a throng of singing angels that only just parted to let me through, and was closed in front of me and shut to again behind me ... And that was noise and was about me and drowned out all thoughts in me and all my blood; was like a Buddha of voices, so big and commanding and superior, so without contradiction, vibrating so, up to the very boundary of the voice, where it becomes silence again, vibrating with the same intensive fullness and evenness with which the stillness vibrates when it grows large and when we hear it... (Rilke 1930).

It is not a contradiction that those species of songbirds which we count amongst the most talented singers belong both to the upper and lower levels of territorial song to a greater degree than other songbirds. They have a broader musical repertoire. Due to their extraordinary musical talent, master singers show much more developed territorial behaviour than birds which sing less well. They defend their acoustic space more vigorously, more aggressively, as can often be seen in the case of the robin. And just as the best singers have the greatest ability to *soar* to the spherical song, they are also able to *slip down* correspondingly rapidly into excited aggressive song.

⁶ The risk of descending into the excited conflict song is absent in the nocturnal chorus sound of the nightingale. Besides, the lack of visual contact prevents any conflicts.

ing on new and varied motifs).

7. In addition, mood can influence both the song and the performance tempo. Depending on whether a singing bird is excited or relaxed, this leads to irregularities or playful compositional options.

Spherical song

The entire wealth of song of our songbird world unfolds in the relaxed motif song, the most commonly heard territorial song. But there is another form of territorial song which goes beyond the relaxed motif song. I would like to call this song, which sounds completely unpremeditated, the 'spherical song'. This can be experienced in a striking manner in the beautiful evening song of the blackbird, when a male pours out his song into the quiet of the evening as though oblivious to the world. In the twilight realm between day and night, in a relaxed calm, blackbirds appear to become particularly creative. This type of song is like a free playful improvisation. The difference in quality of the motifs from the daytime song can be heard. The term I have chosen may appear unsuitable, but it characterises two important aspects:

1. The spherical song sounds as though it is expanded widely over the boundary territory and it is removed from all biological functions, unfolding in a far larger context. It appears to be completely unconnected to territorial functions and to be less directed at members of the same species, although it is produced during the breeding season and in the middle of the territory.
2. Just as the excited conflict song displays an influence from the earth and its necessities, the spherical song gives the impression that the individuals are inspired by the cosmos. It gives the immediate feeling that the songs which pour out into the world return to the earth again as a blessing (Steiner 1923). There is something in the spherical song, which is reminiscent of both the song of some juvenile birds and of the musical enhancement of the songflight, chorus sound, duetting and imitation song.

Male birds often sing alone in the spherical song, such as blackbirds or song thrushes in the late evening, as though they did not even expect a response from male members of the same species. From a musical point of view, these songs rise above the relaxed motif song. Karl Groos gave a beautiful description of this in his original and fundamental work *The Play of Animals*: 'The song of a song thrush or blackbird sitting on the very edge of the roof or in the highest treetop on a beautiful evening, letting its low tranquil but so joyful-sounding voice ring out, is perhaps the aesthetic peak of anything to be found in the world of feathered singers' (Groos 1907).

A similar experience can be had when a robin sings alone in the very early morning or late in the evening, as though it wished to join soft pearls of song into a wonderful musical necklace with its playful composing, or again on a sunny winter's morning when a robin sings in a somewhat more restrained manner (Fig. 4).

This musical enhancement can also be heard in chorus sound, when hundreds of nightingales sing together in the night. You only need to take the time, for example at four o'clock in the morning at the beginning of May in the natural alluvial woodland on the

"natural selection": if I had to commence de novo, I would have used "natural preservation"."

That would have been the value-free description. But the militaristic interpretation had already been taken up widely and was soon being liberally applied also to human society, providing spurious justification for what was soon labelled 'social Darwinism'. Darwin had taken over the idea of a competitive struggle for life from his fellow-countrymen: the economist Thomas Malthus (1766-1834) and the philosopher Herbert Spencer (1820-1903), who in turn had cited the 'father of economics' Adam Smith (1723-1790), the founder of neo-liberalism.

Today's biology is still full of linguistic militarisms, not only in popular scientific writings, but even in academic publications. Even viruses and bacteria are said to 'develop offensive strategies' and 'invent intelligent tactics' out of 'pure self-interest'. Plastids are 'enslaved cyanobacteria', and in Schaede & Mayer (1962) symbiosis is merely a condition of 'stalemate between equally strong opponents'. A 1990 book by Straass (1990) is entitled *Nature's Game Rules: Tactics, Tricks and Subtlety*. Especially tragic in its trivialising effect is his labelling of apoptosis – the healthy destruction of superfluous cells – as 'suicide'. All areas of biology are now routinely described in terms of military strategies, with 'generals' of one kind or another bent over their battle plans. But if one then asks who these 'generals' really are, and whether Darwin had not primarily argued for the demythologising and de-anthropomorphizing of science, then one receives the reply: 'It's not meant to be taken literally! These are all just verbal jokes'. But why then do these authors not seem to be able to manage without them? Freiburg-based Professor Emeritus of German Language and Literature Uwe Pörksen [author of *Plastic Words*] offers a telling critique of the unconsidered – and therefore inappropriate – use of metaphor in modern biology (Pörksen 1986, 1992).

If the martial (and anthropomorphic) language of current biology cannot be renounced – a classic case is Richard Dawkins' 'selfish gene': how can it be 'selfish' without having a 'self'? – then we are at least justified in asking for reasons. I see two: one sociological, the other biological.

The sociological aspect was examined by Daniel Todes in his 1995 essay: 'Darwin's Malthusian metaphor and Russian concepts of evolution', in which he pointed out that the ideas of a struggle for resources and for one's own existence found in Malthus, Spencer and Darwin can be seen as a consequence of the First Industrial Revolution (the introduction of the steam engine and the mechanical loom). Population numbers increased significantly as a result of the wealth created by the new industries, and the concurrent expansion of the British Empire led to pressure for emigration. Britain's population had exceeded the island's capacity to produce sufficient food for all; the idea of a competition for resources then influenced thinking in science.

The opposite was the case in Western Russia. Settlement was sparse – even more so than today – and the next village might be several days' journey away. When people did meet, they tended to co-operate for mutual survival. Thus Russian biologists of the 19th century long rejected the idea of selection as the primary factor in evolution, and placed equal importance on cooperation, in both the animal and vegetable kingdoms. The St.

Petersburg zoologist K. F. Kessler (1815-1881) and Moscow's Prince Peter Alexeyevich Kropotkin (1842-1921) were most influential. This alternative view of the majority of Russian biologists of the end of the 19th and the beginning of the 20th century must be clearly distinguished from the school of biology around Trofim Lysenko (1898-1976), which was subject to corruption through political pressure from Stalin and whose influence ceased only under Khrushchev and Brezhnev. The anarchist Kropotkin, by contrast, was completely opposed to accommodation with a totalitarian state. But the awareness by the western scientific community of earlier evolution research in Russia was significantly hindered by the language barrier. The relevant literature has only recently been translated and made available to a wider readership (Khakina 1992).

Even in the absence of any form of totalitarian state interference, modern science has never operated in a social vacuum – despite all its attempts at objectivity – but has frequently been more influenced by and dependent on social trends than it has been aware of itself. Its own methods and findings have, of course, likewise exerted an influence on those trends; that there is here a mutual give and take is probably only to be expected, and appears to be confirmed by the work of Daniel Todes.

The biological aspect of the use of martial language is clearly connected with the principle of divergent evolution described by Darwin. The microevolutionary division of a population into two and the development of genetic (reproductive) barriers between them represents a split which can easily lead to an assumption of mutual competition – even of antagonism, strife and war. It is psychologically easy to make the anthropomorphic projection, as Darwin did when he developed his paradigm.

If eyes are increasingly opened to the importance for macroevolution of the symbiotic principle of convergence, it becomes necessary also to speak of organisms mutually complementing each other, of their mutual support and assistance, and of altruism (Ernst 1998). If, on the other hand, reference is made to physico-chemical neutrality in relation to all interpersonal metaphors, then an end should be put to the use of any and all militarisms in modern biology. The facts themselves remain unchanged; but the way we speak of them – and thus also the way we see them – would change.

If we look more closely at the problem of interpretation, we can see that it is connected with the fact that the idea of individuality was applied far too quickly to living organisms. Whether we are talking of a cell, a daisy, a tree or a deer: we have a tendency to see them as individuals because, endowed as we are with an individual self-awareness, we project our sense of identity onto the beings of nature. But a cell is not an individual (literally 'something which cannot be divided'), because it normally divides itself in every mitosis into two equal daughter cells, leaving nothing behind. It is thus a 'dividual' (Braun 1851, Troll 1943). All metazoa can be made today into genetically identical clones of themselves, even if the process became increasingly difficult in the course of evolution: the degree of biological autonomy, and thus of individualisation, increased over time, though it never reached completion.

And despite our own internalised respiratory system, our relatively well-closed circulatory system, our remarkable homeothermy and advanced immune system, our non-specialised, universal, mode of nutrition, our internalised reproductive system, and our relatively biotope-independent locomotion, humans are also not closed 'holons', as 'holism'

female songbird nestlings get to know the song of the father and later choose their partners without ever singing themselves' (Wickler 1986).

Frequently the young birds' learning phases correspond to the prominent singing activity of the father at least in terms of frequency as well as timing, varying depending on species. In the case of some songbird species such as the blackbird and marsh tit it might even be appropriate to speak of 'lessons'.

While songbirds learn the song of their own species and pass it on through tradition, even in the initial learning process there is scope for freedom in individual song variations, because learning introduces increased flexibility in comparison with purely inherited behaviour (Rosslenbroich 2007). Learning song implies an important increase in autonomy, enabled by the development of vocal diversity as can be seen in the talented songbird species of the present day.

Using the example of song learning, which can only be touched on here, attention should be drawn to the behavioural flexibility of songbirds on a musical level as a reflection of the differing degree of emancipation from inherited modes of behaviour which are actually only apparent when the acquisition of individual learned adaptations can be excluded (Franck 1997).

Genetic patterns and instinctive actions, known as 'fixed action patterns' (FAP) nowadays:

form the basis for the behaviour modes of all animals. They can be supplemented and expanded to differing degrees through the ability for more flexible behaviour, but are always present in outline and therefore form the basis primarily for life-preserving behaviour modes and reproduction. They are as typical for an animal species as its form. In contrast, learning contains a greater degree of behavioural flexibility. It is a behavioural modification based on experience and introduces an increased plasticity of behaviour in comparison to fixed behaviour patterns (Rosslenbroich 2007).

This is particularly apparent in the skilful and complex songs of a large number of particularly talented songbirds. The ability to mimic other voices is a further stage in song development which, with the exception of dolphins, is quite unique in the animal world.

It is the diversity of song variations which make the study of birdsong very time-consuming but also – due to direct experience – so extraordinarily exciting and stimulating:

1. Numerous species of songbirds, even simple singers such as the house sparrow and zebra finch, have more than a single type of phrase.
2. Species which are musically highly developed sometimes possess an almost inexhaustible range of motifs and phrases.
3. Within a species, song phrases can be performed in shortened, lengthened or incomplete forms.
4. In addition to full song, distinctions can be made between juvenile song, subsong and autumn and winter song.
5. Numerous species have developed geographical song dialects.
6. Individuals are not all equally talented, so that both the range of repertoire and the artistic performance can display large differences within a species. Sometimes a single highly talented song thrush can raise the musical level of a region (by pass-

3. One part of the song (mostly the opening phrase) is innate, other parts (often the closing phrases) are learned (for example chaffinch, yellowhammer).
4. Although the song is inherited, its phrases can be varied due to sometimes astonishing learning ability or be extended in diverse ways by mimicking other motifs (for example some warblers of the Genus *Sylvia*).
5. Certain basic components of the song are genetically determined but can nevertheless be varied in many ways (for example song thrush, grey catbird).
6. There seem to be almost no limits to what the most musically talented songbird species are able to do with notes (for example blackbird, nightingale). However, they also have a marked predisposition for the song of their own species.

The developmental stages indicated here – from the inherited determination of the voice up to playful vocalisation – indicate increasing levels of freedom in birdsong.

Laurens van der Post dealt with this biological/musical lawfulness in his inimitable way. He has his African friend, Ben Hatherall, relate his experiences of how nothing is comparable with the sound of birds. It was as if the sky made music in their throats:

One could hear the sun rise and set, the night fall and the first stars come out in their voices. Other animals were condemned to make only such noises as they must, but birds seemed free to utter the sounds they wanted to, to shape them at will and invent new ones to express all the emotions of living matter released on wings from its own dead weight. (Post 1961)

This touches on an important level of autonomy, that the songbird world has in fact freed itself from the constraints of the naturally fixed vocal repertoire. To the extent that most songbirds do not produce their songs innately but have to learn them, this gives rise to diverse developmental opportunities which are not hard to recognise in the individual song variations – even to dialects – within a bird species. Most songbirds possess a disposition for learning their own song, but have to learn from an older member of the species – mostly the father. The inner acoustic pattern is present but has to be stimulated from outside so that the species-specific song can develop through imitation.

The learning capacity varies from species to species and the sensitive phases in nestlings and young birds for learning to sing are of different length. Numerous species of birds have only a short, usually early formative phase, for example from directly after hatching to shortly after leaving the nest. For goldcrests, the learning phase starts from day eight. In the marsh tit the learning period is from leaving the nest for approximately three weeks. In other species the sensitive phase runs from 10 to 70 days.

In the marsh warbler, probably our best mimic, the learning phase begins in the sixth week and ends at around eleven months. There are two sensitive phases for learning in young chaffinches: the first is in the first summer, the second between February and April in the following year. Numerous birds noted for mimicry are probably capable of learning for years or even throughout their lives. This also applies to the blackbird, canary, linnet, siskin and goldfinch as well as related species.

The greenfinch, for example, in contrast to the chaffinch, is still able to learn after reaching 13 months of age. 'In many bird species, nestlings are conditioned by the song of their father shortly after hatching, but only produce the song much later, true to the original, even if they have not heard it again during the intervening period ... Likewise,

assumes. Our health depends on a rich palette of symbioses with bacteria living on the skin, the mucous membrane and the rectum. And even the human immune system cannot ensure complete protein autonomy: after an infection, the herpes virus is not completely removed, remaining for the rest of one's life in certain nerve ganglia.

Looking through the lens of symbiosis we can say in summary: all life of all organisms consists in symbioses, not in clear and distinct individuals. A sense of personal distinctness, of identity, of self, can exist only in humans, as a result of our unique mode of consciousness – it cannot be derived from our biology. For the realm of biology – including the human organism, as we have shown – we can count on the words of the 'great biophile', as Erich Fromm described Goethe (cf. Jungk 1974):

Freuet euch des wahren Scheins,	Enjoy the true seeming
Euch des ernsten Spieles:	And the serious play,
Kein Lebendiges ist ein Eins,	Nothing lives as a One,
Immer ist's ein Vieles.	Always it is a Multiple.

(from: Epirrhema)

The Danish marine biologist J. Steenstrup found his imagination severely challenged when in 1842 he discovered that in the course of a single life-cycle an animal can appear in two quite different-looking forms, both deriving from the same hereditary material: a sessile polyp and a free-swimming medusa. He had discovered metagenesis (the alternation of generations) in the Coelenterata. A similar arrangement had already been found among the lower plants: the protonemata in mosses or the prothallia in ferns which grow out of them are completely different in appearance. Wilhelm Hofmeister, son of a Leipzig music publisher, became obsessed with the microscopical study of plants. In 1851, when only 27, he published his ground-breaking discovery that *all* plants experience a similar alternation of generations between asexual and sexual generations with mostly very different forms, and linked in most cases to the genetic switch from a simple to a double set of chromosomes. He was able to show that in the course of the macroevolutionary development of the higher plants from the lower ones, the haploid generation had been more and more internalised spatially into the fruits' ovules, achieving a higher degree of autonomy from the environment. Among the lower animals there is also sometimes an alternation of generations with an alternation in nuclear phase (for example in the Hymenoptera, such as the bees: diploid queen > haploid drone > diploid queen).

In the higher animals and humans the haploid nuclear phase is restricted solely to the sexually polarised germ cells (gametes), which in the haploid nuclear phase thus also represent their own generation – and which as spermatozoa are even autonomously motile. In a strict sense, therefore, the human organism, too, passes through two different, genomically distinct, generations, only one of which has been reduced to the existence of a single cell generation, i.e. the haploid germ cell.

As long ago as 1990, the cytologist Peter Sitte said that it made the head spin to see so many ideas in biology, hitherto thought to be solid, now dissolving before one's very eyes. The eukaryotic cell is no longer the fundamental organism (except in many textbooks); the genome and thus the germlines are not fully autonomous; the central dogma of mo-

molecular biology (the transcription of DNA > RNA > protein) is no longer wholly valid. The concept of the strictly individual organism has become progressively dissolved; transmission of heredity is no longer held to be solely from the parents. The definition of a gene as the sequence of bases which codes for a protein had recently been shown to be false (Pearson 2006). It was likewise a complete surprise when it was revealed that the universality of the genetic code for the base triplets in DNA does not actually apply universally to all organisms (Osawa et al. 1992). In fertilisation, paternal mitochondria can in some instances also be passed on – not solely the usual maternal ones (Gyllenstein & al. 1991). Bahnsen (2008) reports on the huge genetic change in the early ontogeny of the human being from the 6th day on. As a result of ‘monoallelic expression’, monozygotic twins are not genetically identical.

In order to remove any possible misunderstandings, it should be stressed that nothing is here meant to imply a denial of the evolutionary trend towards the individualisation of organisms. That is beyond question – it is clear simply from the enclosure of each cell within its own membrane. Then there is the cellular ‘division of labour’ in every genuine metazoan; the increasing homeostases and/or homeodynamics of physiological processes; the increasing autonomy, first from a watery environment, then from external warmth; the internalisation of embryonic development in the seed-bearing plants and in mammals; the extension of the immunological response of each ‘biological entity’ towards everything which is ‘not self’ etc. Many, if not most, of these evolutionary steps were achieved through symbioses (Rosslenbroich 2007).

The ecological symbioses which predominated at first were increasingly internalised into intra-systemic symbioses, without this evolutionary process going so far as ever to exclude the external factors – the *oikos*. Nonetheless, over time, the transition from the exosymbioses to the endosymbioses came to favour the latter. In any organism the extrinsic and intrinsic processes are always in balance with one another, even if the shift in their relative influence has moved in the direction of increasing individuation, without ever achieving it fully. We always need to take two perspectives into account at the same time: convergence, and divergence through descent over the course of evolution. The central task of theoretical biology is to determine where the one or the other evolutionary principle was in play in the past – and perhaps also how they will interact in future.

Molecular biology plays an important role in the above-mentioned discoveries which are revealing the porosity of the biological dogmas. It suggests the heuristic approach that life can never be comprehended solely by one theorem, but requires a pluralism of paradigms. We appear to need far more than one way of looking at life in order to approach it with real understanding.

Biology textbooks are still full of outdated hypotheses. It’s a bit the same as with the Copernican model: we’ve been taught it and have understood it, but day-to-day we still operate according to the geocentric model. American astronaut Brian Swimme recently suggested (1997) that people should go out once, lie down in the open, look up at the night sky, and remind themselves that there’s no ‘above’ or ‘below’ in the cosmos; that it’s only gravitation that keeps us on the Earth. They should then imagine that they are hanging on the Earth, not looking up, but *down* into the vast starry cosmos. Because we’re not used to thinking of it in that way, we might well feel dizzy and even be over-

male of the same species at too close quarters and reverts (temporarily) to old aggressive response patterns or innate song structures, with the transitions from excitement and stimulation being fluid.

2. Solitary breeders without any singing neighbours are *not stimulated* in their singing and the variety of song is in danger of declining (in the long term).

When Konrad Lorenz talks about a songbird which ‘*composes* its song in a quite ordinary state of excitement’, this is not referring to the realm of excited conflict song but to the relaxed motif song, in other words to a freedom which is enlivened and pervaded by the vibrating stimulation of a singing neighbour.

I believe this to be the biological/musical reality in the life of most talented songbirds.

Learning songs

I would like to mention a phenomenon here which has a fundamental connection to the increase in autonomy in birdsong and which also explains the extraordinary richness in variety to be heard particularly at the level of the relaxed motif song. For evolutionary progress in the direction of a ‘biology of freedom’ the important elements are openness, inquisitiveness, flexibility and intelligence, which are closely connected to learning and playing in terms of behavioural biology. These areas cannot always be clearly distinguished, however, as they can easily merge with one another.

As soon as we start to look at vocal development, it can be seen that animals acquire their vocal repertoire from nature in very different ways, but that the extremes of ‘genetically fixed’ and ‘completely free’ never arise in the animal world:

1. Almost all terrestrial vertebrates have the innate ability to vocalise.
2. In terms of vocalisation and the learning of different acoustic signals, it appears that apes, elephants and dogs, depending on the species, have greater freedom than other terrestrial mammals.
3. It has been shown that marine mammals such as dolphins and whales possess a very large vocal repertoire which is always capable of modification or expansion. It is likely that the communication abilities of these animals are significantly greater and more differentiated than was previously supposed.
4. In a large proportion of birds (Non-passeriformes, for example water birds, game birds, waders and birds of prey) the range of sounds is hereditary.
5. Songbirds (Passeriformes) also have innate calls such as alarm calls and contact calls.
6. Most songbirds, with a few exceptions (for example warblers and buntings), have to learn from older members of the same species in order to acquire their typical species song.

In connection with autonomy, attention has been drawn to important developmental stages in the songbird world:

1. The faculty for producing the species’ own song is inherited and does not require to be learned (for example almost all the bunting species in the Genus *Emberiza*).
2. Harsh and aggressive song components as well as pitch and tone quality are innate whereas rhythm and type of modulation have to be learned (linnet).

of their own singing, how they encourage each other in a musical competition, build up the singing intensity and in this way perfect their song. It has been shown that the songs of highly evolved songbirds even have a compositional effect on neighbouring individuals. Likewise, as soon as the so-called rivals are missing and no response is forthcoming, surely something of this outstanding musical talent must be lost?

In answer to this question there are now numerous scientific studies which show that songbirds nesting in isolation sing less both during the day and also during the entire singing period than those in scattered nesting colonies, and that the quality of the song phrases declines significantly in birds nesting singly. So we should not assume that song serves only to drive rivals completely away.

Anyone who has experienced the nocturnal many-voiced chorus sound of nightingales knows that the song of a nightingale singing alone can be further enhanced. After such an unforgettable experience, every bird lover and ornithologist must be convinced that a single singing nightingale would wish for at least *one* opponent for the musical contest. A rival singing male which ventures too near to another territory will definitely be driven off, but not too far, because the territory owner wishes to go on hearing him as a singing neighbour.

This illuminates an important principle in autonomy. The increase in autonomy is shown both in the fact:

that the individual organism becomes more stable, independent and flexible in the face of environmental effects and the balance is ensured between being open or closed to the environment. Even the simple example of the cell membrane shows that, in a biological system, a complete separation from the environment is never achieved. The cell membrane always has the double function of separation from and exchange with the environment. Both have to be guaranteed at the same time. On the one hand cells and multicellular organisms have independence in relation to environmental influences. On the other hand they require constant exchange with their surroundings. Each organism needs to balance these two requirements and each solution takes a different form. (Rosslenbroich 2007)

Talented songbirds find themselves in a similar situation with their vocal disputes and communal singing. **The double message contained in the relaxed motif song is both to define their own acoustic area and to cultivate a singing communication with the territorial neighbours.** In this sensitive boundary realm, the songbird world gives us a telling image, which we know well from a related phenomenon in human relationships, namely the fragile balance between distance and closeness. The difference being that in the case of songbirds, this requirement for equilibrium is connected with musical ability. A relaxed singing atmosphere arises primarily when a territorial neighbour respects the acoustic space of the other by singing at an adequate distance. But a balanced relaxed environment is not only threatened by a singing rival trying to intrude, but equally when there is no singing male member of the same species in the immediate vicinity!

The relaxed motif song, which produces a *stimulating* effect and which is always to be heard when biological functions are not to the forefront, can go astray or degenerate in two ways:

1. The territory owner becomes *excited* by the insistent singing of a neighbouring

come by a sudden fear of falling down into the black hole of infinite space. Yet we mostly feel that we are standing securely *on* the Earth.

The findings of recent biological research may be producing a similar feeling. Much of what has been presented here is now common knowledge, but most people appear not to have understood the implications. It would be very worthwhile to reflect on them; they are what is making biology such an exciting field today – even if we still lack the right language in which to speak of them. The right language would allow us, not only to describe in more appropriate terms the biological problem of the juxtaposition of competition and cooperation, of divergence and convergence, but also to discuss – without falling prey to a crude biologism – similar phenomena in human society. Of course, the latter cannot be explained in terms of natural laws. Whenever biology has been made to serve politics it has always led to totalitarianism – simply because the principle of full individuality does not exist in Nature. That principle is expressed in the cultural recognition of the dignity of every human being – as declared in most constitutions and in international human rights law.

Evolutionary biology and society

On his round-the-world voyage on the Beagle, especially during the time spent in South America and the Galapagos, Charles Darwin (1809-1882) made the observations on which he based his principle of divergence, the value of selection, and his theory of a struggle for life in nature in which the survivors survived by virtue of possessing superior qualities of some kind. His slightly younger compatriot Alfred Russel Wallace (1823-1913) had come to the same conclusions while working as a specimen hunter in Borneo. Wallace generously refused to claim his due priority. Wallace was an even stronger advocate of the theory of selection than Darwin, but differed from Darwin in rejecting its application to human society. Darwin was unable to resolve the dilemma. He wrote to Wallace, begging him to come over to his way of thinking, as even one exception would shake the foundations of his theoretical structure. Yet he, too, saw the dilemma. His theory for the improvement of Nature – including the human race – included the provision that it would be necessary to organise ways of denying assistance to the feeble and the sick before they reached reproductive maturity, to prevent them from passing on their infirmities. Yet he hesitated. In *The Descent of Man*, published in 1871, he wrote:

There is reason to believe that vaccination has preserved thousands, who from a weak constitution would formerly have succumbed to small-pox. Thus the weak members of civilised societies propagate their kind. No one who has attended to the breeding of domestic animals will doubt that this must be highly injurious to the race of man. (1871; 1992:148).

Darwin was well aware of the potential socio-political implications of what to him was a scientific statement. Thus he also concerned himself with the question as to how the unfortunate consequences could be avoided:

The aid which we feel impelled to give to the helpless is mainly an incidental result of the instinct of sympathy, which was originally acquired as part of the social instincts, but subsequently rendered, in the manner previously indicated, more tender and more widely

diffused. Nor could we check our sympathy, if so urged by hard reason, without deterioration in the noblest part of our nature. [...] Hence we must bear without complaining the undoubtedly bad effects of the weak surviving and propagating their kind. (ibid)

Darwin appeals to an inborn or instinctive sympathy, which as the ‘noblest part of our nature’ must not allow itself to be supplanted by our reason, but must accept ‘the undoubtedly bad effects of the weak surviving and propagating their kind’. He does not explain how this instinct could have been favoured by natural selection – against a ruthless, uncaring selection itself – with the result that Social Darwinism could later simply take at face value an unproven, ill-considered line of argument. In the preface to the first French translation (in 1862) of Darwin’s *Origin*, the translator, Clémence Royer, presented a naturalistic ethics for human society – one irreconcilable with a Christian humanism. After reading the preface Darwin declared Royer to be ‘the most remarkable and cleverest woman in Europe’. She had declared that ‘natural selection and the struggle for life will explain all morality, nature of man, politics etc.’ (cf Harvey 1995; 231f).

Of those around Darwin, Herbert Spencer asserted the unbroken validity of the selectionist theory of evolution for both Nature and human society, while Wallace and Mill took an equally firm ethical stance against such equivalence. Huxley thought there had been a gradual transition: at earlier stages of the evolution of humans from animals, natural selection had dominated, but had then been progressively supplanted in the course of human cultural development by a humanitarian ethic which sought to protect each individual in all cases. Darwin’s view should be seen against this background. In his scientific thinking he believed selectionism must necessarily apply also to humans; as a compassionate member of society, however, he toned that position down in his publications. Thus Darwin see-sawed between the positions of Spencer and Wallace. He did not want to see his theory of selection restricted in its application to human evolution and the human cultural sphere – but neither did he wish to abandon his practical humanitarian ethical approach.

Darwin was not able to resolve the dilemma of the application of natural selection to human evolution and human history. That was exactly a century and a half ago. In this essay the attempt has been made to show that recent findings in biology have brought an extraordinary widening of the rather narrow perspectives of Darwin’s time. In terms of the current state of biological knowledge, there is no longer any justification in being satisfied with ‘one-track’ explanations. The natural evolution of life existed and exists in the tension between opposing antagonisms. Finding out where competition and where cooperation in human society properly belong – whether in economics, politics or art – is the task of the present and of the immediate future. The most recent findings in evolutionary biology mean that there is no longer any justification for a restricted approach to this question.

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songbirds or individuals may even possess the ability to find musical *outlets* in a tense situation. This example gives us a glimpse of the deeper secrets of imitative or mimicking song and raises the question as to how far birds are able to perform imitations in the correct context.

When the purpose of the territorial song is discussed nowadays, it is almost always the lower level of territorial song, that is, the aggressive song, that is meant. The science of ornithology is primarily concerned with this lower realm, without stating this explicitly. Functional arguments have a certain justification here, but not for the whole territorial song. Interpretations of a Darwinistic nature only sound so convincing because, due to a lack of differentiation, the aggressive side of territorial singing is brought to the forefront in a one-sided manner. This again proves the necessity and justification of musical differentiation.

Relaxed motif song

Birdsong sounds quite different from the excited conflict song when it is produced in an environment with little disturbance, in a calming relaxed atmosphere. As already mentioned, in the excited song the phrases are frequently shorter, more monotonous and aggressive, while in the relaxed motif song (or full song) they are more perfect, differentiated, with a more beautiful sound and wealth of motifs. In many songbird species the relaxed song has a more coherent effect in general and the individual acoustic elements are often more clearly separated from one another. In the relaxed motif song a completely new range of variation potential opens up, because the birds do not feel themselves cramped by any outer influences. Opportunities arise which are *made use of* by the birds.

The entire musical wealth of our best songbirds is produced in a playful manner and in a relaxed peaceful atmosphere. Everything which develops beyond the excited conflict song, in terms of fine structure, melody and the art of variation, is an audible result of individual opportunity, the living expression of an increased level of freedom, so to speak. The initial discussion of the excited aggressive song should show that birds actually sing *against one another* at this level and are ready to fight if need be. But this only applies to the lower level of territorial song. In the relaxed motif song on the other hand – and this forms by far the larger part of song activity in European songbirds – neighbouring male songbirds sing *with each other*.

The songs sound most beautiful and varied, as already mentioned, when the territorial neighbours sing at an adequately large distance in their territories, in other words quite relaxed but not, as might be thought, when there are no territorial neighbours at all. It is always a pleasure to see how members of the same species (with adequate distance) encourage each other and foster each other’s singing. A nightingale, for example, which was able to drive away all singing members of the same species from its vicinity, would then have an extensive territory and no more rivals next door, but would no longer hear any male members of the same species. Just as during the course of evolution musical communication was required for the development of song, nowadays so is a vocal exchange between singing neighbours necessary.

We know how important acoustic stimulus is for our *master singers* in the development

Bernhard Hassenstein, made similar remarks a few decades later. He describes one of the most impressive things a naturalist can experience when he notices that:

The song is loudest and most aggressive when it fulfils its biological purpose of fighting a rival. But it is most varied and to our ear most beautiful when there is no rival, in other words when the song does not fulfil its biological purpose. It is only then that the bird appears to be in a sufficiently relaxed situation to display its whole musical inventiveness. A bird in this mood can be said to compose. The nightingale's richest variety of musical invention is revealed – as when animals play – in a relaxed environment when instinctive goals are absent ... A state of freedom from biological necessity in the behaviour of animals is demonstrably attained which cannot be imagined in a more perfect form (Hassenstein 1969).

The excited conflict song, which would be totally sufficient for territorial defence, demonstrates that the relaxed motif song has developed far beyond biological necessity. The (temporary) loss of a degree of freedom in the excited conflict song is audible as regression to innate song structures, at least in part. This explains why, with few exceptions, elaborate imitations that indicate an enhancement of song development are almost completely missing on this level. It is very instructive that the blackcap, for example, introduces imitation in excited conflict song.

In comparison with the relaxed motif song (Fig. 2), the more monotonous and shorter aggressive song (Fig. 3) is immediately noticeable: in the sonogram the last part of the excited song displays a short powerful phrase. The initial soft notes and the central part are imitations of blackbird alarm calls. This phrase begins with a rapid series of imitative 'tack' sounds followed by the imitation of a sequence of high scolding calls (Glutz & Bauer 12/II).

The song of the blackcap is not musically enriched by mimicking other bird calls, but imitations of harsh alarm calls are produced, something characteristic of the lower territorial song level. In this case imitation in the excited conflict song is therefore not a contradiction, but very nicely confirms the rule of musical reduction. Some species of

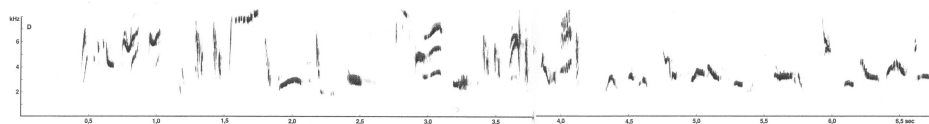


Fig. 2. More varied relaxed motif song lasting 6.5 seconds of male blackcap with striking almost thrush-like final phrase, what is known as the 'cracking voice' (Sonogram: E. Tretzel, in Glutz & Bauer 12/II).

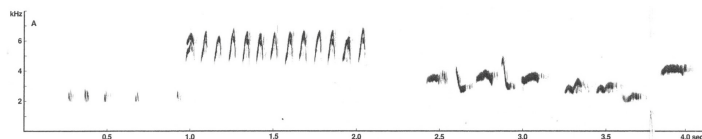


Fig. 3. Excited, 4 second aggressive song of male blackcap with imitation of alarm calls of a blackbird. (Sonogram: E. Tretzel, in Glutz & Bauer 12/II)

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The audible changes in song performance are obvious, but can be different and varied depending on the species. For instance, the ciril bunting sings its song incompletely, loudly, muted or quietly, depending on the degree of excitement (Groh 1975), while it is said of the rock bunting that: ‘after the end of a fight, particularly after driving out another male and returning to its own territory, the male sings aggressively harshly, then increasingly softly until reaching its normal song mode’ (Schuphan 1972). It is important to pay attention to the transition from the excited to the relaxed song. This change, which reflects the bird’s inner mood, will be discussed later.

What is unusual is that in most musically talented songbird species, when the territory is being defended – in other words when the biological purpose for which the song is supposed to have been evolved is actually happening – paradoxically the territorial song is musically diminished. From a musical point of view it descends to the lower level of territorial singing. The stimulus-response arises from which the songbirds on the higher singing level have freed themselves. The full song only unfolds again in its whole charm when the function of defence is no longer present. It is certainly not difficult to observe how quickly songbirds usually return to the level of relaxed motif singing.

If, during the course of evolution, the sometimes highly musical sound figures had developed primarily for the purpose of territorial defence, then the whole diversity of singing ability would have to emerge precisely at the point when the current biological necessity of territorial defence occurs. But this is not what happens. On the contrary: as soon as two neighbouring males approach the border of the territory singing at full volume, their song loses its diversity and beauty of sound. If the increase in autonomy is responsible for the fullness of song, then it is not surprising to find clearly noticeable differences in the acoustic qualities in different stages of arousal of the male birds. Every bird watcher can notice how differently the songs develop depending on whether a male bird produces them in an excited state or in a relaxed atmosphere.

Konrad Lorenz pointed out this phenomenon over 70 years ago. He confessed that birdsong repeatedly prompted him to the deepest philosophical contemplation and wonder. Of birdsong he wrote:

We are well aware that it performs a species-preserving service through territorial demarcation, attracting the female, intimidation of rivals. However, we also know that birdsong reaches its highest perfection, its richest differentiation when these functions are actually missing. A bluethroat, a shama thrush, a blackbird sing their most skilful and to our ear most beautiful, objectively their most complexly constructed songs when they *compose* their song in a quite ordinary state of excitement. When a song becomes functional, when the bird sings to an opponent or displays in front of the female, then all the finer details are lost. All that is to be heard are uniform repetitions of the loudest phrases and, in the case of mimicking species such as the bluethroat, the most beautiful imitative phrases disappear completely and the characteristic but unattractive rasping innate part of the song becomes dominant. It has always really shocked me to realise that a singing bird attains its top artistic performance in exactly the same biological situation and in the same prevailing mood as the human being, that is, when in a certain balanced situation, removed from the trials of life as it were, it produces its song in a purely playful manner (Lorenz 1935).

example, while males in an irritated and aggressive mood often produce significantly shortened phrases (Glutz & Bauer 13/II). The voice can also crack during singing, as is familiar with the cuckoo. Even though this species is not one of the songbirds, its ascending and accelerating three note phrases nevertheless demonstrate its excitement very clearly.

The sonograms (Fig. 1) show the full territorial song phrases of the golden oriole in A – B. Excited phrases often increase in volume: they exhibit higher modulated elements, especially at the start (C – H), but can subsequently be very similar to the normal song (E, F, G) or sound like a *stammer* (C) or resound in partial phrases (D, H) which are clearly separated from one another (Glutz & Bauer 13/II).

The willow warbler shows similar changes in its call, the excited phrases generally becoming increasingly louder with shorter intervals between the phrases. The impartial scientific explanation, that a bird in such a situation uses double phrases, gives no feeling for the bird's degree of inner excitement.

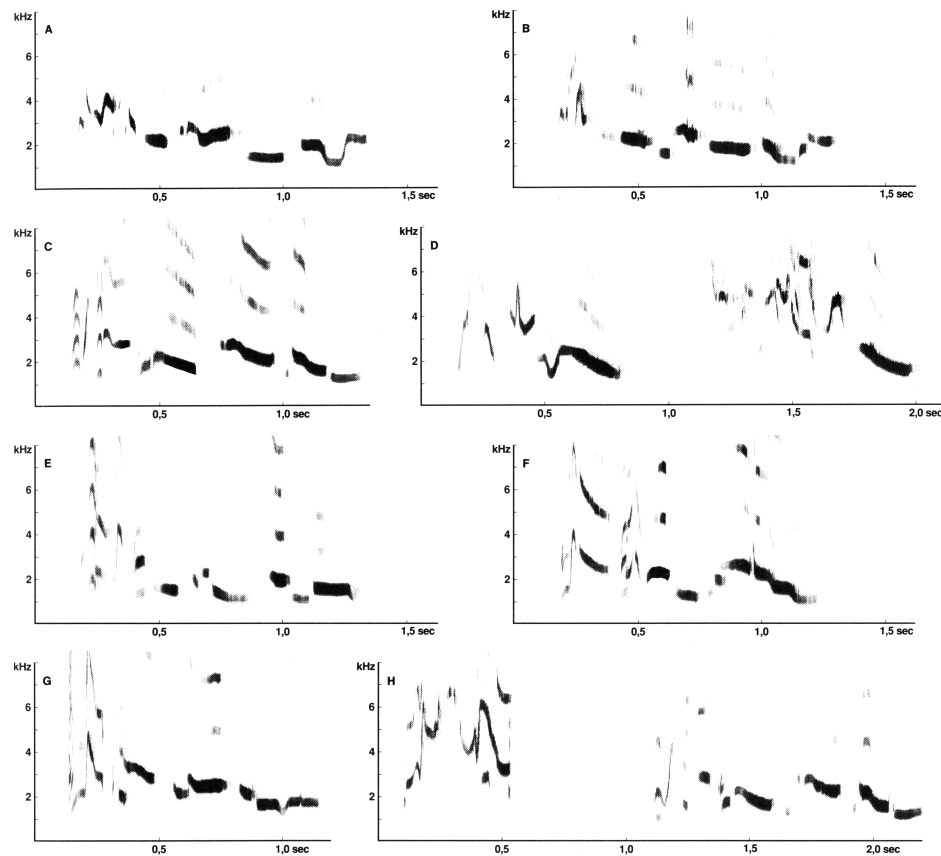


Fig. 1. (A and B) Typical motif song of the golden oriole and (C to H) various excited phrases. (Sonogram: E. Tretzel, in Glutz & Bauer 13/II)

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We therefore not only have a connection between singing and territorial behaviour, but also a close relationship between the quality of the song and the territorial behaviour, with musical ability generally being correlated with the territoriality of the bird species concerned.

It could almost be said that a talented songbird, irrespective of when and where it sings, behaves in a territorial manner such as, for example, a nightingale singing in its wintering areas. Likewise, most talented singers amongst the songbirds also display territorial behaviour if they sing during the return migration, while some songbirds, which sing throughout the year are territorial all year round as a rule. Insight into why the blue rock thrush from southern Europe and the native robin are almost always found alone can also be gained from a musical standpoint: the females of both these European bird species, in contrast to other songbirds, have developed a full song and therefore lay claim to their own acoustic territory almost all year round (with the exception of the breeding and moulting periods), defending this even against their own males!

Excited conflict song

From a musical point of view, which should play a central role in the behavioural biology of songbirds, I believe it necessary to make a distinction in the territorial song and to recognise three different levels.

In contrast to the full song, which I call the 'relaxed motif song', I should like to call the lower level of territorial song 'excited conflict song'. This type of song is also known as the *aggressive* or *excited song* in ornithology.

The excited conflict song does not constitute a completely different type of song but is territorial song which undergoes musical changes, mostly a reduction, due to the excited state of the singer. For example, if an intruding male songbird is vocally attacked by the owner, then even someone with little musical training will soon notice the significant, mostly discordant changes in the song of both the opponents. The excited conflict song can always be heard when territorial conflicts arise, in other words when one territorial neighbour sings too close to the territory boundary or even inside another territory. The song phrases in the excited conflict song are aggressive and harder, often more uniform and louder than in the relaxed motif song because the song, in accordance with the lower level, is more strongly governed by the pressures of territorial defence.

The phrases are very often shortened, as can be heard in the case of the golden oriole, wood warbler, willow warbler, collared flycatcher, grasshopper warbler and other songbird species. For species which sing only short phrases, any further shortening is almost impossible. But changes in the song can be detected here as well.

In aggressive territorial song, great tits and marsh tits reduce their diverse variations to only a few distinctive motifs and competing chiffchaffs begin to sing irregularly and the phrases are generally performed faster and more loudly. In rare instances excited phrases can be sung more quietly. For instance, the excited song of the nightingale sounds quiet and compressed, while the song of the dunnoek becomes increasingly shorter, quieter and more rushed the closer the territorial neighbours approach (Glutz & Bauer 11/I). Undisturbed male golden orioles singing cheerfully often vary the sequence of phrases, for

territorial behaviour in descending sequence. This clearly shows that with decreasing musical song quality territorial behaviour also declines.

This rule applies to most European songbird species.⁴

As soon as we consider the interspecific behaviour of thrushes, a ranking (C) results which corresponds more to the size and strength of the individual species: 'In the dominance sequence of mistle thrush, fieldfare, blackbird, ring ouzel and redwing, the song thrush occupies the bottom position. Mistle thrushes and fieldfares do not attack one another; redwings know to get out of the way of blackbirds more than of song thrushes which themselves are more often attacked by blackbirds' (Davies & Snow 1965).

The relationships between song and territory size in northern species of thrush have been known for a long time. While the social fieldfare only displays the rudiments of a song, the blackbird, song thrush and mistle thrush have large territories and well developed songs. The redwing occupies an intermediate position in both these respects (Glutz 11/II).

It should be stressed that, despite the fieldfare's ability to defend itself – leading the dominance sequence with the mistle thrush as it does – its territorial behaviour towards members of the same species is only weakly developed. However, this is in line with the poor singing ability and shows how closely territorial behaviour and musical development are linked. These thrush species even show significant differences in their migration behaviour (D). Despite their abundance, song thrushes and blackbirds migrate largely alone or in small loose groups and are also more frequent nocturnal migrants than the other thrush species described. Being singing soloists, as it were, they do not abandon their autonomous position even during migration when the majority of birds join up sociably and combine into flocks (Streffler 2005).

Ring ouzels usually also occur singly during migration (Busche 1993). The formation of larger flocks is primarily found in species with a lower level of intraspecific aggression, so it is not a matter of chance that mistle thrushes, but above all redwings and fieldfares, form larger groups during migration (Gatter 2000). The two last-named species frequently even form mixed groups. Similar relationships between singing ability and territorial behaviour have been demonstrated within most genera of Central European songbirds (Streffler 2003).

The barriers at territorial boundaries have much less to do with competition for food than previously assumed: they are primarily of a musical nature. This is connected to the fact that talented songbirds are not so much defending a food territory as an acoustic territory. This proves to be a significant aspect of autonomy.⁵

⁴ I should like to make a metaphorical comparison with the performance of a choral work of music: the choir members sing standing close together whilst the soloists step forward and occupy a larger acoustic space due to their more highly trained voices. Likewise songbird species, which are talented singers, lay claim to a correspondingly larger acoustic territory in comparison with simple singers. Naturally, nesting place and food availability play an important role in a bird's life: however, in relation to good singers, attention is always focussed on defence of the breeding and feeding territory in a one-sided way.

⁵ Friedrich A. Kipp (1908-1997) is the first ornithologist to my knowledge who adopted the concept of the acoustic territory and to whom I am indebted for many suggestions in this respect.

An outline for a biology of freedom using songbirds as an example – concerning the differentiation of the territorial song¹

Walther Streffer

Everything perfect in its kind has to transcend its own kind,
it must become something different and incomparable.

In some notes the nightingale is still a bird;
then it rises above its class and seems to suggest to every winged creature
what singing is truly like.

(J. W. v. Goethe, *Elective Affinities*, bk. 2, ch. 9)

In the above saying Goethe is not describing a law as to how species evolve or how one species is distinguished from another, but is pointing to the development process of species, how a species can rise above itself, *must surpass itself*. Using the musical image of the nightingale he provides us with a wisdom-filled approach to the study of evolution in poetic form.

Nowadays the purpose of birdsong is considered to be explained biologically. According to this, the primary purpose of song is to mark out and defend a territory, to keep males of the same species at a distance and to attract females. There appears to be almost no need for the aspect of autonomy in birdsong. In addition, two 'ornithological rules' make access to this field difficult.

After reducing birdsong to the function of territorial defence, it was later concluded that every bird which vocally demarcates and defends its territory, sings. From a biological point of view it is nowadays considered beyond question to apply the term song only to songbirds (Thielcke 1970)². The second rule is closely connected to the first, being that the study of birdcalls from a musical viewpoint is considered unscientific in ornithology and at best enjoys a certain entertainment value as *scientia amabilis*.

Whether it is reasonable to describe the noisy voice of a pheasant or the dull foghorn-like calling of a bittern as song – to the extent that these are used for territorial marking – can be left open. By reducing the differences in vocal quality to the same level, however, the musical consideration of birdsong was pushed further into the background. The consequences of this are all the greater as the subject of freedom in the territorial singing of songbirds has in general received little attention up until now.

There is therefore no sensible reason to submit to these rules. On the contrary, I believe it to be imperative to establish a musical ranking amongst songbirds. This requires a musical differentiation of the territorial song and a comparative study of singers of varying ability in relation to their territorial and social behaviour. This is entirely justified

¹ This article is part of a more comprehensive study on the topic of 'The increase in autonomy in birdsong' which is published in book form under the title *Klangsphären. Motive der Autonomie im Gesang der Vögel*. (Spheres of sound. Motifs of Autonomy in the Song of Birds). Verlag Freies Geistesleben, Stuttgart 2009.

² A consequence which was probably due to the ability to carry out exact evaluations of song using sonography.

biologically, as the song usually also constitutes an important species characteristic.

Acoustic territory

Territorial demarcation amongst songbirds generally takes place from members of the same species, whilst the habitats of different species can penetrate or overlap each other. In native species of thrushes, however, interspecific territorial disputes can also occur. Naturally the older males who have arrived first in the nesting area assert their claim to particularly favourable areas. However, it is always noticeable that representatives of species which are talented singers usually lay claim to a larger area and defend this more vigorously than do those with a simple song. These latter usually show a clear tendency for tolerance and sociability. Some of them make no claim to a territory at all (for example house martin, bearded tit, house sparrow) and merely maintain a certain minimum separation (individual distance). This points to the connection between singing ability and territoriality, where it should be noted that conflicts at the territorial boundaries are solved for the greater part by means of song.

Moreover, songbird species display a form of behaviour which so far has been more or less ignored in relation to song quality: numerous talented songbirds which are correspondingly territorial often spend time in other territories even during the nesting period. Male chaffinches³ regularly use neighbouring territories for feeding, for example, and are tolerated by the territory owner as long as they do not sing (Hanski & Haila 1988).

It has been shown that chaffinches forage outside their own territory for more than a third of the day (Maciejok *et al.* 1995). You could propose a rule for talented songbirds: no singing in other territories on any account! This shows that musical development is connected with territorial behaviour because development of the territorial song cannot be explained by functional aims alone. This raises the question as to what relationship musical ability has to territorial defence.

The phenomenon becomes clearer if song and behaviour are compared within one bird genus. I wish to demonstrate this using the most common European thrushes as an example.

The song of the blackbird appears perfect in its complexity and richness of sound. The song thrush also belongs to our most talented singers. Its song can be extraordinarily varied, however the compositional aspect is less developed. The phrases of the mistle thrush are also rich but shorter and do not possess the wealth of variety of the aforementioned species: the song is somewhat more uniform. The ring ouzel has a simple song similar to the blackbird, with grating sounds and motifs which are akin to the song thrush, though less melodious. The short warbling phrases of the redwing, a characteristic bird of the Northern European coniferous forests, and a regular passage migrant in Germany, carry over long distances and usually end in a rasping strident chatter. ‘The start of the phrase in each individual remains more or less constant during the entire nesting period. Only a few males occasionally produce a second opening motif’ (Espmark 1981). The song of the fieldfare is little developed. Its commonly heard call sequence is a harsh

³ For Latin names of species mentioned, please see the comprehensive list at the end of this article.

‘tchack, tchack, tchack’. These sounds are reminiscent of the call of young thrushes: melodious notes are rare. The actual song is a compressed sequence of high notes produced during flight.

Now let us consider the interspecific behaviour of these thrushes as we have done with the songs.

Blackbirds are distinctly territorial, song thrushes somewhat less so. Both species defend their territories vigorously. Blackbird territories in towns can be smaller than those in woodland. Foraging blackbirds in city parks can frequently be found very close together (2 – 5 m), but singing males would never be found in such proximity.

The territories of song thrushes overlap more than the exclusive territories of blackbirds (Davies & Snow 1965). Song thrushes occasionally visit other territories or fly through them and as long as they do not sing there are rarely any conflicts. Mistle thrushes are also territorial and usually have fairly large territories. However, members of the same species are tolerated in the territory more often than in the case of song thrushes. Now and again several pairs nest close together. In Denmark more than 30% of mistle thrushes even nested colonially, often at distances of only a few metres (Glutz & Bauer 11/II). Even the ring ouzel is considered to be territorial. However, it does not defend a territory with fixed boundaries and other members of the same species can fly over the nesting area or use it for feeding. Loose assemblages of several pairs in a small area are relatively common. The redwing only defends an area close to the nest as a rule. In some areas considerable concentrations of nesting redwings can occur along with colonies of fieldfares (Glutz & Bauer 11/II). When searching for food, which takes place partly in other territories, members of the same species can be attacked. A ‘redwing which has entered another’s territory generally withdraws if the territory owner approaches singing. Fights are uncommon in the area of the nest’ (Tyrvaenen 1969). While mistle thrushes display the beginnings of local aggregations of nesting pairs and this occurs more or less regularly in ring ouzels, the phenomenon is further developed in the case of fieldfares to the point where closed colonies are formed (Glutz & Bauer 11/II). The last named can also nest singly, but colonial nesting is the norm.

A. Musical ranking	B. Territorial behaviour	C. Dominance behaviour	D. Variation in autonomy of migration behaviour
blackbird	blackbird	mistle thrush	blackbird
song thrush	song thrush	fieldfare	song thrush
mistle thrush	mistle thrush	blackbird	ring ouzel
ring ouzel	ring ouzel	ring ouzel	mistle thrush
redwing	redwing	redwing	redwing
fieldfare	fieldfare	song thrush	fieldfare

Table 1. The musical ability of European species of thrushes in comparison with territorial and migration behaviour (decreasing from the top downwards).

The musical ranking (A) in Table 1 shows the varying singing ability of a number of thrush species. The order of territorial behaviour (B) reflects the differing intraspecific