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The Colour of Birds: Hans Duncker, Pioneer Bird Geneticist*

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Summary

Hans Duncker (1881–1961) is among the first avian geneticists, but remains poorly known. He trained as a biologist, completing his PhD at the University of Göttingen in 1905 and then became a high-school teacher in Bremen where he remained for the rest of his life. In 1921 he met Karl Reich (1885–1970) who was the first person to make recordings of bird song and was well-known for creating a strain of canaries that sang Nightingale (*Luscinia megarhynchos*) songs. Duncker provided a novel Darwinian/Mendelian explanation for how Reich's canaries acquired their songs. In the early 1920s, a time during which the field of genetics was rapidly developing in the USA and Britain, but not Germany, Duncker and Reich conducted large-scale breeding experiments to establish the pattern of inheritance of variegation and other traits in canaries. In 1925 Duncker met Generalkonsul Carl Cremer (1858–1938), who provided the financial backing for a massive and comprehensive study of inheritance of colour patterns in Budgerigars (*Melopsittacus undulates*). At the same time Duncker also initiated a project to create a red canary by hybridising canaries with the Red Siskin (*Carduelis cucullata*). Duncker recognized that bird-keepers had much to offer professional scientists (and vice versa) and was keen to bridge the gap between them and to this end in 1927 began his own journal "Vögel ferner Länder". His research on the genetics of the canary and budgerigar resulted in the publication of a large number of papers in ornithological journals and magazines and several books. Duncker was a eugenicist, and when the National Socialists came to power in 1933 he supported and promoted the notion of positive eugenics. He was later (in 1990) condemned for these activities and for having been a Nazi, but we show that Duncker joined the Party only reluctantly. After WWII Duncker restored and re-catalogued the bird collections at the Übersee-Museum in Bremen. We discuss the possible reasons why Duncker's research, much of it very innovative, has been largely ignored internationally.

Keywords: Hans Duncker, Karl Reich, Carl Cremer, ornithology, avian genetics, canary, budgerigar, red canary, budgerigar mating expectations.

Zusammenfassung

Die Farbe der Vögel: Hans Duncker, ein Pionier der Vogelgenetik

Heute ist weitgehend vergessen, dass Hans Duncker (1881–1961) einer der ersten Genetiker in der Ornithologie war. Aufgewachsen in Ballenstedt am Harz studierte er in Göttin-

* *Dedicated to Rolf Schlenker on the occasion of his 65th birthday*

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gen Naturwissenschaften und promovierte bei Ernst Ehlers über ein morphologisches Thema. Ornithologisch wurde er durch seine Übersichtsarbeit „Über den Wanderzug der Vögel" (1905) bekannt, die den Petsche-Labarre-Preis erhielt. Nach der Promotion fand er eine Anstellung als Lehrer für Mathematik und naturwissenschaftliche Fächer in Bremen, wo er bis kurz vor seinem Tod lebte.

1921 begann seine Zusammenarbeit mit dem Kanarienzüchter Karl Reich (1885–1970), der als erster Vogelgesang auf Platte aufgenommen und einen Kanarienstamm gezüchtet hatte, der perfekt Nachtigallen imitierte. Duncker bot eine darwinistische Erklärung für dieses Phänomen, indem er klarstellte, dass Reich nicht Kanarien mit Genen für Nachtigallengesang, sondern lediglich Vögel mit besserem Lernvermögen herausgezüchtet hatte (Duncker 1922a). Zu Anfang der 1920er Jahre, als die experimentelle Genetik noch weitgehend Neuland war, begannen Duncker und Reich mit Kreuzungsversuchen in großem Stil, um die Erblichkeit von Gefiederfarben und -strukturen, wie z. B. der Haubenbildung, zu erforschen. Ab 1925 kooperierte Duncker auch mit Carl Cremer (1858–1938), einem wohlhabenden Bremer Kaufmann. Cremer ermöglichte die Finanzierung und stellte seine Volierenanlagen für die Untersuchungen der Vererbung von Farbmustern bei Kanarien und insbesondere Wellensittichen zur Verfügung. Durch die Kreuzung mit dem Kapuzenzeisig (*Carduelis cucullatus*) wollte Duncker einen roten Kanarienstamm erzeugen. Dies war deshalb so schwierig, da erst nach mehreren Generationen komplizierter Kreuzungskombinationen fertile Nachkommen möglich sind. Letztlich gelang es, das Gen für rote Farbe vom Kapuzenzeisig auf Kanarien zu übertragen. Dies ist das erste transgene Experiment in der Ornithologie. Wirklich rote Kanarienvögel wurden jedoch erst Anfang der 1950er Jahre in England erzeugt (Gill 1955).

Mit seinen großangelegten Kreuzungsexperimenten hat Duncker die Praxis der Vogelhaltung und die theoretische Naturwissenschaft erfolgreich miteinander verknüpft. Er hatte begriffen, dass Vogelhalter und Wissenschaftler gleichermaßen voneinander profitieren können. Ab 1927 gab er eine eigene Zeitschrift, „Vögel ferner Länder" heraus, die rasch zur Verbandszeitschrift der AZ (Austauschzentrale der Exotenliebhaber und -züchter) wurde. Der enorm produktive Duncker publizierte ca. 75 Arbeiten, die Mehrzahl über Kreuzungsexperimente und Vererbungsregeln bei Wellensittichen und Kanarien. Seine Vererbungstabellen für Wellensittiche sind heute noch in Gebrauch (Elliott & Brooks 1999).

Als engagierter Eugeniker befürwortete Duncker die Zwangssterilisation von Behinderten (Meyer & Duncker 1933), was ihm später vorgeworfen wurde (Walter 1990). Unterlagen und Entnazifizierungsprotokolle im Bremer Staatsarchiv zeigen jedoch, dass Duncker wegen fehlender Loyalität mehrfach in Schwierigkeiten geriet und erst 1940 unter Druck Parteimitglied wurde.

Nach dem 2. Weltkrieg reorganisierte Duncker die Vogelsammlung des Bremer Überseemuseums. Mögliche Gründe für die fehlende internationale Anerkennung Dunckers sind in einer Fehlinterpretation seiner Experimente (Crew & Lamy 1934, 1935) und in der nach dem 1. Weltkrieg einsetzenden Isolation der deutschen Wissenschaft zu suchen.

I. Introduction: Birth to 1918

Hans Julius Duncker was born in Ballenstedt in the eastern foothills of the Harz Mountains on 26 May 1881, the second of three sons. His father Dr. Ernst Eduard Heinrich Duncker (born 7 September 1848) was a high ranking judge and businessman, whom Hans later described as a dynamic and out-going person. His mother was Marigrita (Marie Elisabeth)

Duncker, (formerly Uhde, born 24 August 1847 in Valparaiso, South America). It was his grandfather who roused Duncker's interest in natural history and birds in particular, for this was a period when bird-keeping was especially popular in Germany and elsewhere in Europe (Haffer 2001). The family lived in Dessau, which is where Duncker went to school, attending the Herzogliches Friedrichs-Gymnasium (Ducal Friedrich's Secondary School) until 1900. Hans did well at school, especially in maths, physics, sports and singing, but he found French and English language less easy.

In the autumn of 1900 at the age of nineteen Duncker went to the university at Göttingen to study Mathematics and Natural Sciences, including botany and physics. Between Easter 1901 and 1902 he made a year-long visit to the University of Leipzig during which he decided that zoology would be his main subject. On returning to Göttingen he found a mentor in the grandsigneur of morphology, Ernst Ehlers (1835–1925), a close friend of Ernst Haeckel, Germany's greatest popularizer – some would now say vulgarizer – of Darwin's ideas (Stein 1988). One of Haeckel's several claims to fame was plotting the branching paths of common descent-evolutionary trees, and although Ehlers was much less obsessed with Darwin's ideas, he was nonetheless influenced by Haeckel (Nyhart 1995), and his comparative morphology had its roots in evolution. In the early 1900s comparative morphology was one of the main areas of zoological research, and Duncker's PhD project which Ehlers supervised involved comparing the internal structure of two genera of marine worms. It was undoubtedly through Ehlers and indirectly through Haeckel whose popular works on evolution were best-sellers in Germany during the first decade of the twentieth century (Gould 1977, Stein 1988), that Duncker became a firm Darwinian.

Duncker was a model student and an active member of two student bodies in Göttingen, 'Germania', the National Christian student fraternity, and 'Schwartzburgbund' another Christian society which approved of chastity and disapproved of duelling, then popular among Göttingen's male students. Interestingly, any Christian beliefs that Duncker may have held were not incompatible with his evolutionary views.

Before completing his PhD thesis Duncker was persuaded in 1904 by a student friend, Friedrich Voss, to give a talk in the university on bird migration. This was probably Duncker's first public performance, and it was immediately clear that he had a natural talent for lecturing; the talk was an enormous success. Duncker went on to make a more detailed study of Eurasian bird migration routes, and in 1905 published a paper, 'Über den Wanderzug der Vögel' on the topic. On 15 February 1905 he had the oral examination for his PhD thesis which was entitled "Über die Homologie von Cirrus und Elytron bei den Aphroditiden. Ein Beitrag zur Morphologie der Aphroditiden" (About the homology of Cirrus and elytron among the Aphroditids. A contribution to the morphology of the Aphroditids: Duncker 1905a) and graduated with 'magna cum laude' (second best grade) in Zoology, Botany and Mathematics. One month later in November 1905 'The Migration Paths of Birds', which Duncker dedicated to 'his greatly admired teacher Ernst Ehlers on the occasion of his 70th birthday', was awarded a prize by the Labarre foundation (Faculty for Philosophy at Göttingen University) and published by Gustav Fischer, Jena as a book (Duncker 1905b). Duncker then spent a year training as a high-school teacher (of zoology, botany, mathematics and physics), graduating in May 1906, when he moved to Bremen to take a position as an auxillary science teacher at The Old Gymnasium, a classical state school. He had hardly started as as teacher when he had to undertake one year of military service. Within a week of completing his military obligations, he married Elsa Zwernsmann (born 4 June 1884 in Dessau) on 5 October 1907 in Dessau. Duncker now switched schools, moving briefly to the Realschule am Doventor. In August 1908 Hans and Elsa's first child Marigrita, was born – named after

Fig. 1. Hans Duncker aged 32 in 1913 (photograph courtesy of Rolf Gramatzki).
Abb. 1. Hans Duncker im Alter von 32 Jahren im Jahr 1913.

Duncker's mother. In 1909 Duncker changed schools again, moving to the Realgymnasium, an imposing boy's school on Hermann-Böse-Strasse where he remained until the end of his teaching career[1]. Between 1907–1911 the Dunckers lived at Moselstr. 38; and from 1911–1914 at Rheinstr. 6. In 1912, at the age of 31 (Fig. 1), Duncker joined the German Ornithological Society. He conducted a study of the biogeography of buntings in which he assessed whether current and historic geographic distributions could reflect their phylogenetic relationships (Duncker 1912). In 1914 Duncker published a series of school biology text books for teachers, co-authored with a theologian Friedrich Baade (Baade & Duncker 1914). On 24 April 1913 Hans and Elsa had a son, Hans-Eberhard, but he died less than a year later on 27 January 1914. In 1915 the Dunckers moved to Wernigeroderstr. 22, where they remained until 1932. Their second daughter Lotti Hildegard was born on 28 August 1915.

During World War I Duncker served as an officer, first at the eastern front in Hungary, Galicia, and Russia and then between 1915–1918 at the western front in France. He was awarded several medals and badges, including iron crosses II and I, and was wounded once.

II. Duncker and Karl Reich

Duncker met Ernst Karl Reich (1885–1970), famous for his sound recordings of birds and especially for his nightingale-canaries in August 1921 when Duncker was 40 and Reich 36 (Fig. 2). Reich, who ran a family hardware business on Fedelhörenstrasse in Bremen and lived at Am Wall, had been fascinated by birds and had bred roller canaries ever since he was a boy. In 1911 he had bred one particular male with an outstanding voice with a deep, rich song similar to that of that of a Nightingale (*Luscinia megarhynchos*). It was this bird, which Reich named Bär (Bear) that changed his life and inspired him to breed a strain of roller canaries that sang the nightingale's song. In 1912 Reich performed a back-cross, mating Bär to his mother and then provided their offspring with a singing nightingale 'tutor'. It was (and still is) standard procedure to provide young roller canaries with a song tutor during the sensitive song-learning phase (Speicher 1976), but normally the tutor was another canary. In fact, Reich had screened twenty diffe-

[1] This school was known as the 'Realgynasium' from 1905–1937, but from 1937–1938 was the 'Oberschule für Jungen an der Kaiser Friedrich-Strasse' and from 1938–1945 as the 'Lettow-Vorbeck Schule', and since 1957 as 'Gymnasium at the Hermann-Böse-Strasse'.

rent song birds as possible tutors for his young canaries in the previous years (Von Der Grenze 1938), and had decided, as had many previous bird-song enthusiasts before him, that the nightingale had the best song. One of the problems Reich encountered in using the nightingale as a tutor for his young canaries was that they had only a short singing season, and ceased singing before the young canaries had fully learned the song. He solved this by adjusting the timing of the nightingale's moult and hence its endogenous rhythm, following a method described much earlier (Anon. 1772). Reich also used his own recordings of nightingales to train his canaries, although he preferred using real birds (Von Der Grenze 1938).

By the time Reich and Duncker met, Reich's nightingale-canaries were well established and within canary circles at least well known, since song canaries were still very popular at this time (Gasser 2001). Reich believed that his canaries had inherited their ability to sing a nightingale song because, as he told Duncker, after a few generations he no longer had to use a nightingale tutor, and the quality of the birds' song continued to improve with each successive cohort. The tutors of the young canaries now were adult male nightingale-canaries singing nightingale song. Reich believed that his canaries had acquired the ability to sing the nightingale song by a Lamarckian form of inheritance: the inheritance of an acquired characteristic. It was this that piqued Hans Duncker's imagination. Duncker was a firm believer in Darwin's natural selection, and suspected that Reich's Lamarckian interpretation was probably wrong (Duncker 1922a). Duncker was unusual for most ornithologists at this period were Lamarckians and ideas based on natural selection were often dismissed out of hand (see for e.g. Allen 1893a, b, Keeler 1893).

The period between 1910 and 1930 was one during which the study of genetics blossomed (Provine 1971). Following the rediscovery of Mendel's work in 1900 there had been a bitter and largely futile debate between the Mendelians, led by the British scientist William Bateson, who believed that selection operated on discontinuous traits, and the biometricians (led by the British statistician Karl Pearson), who believed that natural selection operated on the almost imperceptile differences between individuals (see Provine 1971). By 1915 it was clear to both sides that selection operated in exactly the same way on both continuous and discontinuous traits. Meanwhile in the USA Thomas Hunt Morgan had focussed on the mechanisms of heredity, using *Drosophila* as his study organism. Morgan had started by trying to create mutations in various ways, including X-rays, but it was a white-eyed fly in his regular stock (of red-eyed flies), that launched the study of inheritance in 1910. Subsequently Morgan and his co-workers discovered and established the mode of inheritance of a large number of mutations among their flies (Morgan et al. 1915).

Fig. 2. Hans Duncker (left) and Karl Reich in the late 1920s (from Von der Grenze 1938).
Abb. 2. Hans Duncker (links) und Karl Reich in den späten 1920ern.

Duncker's explanation for how Reich's nightingale-canaries acquired their song was extremely novel. He concluded that Reich had

not selected for those birds with the genes for nightingale song, as Reich supposed, but instead had unwittingly selected for those birds that could **learn** the nightingale song from their nightingale-canary tutors. A subtle, but important difference, and one that was entirely consistent with a Darwinian view of evolution. Duncker was justifiably pleased with his igenious (and almost certainly correct) explanation, and he wrote a succession of papers in a range of different magazines and scientific journals describing Reich's birds (Duncker 1922a–e; see also Von Der Grenze 1938). Unfortunately, Duncker's clever idea seems to have been completely overlooked by subsequent researchers: we have never seen Duncker's papers on Reich's canaries referred to and Peter Marler, one of the foremost bird-song specialists, admitted (pers. comm.) to not being aware of Duncker's papers on this topic. Similarly, Reich's pioneering experiment of training birds to sing simply by playing them sound recordings was virtually ignored. Twenty years later when the study of song-learning in birds was becoming a major part of the rapidly developing field of animal behaviour, there is a single, tangential and somewhat deprecating comment about Reich's work in "The Modern Synthesis" (Huxley 1942). In a footnote on p305 Huxley says that Ernst Mayr had told him about a study in which canaries had been taught to sing using recordings of nightingale song 'carried out by a fancier named Reich, but complete proof was not supplied'.

Once Duncker had become interested in Reich's canaries he began to ask other questions relating to their genetics, including the mode of inheritance of traits like plumage colour and crest. In 1923, using Reich's facilities, they performed a large number of experimental pairings to establish the basis for the inheritance of colour. They found that two yellow birds invariably produced yellow offspring, two green birds produced green offspring, but crossing a yellow and a green bird or two variegated birds produced variegated offspring. In other words green plumage (the colour of the wild canary) is dominant over yellow (the domesticated form), but not in a straightforward way and Duncker concluded that at least three genes were involved in the controlling of the canary's colour. Two previous researchers had looked at the inheritance of colour in canaries. In 1908 Florence Durham (sister-in-law and research assistant to William Bateson) established the basis for the inheritance of the cinnamon mutation, which turned out to be sex linked (Durham & Marryat 1908). In the USA Charles Davenport (1908) had looked at the inheritance of variegation, and being a firm Mendelian believed the transition from green to yellow had occurred over just a few generations through the selection of sports. Davenport's study was riddled with errors and was heavily criticised (Galloway 1909, 1910, Heron 1910, Duncker 1928c).

The wild canary is predominantly green and grey in colour with a yellowish head, breast and rump. The familiar yellow domesticated canary was produced during the 17th century following approximately one hundred years of selective breeding to eliminate all traces of melanin (Birkhead, Schulze-Hagen and Kinzelbach, in press.; for a history of the canary see Parsons 1987). It was, as Duncker showed, precisely because colour in the canary is a polygenic trait that it had taken so long to produce a yellow canary by artificial selection. Duncker published the results of these canary experiments in a number of different places, including bird-keeping magazines, like "Die Gefiederte Welt" (Duncker 1924c), but also in the scientific literature, including "Journal für Ornithologie" (Duncker 1924e) because he was keen to bridge the gap between the amateur bird-breeder and the scientist and make his scientific discoveries available to bird breeders. As we will see, to a large extent Duncker was successful, in part because bird-keeping continued to be a respectable hobby in Germany long after it ceased to be respectable in Britain, and German scientists and ornithologists in particular were much more sympathetic to bird-keeping than were ornithologists in

Britain, and indeed continue to be so (Anon. 1978, 1987, Löhrl 1989, Samstag 1988).

III. Duncker and Carl Cremer

Duncker was introduced to Generalkonsul Carl Hubert Cremer (1858–1938) in the autumn of 1925 by Reich. Cremer (Fig. 3) was a wealthy businessman, specialising in foreign trade (Anon. 1928, Duncker 1927e, 1938b, Gebhardt 1964, Ringleben 1955). He was a member of the Natural History Society of Bremen which ran the museum, but this society also supported bird-keeping. Cremer was president of the AZ (Austausch-Zentrale der Exotenliebhaber und Züchter), the German Society of bird keepers founded in August 1920 (and which ran until about 1935). At his two Bremen homes, one in the city at Am Dobben and the other much larger property, Rosenau Villa at Vahr about three km from the centre of Bremen (and now built over) Cremer had a large number of aviaries. His main interest was in foreign birds and especially the different colour forms of the Budgerigar (*Melopsittacus undulatus*).

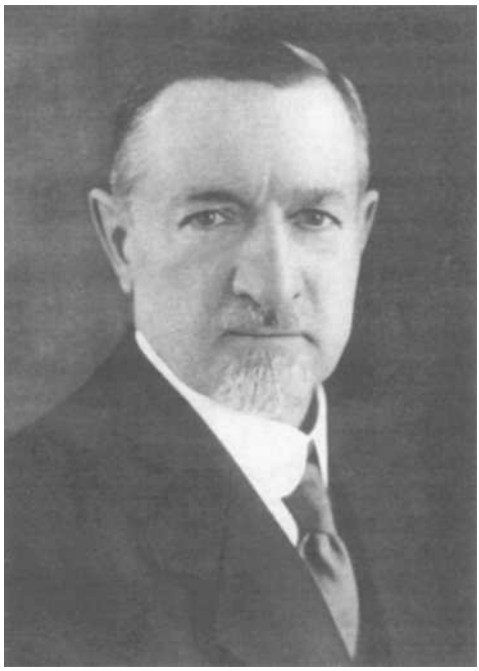


Fig. 3. General Consul Carl Hubert Cremer in the late 1920s/1930s (from Keidel 1960).
Abb. 3. Genralkonsul Carl Hubert Cremer in den späten 1920/1930er Jahren.

Budgerigars had been first introduced into Europe from Australia in 1840. The wild birds are green in colour and the first colour mutations appeared in captive stock; yellow in 1870 and blue in 1878 and others later (Vins 1993). But it was not until the 1920s that interest in budgerigar breeding in Europe really burgeoned, and Cremer was among the foremost enthusiasts. Being wealthy meant that he could buy any new mutations that appeared in other breeders' stock. It also meant that with extensive breeding facilities he was in a good position to establish these new mutations. Cremer was a larger than life character; he was a tall, imposing man with a great sense of humour and was a self-confessed womaniser. Despite Duncker's quieter, more conservative nature, they got on very well and within a short time had agreed to collaborate. Duncker persuaded Cremer that between them (and this included Reich) they could work out the genetic basis for all the budgerigar and canary mutations. There was also another project that Duncker wanted to undertake: to produce a red canary. Having Cremer's generous financial backing was equivalent to Duncker securing a substantial grant from a research council today – except that Duncker's studies of avian genetics were conducted entirely in his spare time while he was a school teacher. Their collaboration provided unique opportunities for Duncker and over the next few years projected him into the position of leading avian geneticist. However, while Duncker's name is still well-known among the budgerigar fancy (Vins 1993, Elliott & Brooks 1999), he remains almost unknown among ornithologists and avian geneticists.

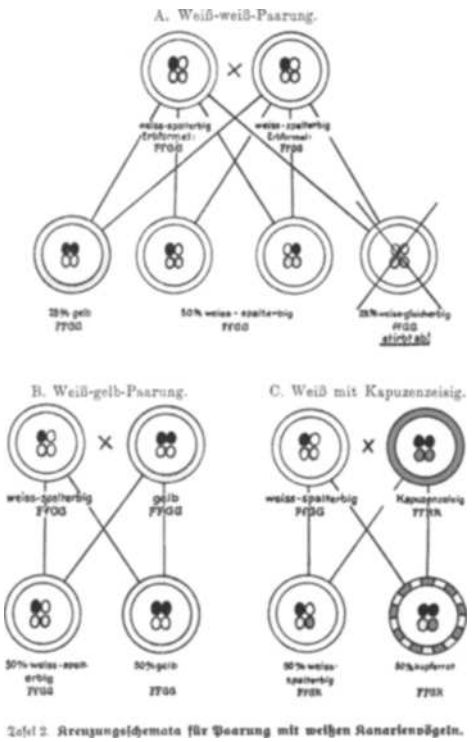
Duncker's idea of breeding a red canary was a bold one. This idea may not have originated

with him, but it was his knowledge of avian genetics that made the red canary a possibility. Duncker's ambition was to create what we would now call a transgenic or genetically engineered canary, taking the genes for red plumage from the Red Siskin (*Carduelis cucullata*) (also known as the Hooded Siskin), and 'placing' them in a canary. The Red Siskin, native to Venezuela, became known to science only in 1820 (Swainson 1820), and did not become a cage-bird in Europe until the early 1900s (Coats 1985, Collar et al. 1992). Before this however, it seems likely that the Spanish, who were enthusiastic bird-keepers, had kept them and transported them back to both the Canary Islands and Spain, where some of them hybridised with canaries (Coats 1985, Collar et al. 1992). Breeding interspecific hybrids between finches (usually European finches, such as the Goldfinch (*Carduelis carduelis*) and canaries had been popular ever since canaries were routinely bred in captivity (Stresemann 1923, Hervieux 1709), so it was not that surprising that the Spanish hybridised Red Siskins and canaries. These hybrids had attractive plumage and voice. Starting in the 1890s Red Siskins were imported into Europe in increasing numbers (Astley 1902 a, b). Today, the Red Siskin is extremely threatened in the wild as a direct result of this trade (Collar et al. 1992).

One of the first people in Britain to hybridise Red Siskin and canaries was Florence Durham sometime between 1908 and 1915 (Durham 1926). In Germany a fancier named Engels of Tilsit, East Prussia also bred some Red Siskin × Canary hybrids in 1912. He gave one of these, a male, to A. Dams of Königsberg who managed to back cross it to a female canary, and although several young were produced they all died. Dams then gave the original hybrid, which was obviously fertile, to Bruno Matern of Rastenburg in central East-Prussia. Matern was extraordinarily successful and over several breeding seasons succeeded in crossing this single hybrid with canaries to produce a dynasty of orange coloured birds (Dams 1926).

Duncker learnt of Matern's success and decided to try to breed a red canary himself. His original plan was to back-cross Red Siskin hybrids to ordinary yellow canaries, and select only the reddest offspring for continued backcrossing. Disappointingly for Duncker, he was unable to produce anything other than coppery coloured hybrids. Duncker's aim was to breed a genetically red canary, not one that relied on colour-feeding, which is what British fanciers had done previously and subsequently did routinely (Gill 1955). This was a frustrating project because the genes from the two parent species did not behave in the way Duncker expected. Initially, he crossed Red Siskins to yellow canary hens, but the offspring were merely orange. Assuming that the genes for producing red plumage from the Red Siskin interfered with those for producing yellow plumage in the canary, Duncker went back to the beginning and created new hybrids using dominant white canaries. These also failed to produce red offspring, and again Duncker assumed this was because the gene for yellow plumage (which is recessive in the dominant white canary) interfered with the production of red colouration (Fig. 4). Duncker then proposed that another white canary mutation, the recessive white (which apparently carried no genes for yellow plumage), would produce offspring of the required colour (see Duncker 1927a, 1931e, f, g, 1932c). Duncker gave up on the red canary project at this point and the crucial experimental pairings were conducted by a British canary breeder, A. K. Gill who was the vice-president of the British White Canary Club and one of only three people in the world (Duncker was another) to own recessive white canaries (Gill 1955). Gill was eventually instrumental in producing a red canary – albeit by a circuitous route (Birkhead 2003).

Soon after they met Cremer and Duncker founded the German Budgerigar Society in 1925. A year later the British budgerigar society was formed and the two groups kept in close contact. Duncker and Cremer's objective was to establish what colours would be produced



Tafel 2. Kreuzungsschemata für Paarung mit weißen Kanarienvögeln.

Fig. 4. Duncker's genetic schemes for predicting the outcome of particular pairings: (A) Two dominant white Canaries (showing the lethal homozygous); (B) a dominant white and a yellow Canary, and (C) a dominant white Canary and Red Siskin (Kapuzenzeisig). (From Duncker 1927a).

Abb. 4. Duncker's Schema zur Vererbung: (A) Zwei dominante weiße Kanarienvögel (mit letaler Homozygotie); (B) ein dominat weißer und ein gelber Kanarienvogel; (C) ein dominat weißer Kanarienvogel und ein Kapuzenzeisig (aus Duncker 1927a).

when two varieties of budgerigar were crossed: so-called mating expectations. There were twelve recognised varieties of budgerigars at this time and hence a potentially large number of different crosses to perform to establish the full range of mating expectations. However, Duncker was extraordinarily efficient and by establishing the genetic constitution of a subset of varieties he was able to predict the likely outcome of all other crosses. Luckily, many of the budgerigar colour mutations involved one or only a few genes, and the budgerigar project made rapid progress. Duncker published the results under his name, but usually with an acknowledgement that the work had been conducted in Cremer's aviaries. For the average budgerigar breeder what Duncker had done was to create order out of chaos, and once breeders knew what to expect from their different pairings the budgerigar fancy could start to develop particular varieties to their (arbitrary) exhibition standards (Vins 1993). Duncker's results were translated and transmitted around the world. The British Budgerigar Society honoured Duncker and Cremer by awarding them a special gold medal each in 1927; they couldn't attend the presentation at the Crystal Palace bird exhibition in London in 1928 because Duncker was ill with kidney trouble (for which he underwent extensive surgery), but they did attend the next National Exhibition in London in 1929 (Anon. 1929).

The late 1920s was an extraordinarily productive time for Duncker (see Appendix A for a list of Duncker's publications). He published relentlessly, in both the ornithological literature and in bird-keeping magazines. His papers were mainly about the inheritance of colour or other traits in birds, but he also made a detailed study of the colour of feathers based on their microscopic structure (Duncker 1927c, k), nest-building in weaver birds (Duncker 1927h), brood parasitism as an adaptation (Duncker 1930a) and the role of X-rays in creating mutations (Duncker 1930f). The idea of bringing together the professional and amateur bird cultures went even further and in 1927 Duncker began his own journal "Vögel ferner Länder". This became the official journal of the AZ. Prior to 1927 the AZ journal had been a thin and poorly produced magazine, but Duncker took it over and revitalised it.

In 1928 Duncker published his book "Genetik der Kanarienvögel" (Canary Genetics) and the following year "Kurzgefasste Vererbungslehre fur Kleinvögel-Züchter" (Concise Genetics for Breeders of Cage-birds) which he dedi-

cated to Reich and Cremer (Duncker 1928c, 1929e). Invitations to speak about his work at conferences around the world started to arrive and in 1930, accompanied by Cremer (who we suspect paid Duncker's way) he gave talks in Vienna, Tübingen and at the International Ornithological Congress in Amsterdam (see Duncker 1931c). Duncker was also invited to the 6th International Congress of Genetics in Ithaca, New York in 1932, at which he would have been able to meet T. H. Morgan who was president, but for some reason he did not accept.

Attempts to officially recognise and reward Duncker in Germany for his extraordinary success failed. In November 1930 Duncker's director at school, Herr Jentsch, asked whether Duncker might be given the title of professor, but this was rejected: because it 'contradicted paragraph 4 of article 109 of the constitution of the Reich'. The next month Alfred Kühn, Professor of zoology at Göttingen sent a petition to the Bremen Senate asking whether they would consider creating a position for Duncker as an independent researcher, but that too was turned down: 'Unfortunately there could hardly be a more difficult moment to create an independent research position for Dr Duncker or even substatially reduce his teaching duties. I certainly do not have to explain the general financial pressure on the Reich...' (see A Note on Sources).

Duncker's experimental bird breeding studies declined during the early 1930s and by 1935 had ceased altogether, apparently through a lack of funding.

IV. Duncker 1933–1945

In 1990 Hubert Walter published a paper highlighting Duncker's membership of the Nazi party and describing his leading role in the Unit of Racial Hygiene which existed at the Natural History Museum in Bremen between 1931 and 1945 (Walter 1990). Walter[2] condemned Duncker's involvement with both these organisations and declared him a disgrace to biology for so enthusiastically promoting eugenic ideas. Walter acknowledged Duncker's ability as a scientist and as a lecturer, but found hard to understand how someone so critical as a scientist could have been so uncritical in his support for racial hygiene. 'Duncker was' Walter wrote 'one of the very many Germans who readily accepted and propagated the aims of the National Socialists' racial politics and hence contributed to the fact that these aims became a cruel and deadly reality for many human beings'. Walter was also particularly critical of Duncker because unlike many other Nazis, Duncker never renounced his views after the war.

Since Walter's important paper was published new information has come to light, and a somewhat different view of Duncker's involvement with both the Unit for Racial Hygiene in Bremen and the Nazi party, now emerges. This new information is the transcript of Duncker's interview with the Allies following the end of WWII: we refer to this as the Allies' Interview (see A Note on Sources).

Duncker was probably always a supporter of eugenic ideas, possibly stemming from Haeckel's popular and influential writings on social Darwinism (Stein 1988). Eugenic ideas were also widespread elsewhere in Europe and in the United States throughout the first two decades of the twentieth century (Allen 1978, Gould 1977, Stein 1988). Duncker appears to have been extremely highly principled inasmuch that if he believed something, he did so in an uncompromising fashion, and it is to this that we attribute his reluctance to retract his eugenic views after the end of WWII.

Duncker became vice-president of the Natural History Society in Bremen in 1931, and in

[2] Walter never met Duncker and obtained the information for his paper from Duncker's own published and unpublished manuscripts. Nor did Walter have access to the transcript of Duncker's interview with the Allies or his personal record held at the Staatsarchiv in Bremen (H. Walter, pers. comm.).

1933 together with the president Hans Meyer (director of the X-ray therapy service in Bremen), he started the sub-unit for racial hygiene. The first society for racial hygiene in Germany had been established in 1905 and Duncker and Meyer's sub-unit was one of many that sprang up in Germany during the 1930s. At this time almost every German university had a chair in racial hygiene and offered undergraduate courses on it. Initially at least, most academic eugenicists were not overtly anti-Semitic, and focussed instead on the mentally retarded (Deichmann 1996). After seizing power in 1933 the Nazis quickly introduced a law advocating the sterilisation of the mentally retarded for the 'common good before the individual'. In response to this announcement Duncker and Meyer organised a series of five public lectures under the umbrella title "The Prevention of Unworthy Life", which were given during March and April 1933 by a biologist, a sociologist, a psychiatrist, a theologian and a professor of law (Meyer & Duncker 1933). The sterilisation law wasn't due to come into effect until early 1934 and these lectures were apparently designed to allow people time to discuss the idea. Given the title of this series of lectures, it is hardly surprising that Walter was sharply critical of Duncker. However, reading them now, they are not as extreme in advocating eugenic ideology as one might imagine. Nonetheless, from 1933 and throughout much of the war Duncker continued to lecture on and publicise eugenic ideas.

On coming to power one of the things Hitler did was to enoble biology as a school subject, much to the delight of biology teachers in schools and universities who had long felt that biology had been under-rated in Germany (Bäumer-Schleinkofer 1995). The new regime provided Duncker with an opportunity to utilise his expertise as a teacher, and together with Dr Friedrich Lange, a high school teacher from Hamburg, he edited a volume which incorporated Nazi ideology into biology teaching (Duncker & Lange 1934). Duncker was not alone in taking advantage of the educational opportunities provided by the new regime, and this book was merely one among many that appeared in the early 1930s (Bäumer 1990, Bäumer-Schleinkofer 1995).

From the foregoing one might imagine that Duncker would have joined the party immediately the Nazis came to power in 1933, but in fact he did not do so until 1940. Duncker revealed in his Allies' Interview that he had been 'encouraged' to join the Nazi party by Senator Richard Hoff (president of the Unit of Racial Hygiene in Bremen) by being offered the prestigious position of director of the Kaiser-Wilhelm-Institute for Genetics in Berlin-Dahlem early in 1933. He declined, partly because he did not want to join the Nazi party and because he did not want to be seen as an opportunist. Moreover, he felt that the position should go to a botanist and professional biologist, rather than a teacher who did research as a hobby (see A Note on Sources). It also seems likely to us that Duncker recognised his own limitations and that he might have struggled in such a position[3]. The Nazis continued to 'encourage' Duncker by offering him the post of inspector of biology books in 1934. He accepted, but this position did not last long however, for in 1934 he was denounced by someone at his school for making insulting remarks about Hitler. The ensuing investigation found no evidence for this however and no formal disciplinary measures were taken against Duncker by the Nazis. Nonetheless, the denouncement did have negative effects: the Nazis actively discouraged him from giving public lectures and his prospects of promotion at school disappeared. The next year Duncker's superiors at school tried once more to persuade him to join the Nazi party, and again he refused. The Nazis then began a more negative form of persuasion, by ap-

[3] The position went to Fritz von Wettstein, then considered to be the foremost plant geneticist in Germany, who ironically never joined the Nazi party.

pointing additional editors, Party members E. Schütze and W. Schinke, to Duncker's journal "Vögel ferner Länder", thereby diluting Duncker's influence, although, as Duncker said in his Allies' Interview, he continued to do all the work. Duncker's contributions to the journal fell sharply during this period.

In 1936 Duncker's application for promotion to senior master at school was rejected by the Nazi party, who in a letter dated 11 August, said: 'We recommend the temporary postponement of the intended promotion of master "Studienrat" Dr. Hans Julius Duncker, Bremen for one year. His attitude towards national socialism does not convince us that he is internally totally dedicated to our movement. Therefore we think that a blocking period is still essential.

Duncker was finally promoted to Oberstudienrat (senior master) in 1939, but as he told the Allies, this was only because by then the Nazis no longer insisted on approving promotions. Early in 1940 he was once again under pressure to join the party and again he refused. Finally, when the Nazis presented him with a completed application form later that year, Duncker capitulated and signed.

Duncker[4] told his Allies interviewers that he had welcomed the racial hygiene laws in 1933 which focussed on the sterilisation of the mentally retarded and the encouragement of large, healthy families, but that he had never personally discriminated against the Jews (but see Walter 1990 referring to Duncker 1933a). Moreover, as the war continued, he became increasingly disillusioned by the Nazis' behaviour. On completing their interview the Allies classified Duncker as a "Mitläufer" – hanger on. However, in itself this is not very informative since "Mitläufer" was one of the commonest classifications made by those involved in the largely ineffectual denazification process (Napoli 1949).

V. Post-war and Retirement 1945–1961

After the Allies' invasion and the end of WWII Duncker, along with many other Nazi schoolteachers, was suspended from his teaching position. This was both a blow to his pride and a serious threat to his livelihood since at start of the war Duncker had been vicarious deputy director and was regarded as both a skilled and popular teacher (M. Birkmann, pers. comm.[5]). Not until 1948, when Duncker was 67, was he allowed to retire and officially receive a pension. He and his wife Elsa continued to live at Mathildenstrasse 78, where they had moved in 1932, but in 1954 they moved further up the street to Mathildenstrasse 37 where they remained. He was appointed honorary curator at the Natural History Museum in Bremen and set about restoring the bird collections which had been damaged and neglected during the war. The bird collection in Bremen was of special significance since much of the material had been collected by the previous curator Gustav Hartlaub (1814–1900). During the late 1940s and early 1950s Duncker restored and re-catalogued the entire collection of 16,000 bird skins (Duncker 1953) for which the museum director, H. Wagner was very grateful (Wagner 1957). Duncker continued to give public lectures at the Übersee-Museum, on topics including birds, inheritance and chromosomes, and judging from contemporary newspaper cuttings, he had retained his ability to inspire an audience.

Although Duncker had long since given up any bird breeding research he continued to be consulted by the editor of "Die Gefiederte Welt", Joachim Steinbacher on avicultural matters, such as nomenclature for the increasing number of colour canary mutations. In

[4] It is difficult to know how honest anyone might be during such an interview, but everything we have been able to check coincides with Duncker's statements, which in turn is consisent with our view that he was highly principled and honest.

[5] M. Birkmann was a former pupil of Duncker's at the Lettow-Vorbeck School.

1951 on the occasion of his 70th birthday the Bremen Natural History Society celebrated Duncker's achievements by making him an honorary member. Throughout his 70s Duncker continued to visit the museum almost every day. In 1960 Duncker's wife died, and a year later in September 1961 he was taken seriously ill. Unable to care for himself he was taken to live with one of his daughters at Saarbrücken, where he died on 22 December 1961.

VI. Overview

Duncker's main achievement was establishing the genetic basis for colour and other mutations of canaries and budgerigars. Some of these were straightforward and involved single autosomal gene effects, others were more complicated, involving sex-linkage and polygenic traits. In this respect Duncker's research followed very much in the mould of that of T. H. Morgan: identifying the genetic basis of mutations. That Duncker was a first rate scientist, is best exemplified by his ingenious interpretation of how Reich's canaries acquired their nightingale song. Duncker (1922a) presented his explanation as an hypothesis and a set of clear, testable predictions, although it is not clear whether he ever conducted the necessary experiments (which would have needed soundproof cages).

It is clear that by 1930 Duncker's success was recognised in Germany and his invitations to international conferences shows that his work was beginning to be recognised elsewhere. There are probably two main reasons why Duncker's scientific work was subsequently ignored internationally. First, he did not discover any general biological principles. In terms of genetics he was a follower rather than a leader, although within the field of avian science he was genuinely innovative, as illustrated by his ideas on the mechanisms of heredity of budgerigar colours. However, these particular ideas, referred to as the 'FOB theory' (see Watmough 1935 for details), were later declared by an English geneticist, Francis Crew to be incorrect (see Crew & Lamy 1934, 1935) and must have been a devastating blow to Duncker. Crew & Lamy (1934) state: 'We do not wish to minimise the work of these scientists [Duncker and Dr Hans Steiner, another budgerigar researcher, Professor of Zoology in Zürich, Switzerland; see Gebhardt 1970]; we merely point out that their theories are not helpful to the breeder. Their analysis of the physico-chemical differences which exist between the various mutant forms of the budgerigar as compared to the wild type light green is a most important work; but it is not genetical analysis, and it is not necessary to the practical application of genetical principles. Moreover, when they assign definite developmental processes arbitrarily to this or that factor, it must be said that they go beyond the conclusions warranted by the facts, and ignore much of the results of experimental genetics of the past twenty years'. In fact, Crew's harsh criticism was based on Duncker's assumption that the biochemical pathways controlling colour was determited by a single gene rather than several genes.

The second main factor contributing to Duncker's lack of international scientific recognition may have been the isolation of German researchers immediately following WWI, and especially after WWII for those working in genetics or eugenics (Deichmann 1996). Duncker's Nazi-links, which were well known to those who worked with him immediately after the war (G. von Wahlert, pers. comm.) and later publicised by Walter (1990), may have contributed to his lack of subsequent recognition. In this respect it may be significant that Duncker never received a proper obituary[6] in

[6] The AZ journal did publish a 'death notice' of Duncker (Keidel 1962), but as far as we are aware the AZ never published any other account of Duncker's scientific contribution or his revitalisation of the AZ in 1927 when he launched "Vögel ferner Länder".

the AZ journal (reinstated after WWII as the AZ Jahrbuch) even though they published a number of articles on the history of the society containing individual photographs of several of the key figures, such as Cremer, but curiously, not Duncker (Keidel 1960, 1962). Other contributory factors probably include the fact that Duncker's papers were all published in German, and that 'real' ornithologists studied wild rather than domesticated birds. Finally, it seems likely that many scientists failed to see the relevance of Duncker's research for wild birds, although now, following the molecular revolution, the study of avian genetics, sexual selection and bird colouration is entering a new and exciting phase (Hill 2002) and may turn the spotlight back onto some of Duncker's pioneering studies.

A Note on Sources

We have pieced together Duncker's private and scientific life from obituaries (Anon. 1962a, b, Steinbacher 1962, Stresemann 1962, Gebhardt 1964), other brief accounts (e.g. Keidel 1962, Wagner 1957, Ringleben 1955) and from Walter (1990). In addition, we used the typescript of the Allies' Interview and his 'personal record' held at the Staatsarchiv in Bremen. The attempts by both Jentsch and Alfred Kühn to promote Duncker is documented in two letters dated 8 November 1930 and 2 January 1931, respectively, held in the Bremen Staatsarchiv. Senator Richard Hoff's offer to Duncker of the directorship of the Kaiser-Wilhelm-Institute in Berlin-Dahlem in 1933 which he reported in the Allies' interview has not been verified. However, the KWI's files for this period are far from being complete, since much was lost during and after the war (Ms. Kazemi, Max-Planck archive in Berlin, pers. comm). Another possibility is that the offer was made only verbally. The Übersee-Museum in Bremen holds a small number of Duncker's personal papers dating from the late 1940s and 1950s. We talked to a few people that knew or knew of Duncker, including Klaus Speicher, Joachim Steinbacher and Gerd von Wahlert. Duncker published 'popular' accounts of many of his findings in avicultural magazines or newspapers, such as Kanaria which came out weekly, (but is no longer published and copies from the 1920s and 1930s are now very difficult to locate). Kanaria had no volume numbers so we refer to it by year and week number. In some instances we had photocopies of Duncker's articles but no page numbers – hardly ideal, but we felt it was better to include them as they are rather than not at all.

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Appendix A.
A list of Duncker's publications

Baade, F., and H. Duncker. 1914. Der menschliche Körper nach Leben, Bau und Pflege. Herman Schroedel, Halle on Saale. [The Human Body according to its Life, Structure and Care]

Duncker, H. 1905a. Über die Homologie von Cirrus und Elytron bei den Aphroditiden (Ein Beitrag zur Morphologie der Aphroditiden). Zeitschr. f. Wiss. Zool., 81, 191–276. [On the morphology of Cirrus and Elytron in Aphrodites]

Duncker, H. 1905b. Wanderzug der Vögel. Jena: Petsche-Labarre-Stiftung. [Migration Paths of Birds]

Duncker, H. 1912. Die Verbreitung der Gattung Emberiza, eine ornitho-geographische Studie. J. Orn. 60, 69–95. [The distribution of the genus Emberiza an ornitho-geographical study]

Duncker, H. 1922a. Die Reich'sche Gesangeskreuzung (Nachtigall u. Kanarienvogel) eine „erworbene" Eigenschaft. J. Orn. 70, 423–430. [The song hybrid of Reich (nightingale/canary); an 'acquired' character – preliminary contribution]

Duncker, H. 1922b. Die „Nachtigallen-Schläger" des Hern Reich, Bremen. Gefiederte Welt, 51, 65–66. [The "Nightingale Singers" of Mr. Reich, Bremen]

Duncker, H. 1922c. Die „Nachtigallen-Schläger" des Hern Reich, Bremen. (part II). Gefiederte Welt, 51, 73–74.

Duncker, H. 1922d. Die „Nachtigallen-Schläger" des Hern Reich, Bremen. Conclusion. Gefiederte Welt, 51, 81–82.

Duncker, H. 1922e. Nachtigall-Kanarienhähne. Kosmos, 5, 129–130.

Duncker, H. 1922f. Der Reichsche Stamm. Kanaria, 15, 00–00. [The Reich's Strain]

Duncker, H. 1923a. Aus der Geschichte der Kanarienvögel. Die Kanarienvögel, 11, 48–49. [Aspects of the History of Canaries]

Duncker, H. 1923b. Die Erblichkeit der Scheitelhaube bei Kanarienvögeln. J. Orn., 71, 421–447. [Genetics of the crest in canaries]

Duncker, H. 1923c. Geschlechtsbestimmunng bei Tieren. Der Kanarienvogel, 12, 13. [Sex determination in animals]

Duncker, H. 1924a. Ein eigenartiger Bastard von Stieglitz und Kanarienvogel. Der Kanarienvogel, 12, 6. [A peculiar hybrid between a goldfinch and a canary]

Duncker, H. 1924b. Einige Beobachtungen über die Vererbung der weissen Farbe bei Kanarienvögeln. Zschr. f. Ind. Abst. u. Ververbl. 32, 363–376. [Some observations on the inheritance of the white colour in canaries]

Duncker, H. 1924c. Exakte Vererbungsversuche bei Kanarienvögeln (parts I-VIII). Die Gefiederte Welt, 53, 2–5, 11–13, 19–22, 26–28, 34–36, 43–45, 50–52, 58–60. [Exact genetic experiments with canaries]

Duncker, H. 1924d. Vererbungsstudien an Kanarienvögeln. Wiss. Beil. d. Weser. Ztg., 12 June. [Genetic experiments on canaries]

Duncker, H. 1924e. Vererbungsversuche an Kanarienvögeln. III. Haubenfaktor. Weissfaktor. Scheckproblem. J. Orn., 72, 314–381. [Genetic experiments on canaries III. crest factor, white factor, variegation]

Duncker, H. 1924f. Wie entstehen unsere Haustierrrassen? Kanaria, 22, 000–000. [How do our domestic breeds arise?]

Duncker, H. 1925. Reingelbe Isabellen. Kanaria, 19, 261–262. [Pure Yellow Isabels]

Duncker, H. 1927a. Bastarde von Kapuzenzeisig und weissem Kanarienvogel. Vögel ferner Länder, 1, 67–74. [Hybrids of hooded siskin and white canary]

Duncker, H. 1927b. Erbformeln und Methode zur Berechnung der Nachzucht eines Wellensittichpaares. Vögel ferner Lander, 1,112. [Genetic formulas and method to calculate the offspring of a pair of budgerigars]

Duncker, H. 1927c. Der Ausfall des Fettfarbstoffes in den epidermoidalen Gebilden auf Grund erblicher Veranlagung (Alipochromismus) bei Kanarien und Wellensittichen. Zschr. f. ind. Abst.- u. Vererbl. 45, 41–86 [Lack of lipophyllic pigments in epidermal structures because of a genetical disposition 'alipochromismus' in canaries and budgies]

Duncker, H. 1927d. Der Geltungsbereich des Mendelismus. Abh. Vortr. Bremer Wiss.fes Reihe D. Bd., 1, 251–279. [The limits of Mendelism]

Duncker, H. 1927e. Die Vogelhäuser von Herrn Generalconsul C.H. Cremer, Bremen. Vögel ferner Länder, 1, 166–174. [The aviaries of General Consul C. H. Cremer, Bremen]

Duncker, H. 1927f. Ein Bastard zwischen Stieglitzmännchen und Weibchen eines weissen Kanarienvogels. Vögel ferner Länder, 1, 106–107. [A hybrid between goldfinch cock and female white canary]

Duncker, H. 1927g. Erbformeln und Methode zur Berechnung der Nachzucht eines Wellensittichpaares. Vögel ferner Länder, 1, 112 [Genetic formulas and method to calculate the offspring of a pair of budgerigars]

Duncker, H. 1927h. Über die Webetätigkeit der Webervögel. Vögel ferner Länder, 1, 145–149. [About the weaving activity of weaving birds]

Duncker, H. 1927i. Von ausländischen Züchtern und Liebhabern. Vögel ferner Länder, 1, 96–100. [About foreign breeders and enthusiasts]

Duncker, H. 1927j. Von Züchtern und von Vererben. Vögel ferner Länder, 1, 7–15. [Inheritance and the breeder]

Duncker, H. 1927k. Wie entsteht die Farbenpracht der Vogelfeder? Vögel ferner Länder, 1, 125–139. [What creates the beautiful colours of birds' feathers?]

Duncker, H. 1928a. Die Vererbung der Farben bei Wellensittichen. Vögel ferner Länder, 2, 9–34. [The genetics of colour in budgerigars]

Duncker, H. 1928b. Faktorenkoppelung bei Wellensittichen. Vögel ferner Länder, 2, 206–220. [The coupling of factors in budgerigars]

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