Inhalt

"[...] In contrast, tropical life seems to have flung all restraints to the winds. It is exuberant, luxurious, flashy, often even gaudy, full of daring and abandon, but first and foremost enormously tense and powerful. Watching the curved, arched, contorted, spirally wound, and triumphantly vertical stems and trunks of trees and lianas in forests of Rio Negro and the Amazon, it often occurred to me, that modern art has missed a most bountiful source of inspiration."

Theodosium Dobzhansky (1950): Evolution in the Tropics.

Synopsis

Introduction

As a mutualistic relationship, frugivory plays an important role for plants benefiting from endozoochory and animals gaining nutrients and energy by pulp digestion of fleshy fruits (Howe & Westley 1988). Seed dispersal enhances the survival and distribution of plant species due to limited germination conditions under the parent tree and the spreading of seeds over a wider area. Hence, seed dispersal due to frugivory is an important factor in forest regeneration and colonisation (e.g. Bullock 2000; Howe & Smallwood 1982; Wenny & Levey 1998). Frugivory and the mechanisms leading to fruit choice have been a major scientific subject in the past century. Different aspects of why a fruit gets chosen and eaten have been investigated, and a number of factors influencing fruit choice in birds has been discussed, like food abundance, encounter rate, crop size, accessibility, nutrient content, seed load, fruit size, secondary compounds, different digestive strategies etc. (Worthington 1983; McPhearson 1987, 1988; Murray 1987; Sallabanks 1992; Stiles 1993; Willson 1994; Moermond & Denslow 1983; Debussche & Isenmann 1989; Levey & Grajal 1991; Cipollini & Levey 1997; Johnson et al. 1985; Murray et al. 1993; Whelan & Willson 1994; Witmer & van Soest 1998). But before all these factors can influence an animal's fruit choice, the fruit has to be detected first. Therefore, fruit colour has attracted major interest over the past 25 years (Levey & Benkman 1999). Suggestions about the role of fruit colour have been made much earlier (e.g. Darwin 1859; Ridley 1930), but it took several decades to gain broader attention. Fruits are often brightly coloured and conspicuous to the human eye. A wide variety of fruit colours exists, but they are not evenly distributed in plants. By now, numerous studies have addressed the colour pattern of fleshy fruits in different habitats and continents (e.g. Turcek 1963; Knight & Siegfried 1983; Wheelwright & Janson 1985; Gautier-Hion et al. 1985). Studies in temperate and tropical zones in different continents all found a similar colour distribution regardless of habitat with a strong dominance of red and black fruits. Even though the relative

amount of both colours varied (see Wheelwright & Janson 1985), these two hues usually amount to over 50% of all fleshy fruits found. Hence, the focus of fruit colour research concentrated on the following question: Why do red and black fruits prevail in the fruit colour pattern? How did the current fruit colour distribution evolve? Various adaptive hypotheses including plant animal interactions and non-adaptive hypotheses including e.g. biochemical and phylogenetical approaches have been proposed to explain this phenomenon (reviewed in Willson & Whelan 1990). The adaptive hypotheses focus either on defence against insects or on interactions with seed dispersers.

While mammals and birds are both important groups of seed dispersers, research concerning fruit colour has focussed on the latter. Mammals are often nocturnal and/or dichromatic lacking the possibility to distinguish between red and green (e.g. Hunt et al. 2001), except for Old World primates and some New World howler monkeys (Jacobs et al. 1996; Jacobs & Deegan 1999; Kainz et al. 1998), which evolved the ability to distinguish between red and green with a third cone type in the visual system. Therefore, the abundance of red fruits cannot have resulted from the selection of fruit colours by mammals.

Frugivorous birds on the contrary are mainly active during daytime and are provided with an excellent colour vision which exceeds human colour perception in several aspects (Goldsmith 1990). Birds, with the possible exception of diurnal primates, are the vertebrates which may rely most heavily on vision to function in their environment (Cuthill et al. 2000). Birds' eyes can make up to 1.5% of total body mass (Welty 1982). The visual systems of birds and humans (as an example of trichromatic colour vision of Old World primates), differ in major aspects. First, the visible spectral range of birds also includes the UV range, while humans lack the UV visibility due to the filter function of the cornea (Burkhardt 1982, 1996; Burkhardt & Maier 1989; Hunt et al. 2001). UV vision seems to be a general property of diurnal birds having been found in over 35 species (Cuthill et al. 2000). The second main difference is the existence of at least four types of cones instead of three (Chen & Goldsmith 1986; Vorobyev et al. 1998) with the absorbance maxima at wavelengths in the UV range and the short-wave, medium-wave and long-wave section of the visible spectrum (Cuthill et al. 2000). The three short-, medium-, and long-wave range cones types responsible for human colour vision differ from avian colour receptor types in wavelength maxima (Hurvich 1981; Hunt et al. 2001). Colour perception stems from contrasts in output between cone classes (Endler 1990; Bennett et al. 1994). The existence of a fourth receptor thus endows birds with more possible receptor pairings, and they probably perceive more different hues than trichromates. Furthermore, birds have oil droplets in their cones, which act as coloured filters

of the entering light, sharpening spectral tuning and thus modifying colour vision (Bowmaker 1980; Vorobyev et al. 1998). Hence, adaptive hypotheses on the evolution of fruit colour due to seed dispersal focus on avian frugivores because of their superior colour vision.

Several adaptive and mutually non-exclusive hypotheses have been reviewed by Willson and Whelan (1990): i) The current fruit colour distribution could be the result of a general colour preference by birds either due to physiological (i.e. visual sensitivity) or behavioural (e.g. learning) reasons. The hierarchy in colour preferences would then reflect the colour frequencies in nature. Red and black should be the most favourite colours. Testing this hypothesis has led to contradicting results. Cage experiments yielded no preference at all, or pronounced individual variation and inconsistencies in colour preference. Therefore, this hypothesis received little support. But most studies used different approaches, i.e. species and methods, and are therefore difficult to compare. Willson & Whelan (1990) also report, that ii) fruit colour might indicate maturity. Immature and ripe fruits differ in their chemical composition (e.g. Schaefer 2002). Birds usually prefer ripe fruits, probably due to the higher concentration in secondary compounds in unripe fruits, such as tannins, which may have adverse effects on consumers (Clifford 1997; Provenza et al. 1990; Clark et al. 1991). Unripe and mature fruits also differ in the viability of the included seeds (Cipollini & Levey 1997, but see Foster 1977). Both partners, plants and birds, would thus benefit from a signal indicating ripeness. The plant would ensure, that fruits only get eaten, when the seeds are viable, while fruit colour would advertise palatability to the birds. The basis for such a signal is, that ripe fruits are conspicuous exhibiting a contrast to their background.

A follow up hypothesis in this context has been proposed by Wheelwright & Janson (1985), that fruit colour might not only indicate maturity, but also convey information about nutrient compounds contained in the fruit. The hypothesis predicts a correlation between the chemical compounds of a fruit and its colour. However, a thorough attempt to test this correlation is yet lacking due to a very limited number of studies approaching both, fruit colour and chemistry. Furthermore, certain fruit colours are not limited to certain ripening stages. Especially yellow, orange and red can be associated with unripe fruits in one species, but ripe in another. Fruit colour is therefore context dependent. Birds are endowed with great learning abilities. They have often been shown to associate food with certain contexts or landmarks (Kamil & Balda 1985; Hurley & Healy 1996; Gould-Beierle & Kamil 1998; Swaddle & Pruett-Jones 2001). Witmer (2001) demonstrated, that Cedar Waxwings (*Bombacilla cedrorum*) could not only distinguish between their food plants, but also select specific food species to complement

their diet. Hence, it might be possible, that fruit colours contain information on chemical compounds for frugivores (Whelan et al. 1998).

Willson & Whelan (1990) further report, that iii) certain colours might be selected due to conspicuousness to avian frugivores and act as a long-range signal. The more conspicuous the fruit, the faster it will be detected, increasing the likelihood to be approached and consumed by avian frugivores. This signal hypothesis therefore postulates, that the most common fruit colours, red and black, will also be the most conspicuous ones. Most studies on fruit colour concentrated on colour itself, rather than conspicuousness. Conspicuousness, defined as the colour contrast between a fruit and its background under natural illumination, is -like colour- dependent on the receiving visual system. Due to the lack of knowledge on the avian colour perception and the focus on fruit colour alone, studies directly testing this hypothesis are scant.

It is also discussed, that iv) colours facilitate quick food recognition particularly for migrant birds (Willson & Whelan 1990). Species often confronted with different environments and food items would greatly benefit from a certain colour being associated with a "good" food source. Following this hypothesis, the most common colours, red and black, would act as a colour cue, facilitating food search under time constraints during migration. Areas with higher abundance of migrant species should contain a greater frequency of red and black fruits than areas with a more resident frugivore community. Quick food recognition could also facilitate food search for juveniles, which after fledging are also confronted with a new environment and would therefore benefit from an intrinsic association between colour and edible food. Then, fledglings without prior experience in fruit consumption, should show a clear preference for red and black.

The aim of the study was, to i) choose an objective method of colour assessment for the avian visual system based on the knowledge currently available, ii) to test, whether birds have a general preference for specific colours, or whether adults of migratory species or fledglings exhibit a certain colour preference. This was tested in various choice experiments. It was furthermore investigated, whether iii) fruit colours could indicate maturity by examining, whether ripe fruits exhibit a general colour contrast against their natural background. I iv) addressed the information hypothesis and tested, whether fruit colour and chemical compounds of fruits show a correlation, and v) I approached the signal hypothesis by investigating the conspicuousness of different fruit colours and testing, whether conspicuousness influences fruit choice by birds. This was again examined in choice experiments.

The field studies have been done in a lowland rainforest in Venezuela. Fruit supply in tropical forests is higher and less seasonal than in temperate zones. Furthermore, the high abundance of avian frugivores and the fact, that up to 75% of neotropical tree species produce fruits eaten by birds (Howe & Smallwood 1982), render the Neotropics an excellent study site for investigations on the interactions between fruits and frugivores.

Visual systems and adequate methods for colour assessment

In chapter 2 and 3, I address the issue of finding an adequate method of colour assessment for the avian visual system. Until recently, all studies used conventional methods for fruit colour description, i.e. the classification into colour categories by different human observers, using devices as the Munsell Colour system. But the differences in the visual system and thus colour perception lead to the consequence, that human colour definition is inappropriate in studies investigating the interactions between fruit colours and avian dispersers. However, knowledge on avian colour perception is too scarce to develop a method for truly adequate colour assessment.

The colour perception of an object contains three processes: (i) light reflectance and transmission to the surface of the eye, (ii) light transmission, refraction and photoreception within the eye, and (iii) the neural processes in the retina and brain, which ultimately lead to the perception of colour (Endler 1990). The first process depends on the illumination of the object and the properties of the object's surface as well as of the transmission medium (e.g. air or water). The latter two are properties of the visual system of the observer. Since in the avian vision, the last two processes remain yet unknown, an objective colour assessment must be restricted to the spectral curves, right before they reach the eye of the observer and enter a specific visual system. This information was obtained by the use of a spectroradiometer, with which the reflectance of a certain amount of light sent to the object's surface as well as the environmental light was measured. Data are available as values in 5nm intervals over a range from 350nm to 700nm (chapter 2). The data points of the spectral curves can then be processed through statistical analyses without the commitment to one specific visual system. To comprise the information contained in the spectral curves, I performed a principal component analysis with the data of all fruit species, a method proposed by Cuthill et al. (1999). This analysis resulted in three principal components explaining *in summa* 98% of the variation in the sample. The first component (hereafter PC1) contributes 70.2% to the explained variance and is an achromatic factor representing the brightness of the spectra. Dark

fruits have low PC1 scores, while bright fruits have high values. The second principal component (PC2) stands for the relation between short-wave and long-wave segments of the spectrum and adds 23.9% to the explained variance. Fruits with a low PC2 score were fruits with a peak in the short-wave segment, or similar values over all wavelengths (black and white fruits). Yellow, orange and red fruits with maxima in the long-wave range have high PC2 scores. The last 4.5% of the total explained variance are contributed by PC3, the relation between the middle-wavelength range and both, short-wave and long-wave range. Thus, PC2 and PC3 are associated with aspects of colour, rather than brightness, but cannot be interpreted as clearly. The advantages of colour assessment with the PCA method versus the colour classification by human observers are self-evident. While the latter is specific to one visual system, the PCA is based only on impartial physical raw data and remains therefore objective. Each spectrum is individually characterised by three values, rather than lumped together into categories of colours of similar shade. The comparison between both methods shows, that fruits classified into different colour categories by human perception can have more similar PC2 values than fruits within one category (chapter 3). On the other hand, also the spectral curves of fruits within one category can vary considerably, which is accounted for in the characterisation of each spectrum by the three PC scores. Principal components depend on the spectra analysed in the PCA, though. For each different sample, a separate PCA has to be performed, and PC scores of spectra from different samples cannot be compared (Cuthill et al. 1999).

When enough information on avian vision is available for the development of a colour assessment based on avian perception, the raw spectral data will form a basis for the avian specific colour appraisal and can then be further analysed.

Fruit colour choice in avian frugivores: general colour preference, cue for migrants, or genetic predisposition?

In all studies on fruit colour patterns, a clear prevalence of red and black fruits has been found. These findings are independent of habitat or geographical position. Furthermore, red and black fruits have been reported to be smaller than fruits of other colours and have therefore been related to avian frugivores due to gape width (Knight & Siegfried 1983; Gautier-Hion 1985). Both results have been confirmed in this study (chapter 3). Red and black fruits add up to 51% of the total sample and are significantly smaller than fruits of other colours. This corroborated the assumption, that the commonness of these fruit colours is

associated with avian frugivores rather than mammals (Willson & Whelan 1990). General physiological (i.e. visual sensitivity) or behavioural (e.g. learning) trends of avian consumers may determine global fruit colour patterns (Willson & Whelan 1990). To test this hypothesis, I investigated, whether avian frugivores exhibit clear preferences for certain fruit colours by conducting choice experiments (chapter 6) with three tanager species, also occurring on the study plot in Venezuela. I used artificial fruits, differing only in colour. Fruits with reflectance spectra matching black natural fruits could not be produced. While Green Honeycreeper (*Chlorophanes spiza*) and Short-billed Honeycreeper (*Cyanerpes nitidus*), preferred red fruits in cafeteria experiments, Blue Dacnis (*Dacnis cayana*) consumed fruits randomly. Winkel (1969) found similar results with two congeners of the Short-billed Honeycreeper, one favouring red fruits, while the other species consumed fruits at random. Both, Winkel's results and the findings of the present study, indicate that no general colour preference inherent to all species exists. If learning was involved in the development of a preference, then adult birds should be more determined in their choice than juveniles due to their experience. Individual variation in colour choice could then reflect differences in pre-experience. The indicated difference among species needs further investigation with individuals of known biography.

Willson & Whelan (1990) suggest, that the distribution of fruit colours could partly be due to red serving as a signal for quick food recognition for migrant birds passing through unknown environment and being confronted with unfamiliar fruit species to feed on. They would therefore benefit from a colour cue advertising palatable fruits in limited time frames during migration stopovers. I presented adults of the migratory Blackcap (*Sylvia atricapilla*) with differently coloured artificial fruits, which do not resemble any natural fruit species. Blackcaps should thus feed mainly on red fruits due to the association with palatable food. Instead, in the experiments Blackcaps fed randomly on fruits. Also, areas with a higher proportion of migrants like North America do not differ in their fruit colour pattern from areas with lower migrant proportion like the Neotropics, where the majority of avian frugivores are residents. Therefore, the findings of this study and the global fruit colour patterns do not support the hypothesis, that quick food recognition in migrants explains these patterns. The random fruit choice in adult Blackcaps does also not buttress the hypothesis, that birds in general show a preference for certain colours, neither due to physiological, nor behavioural origins. To investigate, whether fledglings show a preference for red fruits, i.e. a genetic predisposition, I conducted cafeteria experiments with inexperienced handraised Blackcaps. Why should birds *a priori* exhibit a preference for a certain colour? In early summer in Central Europe, when juveniles start searching for food, the majority of ripe fruits is red

(Bairlein 1978; Snow & Snow 1988). A food search image for red fruits would therefore be advantageous for fledglings to facilitate quick food recognition (Bairlein, pers. comm.). In autumn, birds might broaden their food spectrum by learning due to the more diverse fruit colour pattern. Hence, the predisposition gets overridden by experience leading to random colour choices of adults. In the aviary experiments, juvenile Blackcaps indeed clearly preferred red over other colours. This corroborates the suggestion of a genetic predisposition in juveniles to search for red fruits. These findings have yet to be tested with other temperate zone species. In the tropics, fruit supply is not as seasonal, breeding seasons among species not as synchronised (Stutchbury & Morton 2001), and to my knowledge, no time window with mainly ripe red fruits exists. Therefore, the existence of a genetic predisposition might not be as likely to explain global patterns.

Concluding, birds do not exhibit a general fruit colour choice on a physiological or behavioural basis. Experiments on Blackcaps do not support the hypothesis on the prevalence of red fruits due to quick food recognition of migratory species. However, juveniles in temperate zones might be endowed with a genetic predisposition for red fruits as a search image for quick food recognition after fledging.

Colour as an indicator for maturity or specific chemical compounds: the information hypothesis

The evolution of colour vision has opened a large variety of possibilities for communication and signalling. Colour plays an important role in many ecological and behavioural aspects and is used in e.g. intraspecific communication, warning and cryptic coloration, or the recognition of food items (Endler 1981, 1984,1991a, 1991b, 2000; Alatalo & Mappes 1996; Fleishman & Persons 2001; Church et al. 1998; Espmark et al. 2000). Colours serve as intra- and intersexual signals and for male quality assessment (e.g. Endler 1983; Heindl & Winkler in prep.; Bennett et al. 1996, 1997; Hunt et al. 1999). Plumage colours engaged in quality assessment often derive from carotenoid pigments, which are also essential in the immune system. The display of bright colours can therefore signal the health state of a male (Lozano 1994; Hill & Montgomerie 1994; Saino et al. 1999). Hence, birds use different shades of colour as a very precise information system in mate choice. This ability can also be used in food choice. Mature fruits are often brightly coloured, while unripe fruits are usually green or distinct from the colour in maturity (McPhearson 1987; García et al. 1999). Fruit colour develops during ripening (Ballinger & Kushman 1970; Rhodes 1970). The consumption of

unripe fruits is disadvantageous for most plants due to a reduced viability of the seeds (Cipollini & Levey 1997). To prevent removal of unripe fruits, these can be cryptic and inconspicuous or contain unpalatable compounds. The coloration process might therefore increase detectability and also function as a signal of ripeness and palatability for dispersers (Willson & Thompson 1982). In chapter 4, I investigate, whether ripe fruits are conspicuous towards their background. I performed an ANOVA with fruit and background colour of each species followed by a Tamhane-test and found, that mature fruits are in general conspicuous against their natural background. Since most unripe fruits are green, coloration presumably indicates ripeness. A comparison between the contrasts of immature and ripe fruits has to elucidate, whether ripe fruits are more conspicuous against their natural background. Preliminary results on *Goupia glabra* seem to confirm this assumption (chapter 5), but need to be tested on a larger sample size. Often, premature stages are brightly coloured, which could announce the ripening process to avian frugivores (Stiles 1982). Birds can remember locations in their environment for a long time (e.g. Bednekoff et al. 1997), and the announcement of ripening fruits might induce avian frugivores to revisit the location later on.

Females' judgement of males' fitness from carotenoid dependent plumage coloration (Hill 1999) indicates the ability to use variation in colour shades for information conveyance on a fine-tuned level. These developed skills can also be of advantage for nutrition. Fruits vary not only in colour but also considerably in nutritional and allelochemical contents (Herrera 1987; Schaefer 2002). Avian frugivores possess fine-tuned discrimination abilities (Levey 1987; Bairlein 1990; Schaefer 2002) enabling them to choose those fruits, that meet their dietary demands. Complementary feeding has been proposed for birds to cover their specific nutritional requirements during moult (Murphy & King 1987, 1989; Murphy & Pearcy 1993) and as a general feeding strategy for frugivorous birds (Whelan et al. 1998). Complementary feeding has recently been demonstrated for the frugivorous Cedar Waxwing (*Bombacilla cedrorum*) to meet protein demands (Witmer 2001; see also Johnson et al. 1993), and it has generally been proposed that fruit colour yields the information on pulp chemistry, that lead to avian fruit consumption. (Wheelwright & Janson 1985; Herrera 1987). Plants may benefit from providing one specific nutrient content important for frugivores, not easily obtainable from other sources, and thus lowering production costs in other contents. Furthermore, the advertisement of attractive fruit components may enhance fruit removal resulting in improved seed dispersal. To thoroughly test the information hypothesis, extensive information on fruit chemistry in addition to the obtained spectral curves is needed. Simultaneously to my work, a study on the chemical composition of tropical fruit species was conducted (Schaefer 2002),

which included the same fruit species investigated in this study. I am therefore able to present the first study with a large data set of 45 species, the information on major nutrient contents and the most objective fruit colour assessment currently possible (chapter 4). Schaefer had analysed the following contents: macronutrients as lipids, proteins and carbohydrates as well as secondary compounds such as overall phenols and condensed tannins and the energy yield and water content of fruits. A principal component analysis on the spectral raw data of all fruit species included in both studies resulted in three principal components explaining 98% of the total variance among spectra. A multiple regression with the PC scores of each fruit species and the data on nutrient contents revealed, that fruits with low PC2 values, which were black and white fruits, are high in tannin contents, while fruits with a high PC2 value, i.e. some red, orange and yellow fruits, had high protein contents. This model explained 37% of the variation. Tannins are found as co-pigments in anthocyanin-complexes resulting in dark coloration. Presumably, tannins bound in these complexes are biologically inactive. Due to antimicrobial and antifungal activities (Scalbert 1991; Davidson & Juneja 1990), tannins may function as a defence against fruit pests, especially in unripe fruits due to their long persistence on the plant. In ripe fruits, tannins may then be bound in complexes to signal palatability being both, a cheap and effective signal. However, tannins are a very heterogenic group of secondary metabolites, and their biological activity is often unclear. Bairlein (1996) demonstrated, that birds' tannin intake was only constrained at very high tannic acid concentration (10%). A further investigation of this hypothesis would therefore require information on biological activity of single tannins on consumer species as well as the exact tannin composition in fruits.

Red, orange and yellow fruits partly have a high protein content. The advertisement of high protein contents might be very important, since fruits are in general very poor protein sources (e.g. Herrera 1987) due to the nitrogen limitation of plants. Mainly frugivorous birds, which need to cover all their requirements by fruit consumption would therefore benefit greatly of fruits announcing high protein contents. The high PC2 values of some, but not other red, orange and yellow fruits, result from a high ratio between short and long wavelengths, which cannot be perceived by humans. For primates, there is no colour category including these specific hues, but exclude others of similar shades. We can not rule out, however, that birds can somehow perceive this wavelength ratio, and that they notice information not visible for us. This can not be further investigated, until the knowledge on avian perception allows an appropriate subjective colour assessment on this specific visual system.

Concluding, the 37% of explained variance clearly show, that information on nutrient contents provided by fruit colour is possible. However, clear trends are yet missing, which can have several reasons: i) the analyses were not fine enough. Due to the fine-tuned discrimination abilities of birds, micronutritional food composition and structure as well as effects of secondary compounds have to be investigated more closely, ii) we did not concentrate on the "right" contents important for birds, i.e. secondary compounds (e.g. carotenoids) and essential amino acids as clues of the information system, iii) trends become obvious only when avian colour vision is known in detail, or iv) they are simply not exist as clear. These problems also apply for the few other studies, which tried to approach the information hypothesis. Wheelwright & Janson (1985) investigated fruit colour and quality, but found no connection. But they only analysed few factors of the ones included in the present study and focussed on fruit design. Hence, they concluded that colour conveyed little information about fruit quality, but the colour classification and chemical analyses used did not address fine-tuned relationships. Herrera (1987) also made an attempt to investigate fruit colour and quality including a broader array of nutrient compounds. He classified fruit colours into different categories and analysed the contents of macronutrients (lipid, protein, non-structural carbohydrates, fibre, water) as well as minerals. In his sample he found, that black fruits tended to have high mineral contents, followed by red and orange fruits, while fruits of other colours had low overall mineral contents. But to correctly interpret these results, information on the importance of different minerals for birds is required. He also found, that fibre content increased, and non-structural carbohydrates decreased in the direction black, red to orange and others, but did not present a hypothesis for these results. He did not find any correlations between colour and protein, which might be due to the different colour classification. In this present study, protein content was linked to fruit colours with maxima in the long-wave section and a minimum in the short-wave range, rather than to distinct human perceived hues, as Herrera used in his study. Since he did not include tannins in his analyses, and Schaefer did not measure mineral content, the studies are not comparable in these compounds. Herrera did not exclude a connection between fruit colour and chemical contents, but could not explain his findings either.

It can be stated, that this study has made the first serious attempt to link chemical contents to fruit colours, and the results indicate, that an information system might exist. Both, fruit chemistry as well as avian colour vision are yet to be investigated further, before a final evaluation of the information hypothesis can be done.

Colour as a long-range signal to attract avian dispersers: the signal hypothesis

Signals play an important role for interactions in nature. These interactions can be intraspecific, intersexual, between animal species, and also between animals and plants. Signals are used by senders to try to increase fitness by affecting the behaviour of receivers, while simultaneously, receivers use the same signals to try to increase their own fitness (Endler 2000). Frugivory as an interaction between animals and plants might be an example of a mutualistic signalling system. Plants might use fruit colour to advertise ripe fruit crop in order to attract frugivores. After fruit consumption, the seeds pass the intestinal tract of frugivores undigested and get dropped away from the parent plant thus enhancing the chance of successful seed germination. According to the signal hypothesis, fruits with a more pronounced signal would benefit from this mutual relationship more than fruits with a weaker signal, and would therefore be favoured in a selective process. Concerning fruit colour distribution, this would predict, that red and black fruits are stronger signals than other fruit colours. The strength of the signal lies in the conspicuousness, which is the contrast between fruit and background colour. In chapter 5, I investigate this hypothesis by measuring the contrast between fruit colour and background in their natural light environment in 43 species. As a measure of contrast, I chose the Euclidean distance, which is a common measure for contrasts in colour space models (e.g. Endler 1990). The brightness of the environmental light has a strong numerical influence on the contrast. Humans can adjust for brightness with the ability of light-dark-adaptation, and this is assumed to be also true for birds (Vorobyev et al. 1998). Calculations including environmental brightness do not account for this ability, however, and contrasts increase proportionally with increasing brightness of environmental light. I therefore chose to normalise spectra to the same brightness and concentrated on colour contrast itself. It has been shown earlier, that birds choose fruit colour on the basis of hue, rather than brightness (Puckey et al. 1996). In budgerigars, also plumage hue influences mate choice more than brightness (Pearn et al. 2001). While brightness contrast vary with environmental brightness, the calculation of colour contrast reveals a different pattern. Red and black fruits, the most common fruit colours, are more conspicuous than fruits of other colours. This was true regardless of habitat. In this study, conspicuousness was demonstrated as a measured contrast, a mathematical calculation. To investigate, whether conspicuousness does indeed influence fruit choice in birds, I conducted choice experiments with contrasting fruit displays on captive birds (chapter 6). In one trial, birds were presented artificial fruits in front of both, a background of the same and of contrasting hue. The other trial included a uniformly coloured display of natural, ripe black fruits and a bi-coloured display due to the

addition of several green, immature fruits. In both experiments, birds showed a clear preference for the contrasting display, regardless of the presented fruit colour. The conspicuousness of fruit presentation plays a role in avian fruit choice by enhancing the attractiveness for frugivores, independent of age and experience. Increased conspicuousness was also proposed for bi-coloured displays, thereby enhancing attractiveness and cause higher fruit removal (Willson & Melampy 1983, but see Greig-Smith 1986). But conspicuousness had never been measured. This was further tested by examining multi-coloured displays. I calculated contrasts between accessory structures (e.g. husk, stem, exocarp) or immature fruits and background as well as between these adjacent structures and ripe fruits. In eight out of nine cases of multicoloured displays, secondary structures including immature fruits enhanced conspicuousness in comparison to the contrast between ripe fruits and background only. This also corroborates the assumption, that plants use conspicuousness as a cue to attract avian dispersers.

Conclusion

The distribution of fruit colours shows a strong prevalence of red and black fruits. One explanatory approach is a co-evolutionary process between fruit colour and frugivorous birds. In recent years, co-evolution is " viewed by many as a reasonable but essentially untestable concept" (Wheelwright 1991). In fact, frugivory involves complex plant animal interactions with a very large and heterogeneous group of plants and a very large and heterogeneous group of frugivores. Evolutionary rates in plant animal interactions are slow, with a notable asymmetry in generation length of plants and disperser (Herrera 1985). Selective pressures of single species might be diluted by differently directed selective pressures from other species, since plants will respond evolutionary to the combined overall pressure. Therefore, the greater the species diversity, the lower the probability of a close co-evolutionary process between particular plant and disperser species (Herrera 1985). The diversity of physiological requirements and constraints in the heterogeneous group of consumers operate against tight co-evolutionary patterns. Only those consumer traits that are ubiquitously present have the potential to influence plant traits. Due to different physiological constraints in digestion, avian colour vision is one of the very few traits consistently present in avian consumers. Fruit traits, e.g. conspicuousness, applying to the very general ability of colour vision among fruit eating birds therefore could outlive the differing alternations of generations between plants and birds and even the extinction of bird species, since "new" frugivorous bird species were again

endowed with similar colour vision. Conspicuousness might hence be a fundamental key for plants to increase fruit removal. The fruit trait enhances the detection rate for a given fruit. By acting prior to the number of factors that contribute to the decision of fruit selection, conspicuousness influences the fruit choice of the majority of frugivorous birds and plays therefore a crucial role in the understanding of fruit choice in avian frugivores.

Acknowledgements

Cited literature

Alatalo, R.V. & Mappes, J. (1996): Tracking the evolution of warning signals. Nature 382: 708-710.

Bairlein, F. (1978): Über die Biologie einer südwestdeutschen Population der Mönchsgrasmücke (*Sylvia atricapilla*). J. Orn. 119: 14-51.

Bairlein, F. (1990): Zur Nahrungswahl der Gartengrasmücke *Sylvia Borin*: Ein Beitrag zur Bedeutung der Frugivorie bei omnivoren Singvögeln. Proc. Int. 100 DO-G Meeting, Current Topics Avian Biol.: 103-110.

Bairlein, F. (1996): Fruit-eating in birds and its nutritional consequences. Comp. Biochem. Physiol. 113A: 215-224.

Ballinger, W.E. & Kushman, L.J. (1970): Relationship of stage of ripeness to composition and keeping quality highbush blueberries. J. Amer. Soc. Hort. Sci. 95: 239-242.

Bednekoff, P.A., Balda, R.P., Kamil, A.C. & Hile, A.G. (1997): Long-term spatial memory in four seed-caching corvid species. Anim. Behav. 53: 335-341.

Bennett, A.T.D., Cuthill, I.C. & Norris, K.J. (1994): Sexual selection and the mismeasure of color. Am. Nat. 144: 848-860.

Bennett, A.T.D., Cuthill, I.C., Partridge, J.C. & Maier, E.J. (1996): Ultraviolet vision and mate choice in zebra finches. Nature 380: 433-435.

Bennett, A.T.D., Cuthill, I.C., Partridge, J.C. & Lunau, K. (1997): Ultraviolet plumage colors predict mate preference in starlings. Proc. Natl. Acad. Sci. USA 94: 8618-8621.

Bowmaker, J.K. (1980): Colour vision in birds and the role of oil droplets. Trends Neurosci. 3: 196-199.

Bullock, J.M. (2000): Gaps and seedling colonization. In Fenner [ed.]: Seeds: The ecology of regeneration in plant communities, 2nd ed., CAB International, Wallingford, UK: 375-396.

Burkhardt, D. (1982): Birds, berries and UV: A note on some consequences of UV vision in birds. Naturwiss. 69: 153-157.

Burkhardt, D. (1996): Die Ultraviolett-Tüchtigkeit des Vogelauges und einige Konsequenzen. Naturwiss. 83: 492-497.

Burkhardt, D. & Maier, E. (1989): The spectral sensitivity of a passerine bird is highest in the UV. Naturwiss. 76: 82-83.

Chen, D.-M. & Goldsmith, T.M. (1986): Four spectral classes of cone in the retinas of birds. J. Comp. Physiol., A 159: 473-479.

Church, S.C., Bennett, A.T.D., Cuthill, I.C., Hunt, S., Hart, N.S. & Partridge, J.C. (1998): Does lepidopteran larval crypsis extend into the ultraviolet? Naturwiss. 85: 189-192.

Cipollini, M.L. & Levey, D.J. (1997): Secondary metabolites of fleshy vertebrate-dispersed fruits: Adaptive hypotheses and implications for seed dispersal. Am. Nat. 346-372.

Clark, L. Shah, P.S. & Mason, J.R. (1991): Chemical repellency in birds; Relationship between chemical structure and avoidance response. J. Exp. Zool. 260: 310-322.

Clifford, M.N. (1997): Astringency. In Tomás-Barberán, F.A. & Robins, R.J. [eds.]: Phytochemistry of fruit and vegetables. Proceeding of the Phytochemical Society of Europe, Oxford Science Publications: 87-107.

Cuthill, I.C., Bennett, A.T.D., Partridge, J.C. & Maier, E.J. (1999): Plumage reflectance and the objective assessment of avian sexual dichromatism. Am. Nat. 153: 183-200.

Cuthill, I.C., Partridge, J.C., Bennett, A.T.D., Church, S.C., Hart, N.S. & Hunt, S. (2000): Ultraviolet vision in birds. Advances in the study of behaviour 29: 159-214.

Darwin, C. (1859): The origin of species. Murray, London.

Davidson, P.M. & Juneja, V.K. (1990): Antimicrobial agents. In Branen, A.L., Davidson, P.M. & Salminen, S. [eds.]: Food additives. Marcel Dekker: 83-137.

Debussche, M. & Isenmann, P. (1989): Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. Oikos 56: 327-338.

Endler, J.A. (1981): An overview of the relationship between mimicry and crypsis. Biological Journal of the Linnean Society 16: 25-31.

Endler, J.A. (1983): Natural and sexual selection on colour patterns in Poeciliid fishes. Envir. Biol. Fishes 9: 173-190.

Endler, J.A. (1984): Progressive background in moths, and a quantitative measure of crypsis. Biological Journal of the Linnean Society 22: 187-231.

Endler, J.A. (1990): On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41: 315-352.

Endler, J.A. (1991a): Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. Vision. Res. 31: 587-608.

Endler, J.A. (1991b): Interactions between predators and prey. In Krebs, J.R. & Davies, N.B. [eds.]: Behavioural ecology. An evolutionary approach. Blackwell Scientific Publications, Oxford: 160-196.

Endler J.A. (2000): Evolutionary implications of the interaction between animal signals and the environment. In Espmark, Y., Amundsen, T. & Rosenqvist, G. [eds.]: Animal Signals. Tapir Academic Press, Trondheim: 11-46.

Espmark, Y., Amundsen, T. & Rosenqvist, G. [eds.] (2000): Animal signals. Tapir Academic Press, Trondheim.

Fleishman, L.J. & Persons, M. (2001): The influence of stimulus and background colour on signal visibility in the lizard *Anolis cristatellus*. J. Exp. Biol. 204: 1559-1575.

Foster, M.S. (1977): Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. Ecology 58: 73-85.

García, D., Zamora, R., Gómez, J.M. & Hódar J.A. (1999): Bird rejection of unhealthy fruits reinforces the mutualism between juniper and its avian dispersers. Oikos 85: 536-544.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, P., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J.-M. (1985): Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324-337.

Goldsmith, T.H. (1990): Optimization, constraint, and history in the evolution of eyes. Quarterly Review of Biology 65: 281-322.

Gould-Beierle, K.L. & Kamil, A.C. (1998): The use of landmarks in three species of food-storing corvids. Ethology 104: 361-378.

Greig-Smith, P.W. (1986): Bicolored fruit displays and frugivorous birds: the importance of fruit quality to dispersers and seed predators. Am. Nat. 127: 246-251.

Herrera, C.M. (1985): Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44: 132-141.

Herrera, C.M. (1987): Vertebrate-dispersed plants on the Iberian peninsula: A study of fruit characteristics. Ecological Monographs 57: 305-331.

Hill, G. E. (1999): Mate choice, male quality, and carotenoid-based plumage coloration. In Adams, N.J. & Slotow, R.H. [eds.]: Proc. 22 Int. Ornithol. Congr., Durban. BirdLife South Africa, Johannesburg: 1654-1668.

Hill, G.E. & Montgomerie, R. (1994): Plumage color signals nutritional condition in the House Finch. Proc. R. Soc. Lond. B 258: 47-52.

Howe, H.F. & Smallwood, J. (1982): Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13: 201-228.

Howe, H.F. & Westley, L.C. (1988): Ecological relationships of plants and animals. Oxford University Press, New York.

Hunt, S., Cuthill, I.C., Bennett, A.T.D. & Griffiths, R. (1999): Preferences for ultraviolet partners in the blue tit. Anim. Behav. 58: 809-815.

Hunt, D.M., Wilkie, S.E., Bowmaker, J.K. & Poopalasundaram, S. (2001): Vision in the ultraviolet. Cell. Mol. Life Sci. 58: 1583-1598.

Hurly T.A. & Healy, S.D. (1996): Memory for flowers in rufous hummingbirds: location or local visual cues? Animal Behaviour 51: 1149-1157.

Hurvich, L.M. (1981): Color Vision. Sunderland (Mass.), Sinauer Associates Inc.

Jacobs, G.H. & Deegan, J.F. (1999): Uniformity of color vision in Old World monkeys. Proc. R. Soc. Lond. B 266: 2023-2028.

Jacobs, G.H., Neitz, M., Deegan, J.F. & Neitz, J. (1996): Trichromatic colour vision in New World monkeys. Nature 382: 156-158.

Johnson, R.A., Willson, M.F., Thompson J.N. & Bertin, R.I. (1985): Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66: 819-827.

Johnson, W.C., Thomas, L. & Adkisson, C.S. (1993): Dietary circumvention of acorn tannins by blue jays. Oecologia 94: 159-164.

Kamil, A. & Balda, R. (1985): Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). J. Exp. Psychol. Anim. Behav. Proc. 11: 95-111.

Knight, R.S. & Siegfried, W.R. (1983): Inter-relationships between type, size and colour of fruits and dispersal in Southern African trees. Oecologia 56: 405-412.

Levey, D. J. (1987): Sugar-tasting ability and fruit selection in tropical fruit-eating birds. Auk 104: 173-179.

Levey, D.J. & Benkman, C.W. (1999): Fruit-seed disperser interactions: timely insights from a long-term perspective. Trends Ecol. Evol. 14: 41-43.

Levey, D.J. & Grajal, A. (1991): Evolutionary implications of fruit processing limitations in cedar waxwings. Am. Nat. 138: 171-189.

Lozano, G.A. (1994): Carotenoids, parasites, and sexual selection. Oikos 70: 309-311.

Kainz, P.M., Neitz, J. & Neitz, M. (1998): Recent evolution of trichromacy in a New World monkey. Vis. Res. 38: 3315-3320.

McPhearson, J.M (1987): A field study of winter fruit preferences of Cedar Waxwings. Condor 89: 293-306.

McPherson, J.M. (1988): Preferences of cedar waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. Anim. Behav. 36: 961-969.

Moermond, T.C. & Denslow, J.S. (1983): Fruit choice in neotropical birds: Effects of fruit type and accessibility on selectivity. J. Anim. Ecol. 52: 407-420.

Murphy, M.E. & King, J.R. (1987): Dietary discrimination by molting white-crowned sparrows given diets differing only in sulfur amino acid concentration. Physiol. Zool. 60: 279-289.

Murphy, M.E. & King, J.R. (1989): Sparrows discriminate between diets differing in valine or lysine concentration. Physiol. & Behav. 45: 423-430.

Murphy, M.E. & Pearcy, S.D. (1993): Dietary amino acid complementation as a foraging strategy for wild birds. Physiology and Behavior 53: 689-698.

Murray, K.G. (1987): Selection for optimal fruit-crop size in bird-dispersed plants. Am. Nat. 129: 18-31.

Murray, K.G., Winnett-Murray, K., Cromie, E.A., Minor, M. & Meyers, E. (1993): The influence of seed packaging and fruit color on feeding preferences of American robins. In Fleming, T.H. & Estrada, A. [eds.]: Frugivory and seed dispersal: Ecological and evolutionary aspects. Vegetatio 107/108: 217-226.

Pearn, S.M., Bennett, A.T.D. & Cuthill, I.C. (2001): Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. Proc. R. Soc. Lond. B 286: 2273-2279.

Provenza, F.D., Burritt, E.A., Clausen, T.P., Byrant, J.P., Reichardt P.B. & Distel R.A. (1990): Conditioned flavor aversion: a mechanism for goats to avoid condensed tannins in blackbrush. Am. Nat. 136: 801-826.

Puckey, H.L., Lill, A. & O'Dowd, D.J. (1996): Fruit color choices of captive silvereyes (*Zosterops lateralis*). Condor 98: 780-790.

Rhodes, M.J.C. (1970): The climacteric and ripening of fruits. In Hulme, A.D. [ed.]: The biochemistry of fruits and their products. Academic Press, New York: 521-533.

Ridley, H.N. (1930): The dispersal of plants throughout the world. L. Reeve, Ashford, Kent.

Saino, N., Stradi, R. Ninni, P., Pini, E. & Møller, A.P. (1999): Carotenoid plasma concentration, immune profile, and plumage ornamentation of male barn swallows. Am. Nat. 154: 441-448.

Sallabanks, R. (1992): Fruit fate, frugivory, and fruit characteristics: a study of the hawthorn, *Crataegus monogyna* (Rosaceae). Oecologia 91: 296-304.

Scalbert, A. (1991): Antimicrobial properties of tannins. Phytochemistry 30: 3875-3883.

Schaefer, H.M. (2002): The influence of fruit pulp chemistry on avian fruit choice. PhD thesis, University of Oldenburg, Germany.

Snow, B.K. & Snow, D.W. (1988): Birds and berries. A study of an ecological interaction. Butler & Tanner Ltd, Frome and London.

Stiles, E.W. (1982): Fruit flags: two hypotheses. Am. Nat. 120: 500-509.

Stiles, E.W. (1993): The influence of pulp lipids on fruit preference by birds. In Fleming, T.H. & Estrada, A. [eds.]: Frugivory and seed dispersal: Ecological and evolutionary aspects. Vegetatio 107/108: 227-235.

Stutchbury, B.J.M. & Morton, E.S. (2001): Behavioral ecology of tropical birds. Academic Press London and San Diego.

Swaddle, J.P. & Pruett-Jones, S. (2001): Experimental investigation of the acquisition of learned symmetry discrimination in starlings. Am. Nat. 158: 300-307.

Turcek, F.J. (1963): Color preference in fruit- and seed-eating birds. Proc. XIII Intern. Ornithol. Congr., 285-292.

Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J. & Cuthill, I.C. (1998): Tetrachromacy, oil droplets and bird plumage colours. J. Comp. Physiol. A 183: 621-633.

Welty, J.C. (1982): The life of birds. 3rd ed. Saunders Coll. Publ., Philadelphia, Pennsylvania.

Wenny, D.G. & Levey, D.J. (1998): Direct seed dispersal by bellbirds in a tropical cloud forest. Proc. Natl. Acad. Sci. USA 95: 6204-6207.

Wheelwright, N.T. (1991): Frugivory and seed dispersal: 'La coevolución ha muerto-! Viva la coevolución!' Trends Ecol. Evol. 6: 312-313.

Wheelwright, N.T. & Janson, C.H. (1985): Colors of fruit displays of bird dispersed plants in two tropical forests. Am. Nat. 126: 777-799.

Whelan, C.J. & Willson, M.F. (1994): Fruit choice in migrating North American birds: field and aviary experiments. Oikos 71: 137-151.

Whelan, C.J., Schmidt, K.A., Steele, B.B., Quinn W.J. & Dilger, S. (1998): Are bird-consumed fruits complementary resources? Oikos 83: 195-205.

Willson, M.F. (1994): Fruit choices by captive American robins. Condor 96: 494-502.

Willson, M.F. & Melampy, M.N. (1983): The effect of bicolored fruit displays on fruit removal by avian frugivores. Oikos 41: 27-31.

Willson, M.F. & Thompson, J.N. (1982): Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are 'green'. Can. J. Bot. 60: 701-713.

Willson, M.F. & Whelan, C.J. (1990): The evolution of fruit color in fleshy-fruited plants. Am. Nat. 136: 790-809.

Winkel, W. (1969): Experimentelle Untersuchungen an Zuckervögeln (*Coerebidae*) im Funktionskreis der Nahrungssuche: Über die Bedeutung von Farben, Formen und Zuckerkonzentrationen. Z. f. Tierpsychol. 26: 573-608.

Witmer, M.C. (2001): Nutritional interactions and fruit removal: cedar waxwings consumption of *Viburnum opulus* fruits in spring. Ecology 82: 3120-3130.

Witmer, M.C.& Van Soest, P.J. (1998): Contrasting digestive strategies of fruit-eating birds. Functional Ecology 12: 728-741.

Worthington A. (1983): How rare plants attract fruit dispersers; the role of nutritional rewards. Bulletin of the Ecological Society of America 64: 53.

Conceptual background and methods

Abstract

The perception of the colour of an object depends on illumination, the surface of the object and processes within the eye and the brain of the observer. Therefore, adequate colour assessment is only possible with sufficient knowledge on the receiver's visual system. If information on the receiver's perception is scarce, colour assessment can be restricted to the physical data before the light enters the observer's eye. These physical data are the spectral curves of light reflected by an illuminated object towards the observer's eye. The ambient light is the sum of radiances coming from all light sources, light-emitting as well as light reflecting. The sum of these spectra forms the irradiance spectrum, which falls on the object's surface. According to the properties of the surface, the light gets reflected and transmitted through the medium to the observer's eye, thereby forming the colour spectrum. To obtain these colour spectra, a spectrometer was used for measurements of reflectance as well as measurements of the environmental light illuminating the object. Measurements were conducted in the Venezuelan lowland rainforest. Fruits were collected using a mobile construction crane to reach understory as well as canopy fruit species.

Study plot

Fieldwork was conducted in a lowland rainforest in the Estado Amazonas, southern Venezuela (65°40'W, 3°10'N/ Fig. 2.1). The study plot is located 105m above sea level at the banks of the Surumoni, a small black-water tributary of the upper Rio Orinoco 12km south of the village of Esmeralda. The area consists of pristine rainforest. Annual rainfall average amounts to 2900mm (Anhuf & Winkler 1999; Winkler & Preleuthner 1999). For ecological investigations, the Austrian Academy of Science has set up a mobile construction crane on 120m of tracks. The crane measures 40m in height and has a derrick of 40m. The average canopy height in the study plot is around 25-30m. Studies were carried out either on the ground or from a gondola hooked onto the steal cable of the crane, which can be positioned anywhere in an area of about 1,5ha. Most of the over 50 fruit species were collected inside this area, only five species were gathered in the forest surrounding the plot, and ten species were collected in a savannah location in the surrounding hills of the village Esmeralda, which were not used agriculturally or for cattle ranching. This savannah can be classified as a Llanos type savannah (Huber 1982; Coomes & Grubb 1996). Most of the area is ridge savannah,

characterised by rocky underground and a very dense vegetation cover of scrubs and trees. Trees have a maximal height of 4-6 m and small leaves (Seltmann 2000).

Fig. 2.1: Location of the study plot in South Venezuela near La Esmeralda

Conceptual background

The formation of a colour spectrum

The perceived colour of an object depends on three processes: (i) light reflectance and transmission to the surface of the eye, (ii) light transmission, refraction and photoreception within the eye, and (iii) the neural processes in the retina and brain, which ultimately lead to the perception of colour (Endler 1990). The first process depends on the illumination of the object and the properties of the object's surface as well as the properties of the transmission medium (e.g. air or water). The latter two are specific to the visual system of the observer. An appropriate assessment of colour perception is therefore only possible for species, in which the visual system has been thoroughly studied, and receptor properties as well as neural processes are known. If the knowledge about the visual system of the investigated species is restricted, no adequate colour assessment can be achieved (Bennett et al. 1994). The

limitation to the first process, the spectrum reaching the observer's eye (hereafter called the colour spectrum Q), is then the best approach to obtain the most objective appraisal of colour.

The components of the colour spectrum

The colour spectrum reaching the eye is the product of several different components, the ambient light spectrum, the reflectance spectrum and the transmission spectrum (Fig. 2.2). Illumination is caused by the irradiance spectrum of the ambient light. This spectrum is created by the sum of radiances from all contributing light sources, objects producing light and objects reflecting light. Among these light sources are the sun, blue sky and clouds, illuminated and shaded leaves, other vegetation and soil. These factors contribute different spectra to the ambient light and form the irradiance spectrum illuminating the object, defined by the light integrated over a 180° solid angle normal to the object's surface (Endler 1990, 1993). Due to the different spectral composition of the radiance spectra, a change in the contributing light sources evokes a change in illumination of the object and causes changes in the perceived colour of the object. A part of the irradiance spectrum falling on the surface of the object is reflected towards the viewer's eye, called the reflectance spectrum. On its way through the medium (e.g. air or water) this spectrum can be further modified by particles (dust, fog, turbid water) through absorption or scatter and is called the transmission spectrum. The light beam finally reaching the surface of the observer's eye after being affected by these factors is called the colour spectrum Q:

$$Q(\lambda, x) = A(\lambda) * R(\lambda) * T(\lambda, x),$$

where Q is the distribution of light at all wavelengths reaching the eye at a certain distance x, A is the spectral pattern of ambient light, R the spectral pattern of reflectance, and T the spectral pattern of transmittance , all three as a function of wavelength λ, and T as a function of distance. If viewing conditions are good (not in stained water, fog or heavy dust), and the distance between the observer and the object is not too far (as in some birds of prey), scatter and absorption in the transmission medium can be neglected. Then Q can be defined as

$$Q(\lambda) = A(\lambda) * R(\lambda).$$
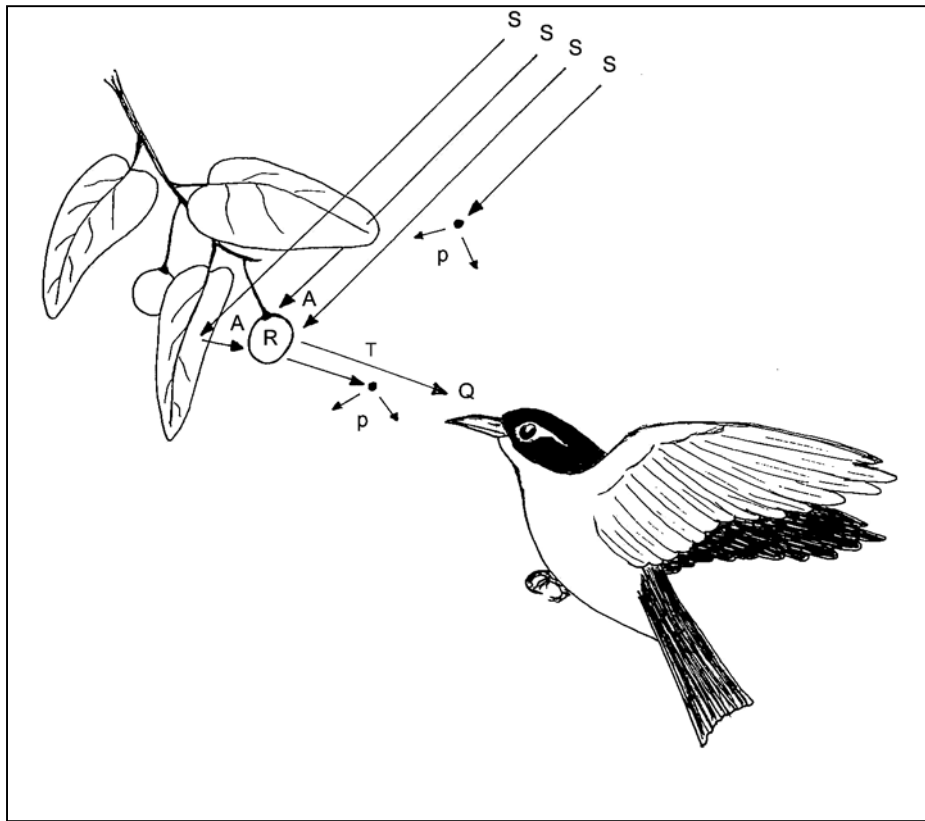
Fig. 2.2: The formation of the colour spectrum (Q), before it reaches the eye of the observer. The fruit is illuminated by the irradiance spectrum of the ambient light (A). A is the sum of radiances of all light sources. Light falling on the fruit comes from the sun (S), and from reflection by and transmission through vegetation. Sunlight gets partially scattered by particles (p). The light reflected by the fruit (R) passes through air, forming the transmission spectrum (T), and gets partially scattered by particles again, before it reaches the bird's eye as the colour spectrum.

Aspects of colour

Colour can be divided into three components, brightness, chroma and hue (Endler 1990). Brightness is defined as the total intensity of light reaching the eye from the object. It is calculated as the integral over the values of the wavelength intervals in the visible range of the visual system of the observer:

$$Qt \equiv \int Q(\lambda, x) d\lambda$$

Apart from brightness, the perceived colour of an object is determined by chroma and hue, which depend on the spectral shape of the colour spectrum. Chroma means the saturation of a colour and is a function of the differences between parts of the spectrum. Spectra with steeper slopes and greater differences will have more chroma than spectra with gradual and smaller

changes. Hue is what we call colour in everyday life, such as "green" or "blue" etc. Hue is correlated with the wavelength of the maximum slope of the curve (most rapid change of Q with wavelength) as well as the sign of the slope (Fig. 2.3. Note the change in position of the maximum slope with hue). Q with a positive slope at a longer λ is an orange or red, while Q with a negative slope at a shorter λ is a blue or blue-green.
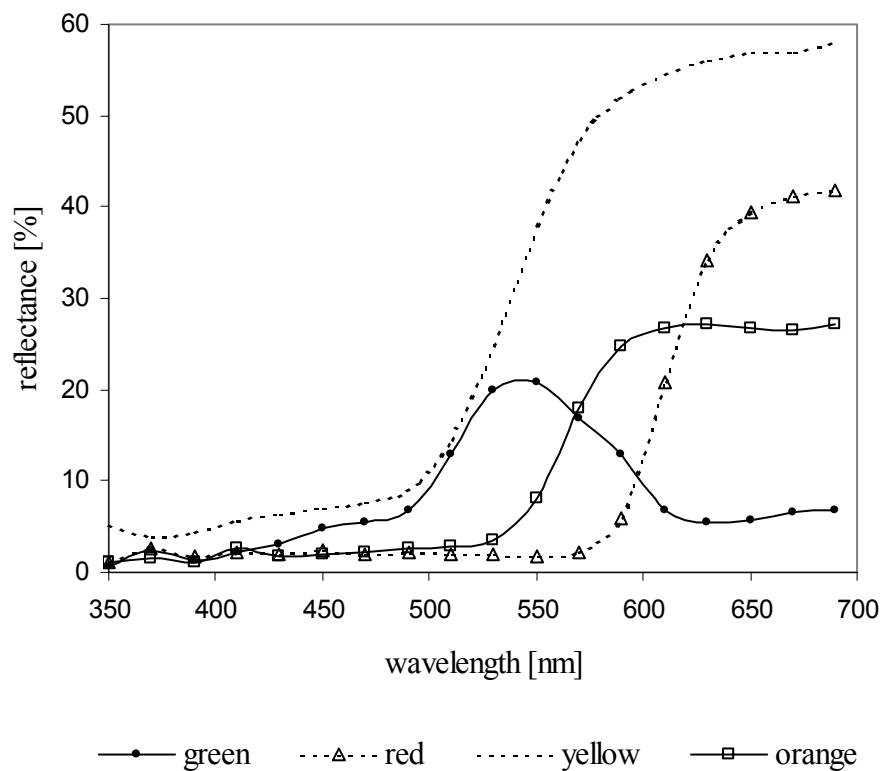
Fig. 2.3: Spectral curves of differently coloured fruits. Brightness corresponds to the area below the curve. Chroma is represented by the differences in reflectance between parts of the spectrum. Hue is characterised by the position of the maximum slope.

Some colours have two slopes with different signs, e.g. purple, yellow-green or green. Purple e.g. would have a negative slope between short and medium wavelengths and a positive slope in long wavelengths, while green has a positive slope between short and medium wavelengths and a negative slope between medium and long wavelengths (Fig. 2.3). Chroma and Hue can be calculated for each spectrum (Endler 1990), but only suitably, if the addressed visual system is sufficiently known. In other cases, measures for chroma and hue cannot be derived.

Methods

Sample collection

Prior to fruit collection, the ripening stage was determined using various factors such as colour change, smell, taste, smoothness, consumption by foragers and the attachment to the plant. Though none of these factors is a clear indicator for ripeness, the combination of all gives good evidence of the ripening stage. I collected up to 20 mature fruits of each plant species and took measurements immediately afterwards to prevent fruits from deterring and changing colour. I also collected a sample of background leaves or bark. Some plants had coloured secondary structures such as the exocarp, capsules or coloured infructescence. These structures were also collected and measured. If possible, plants were identified to species level (Wesenberg pers. comm.). Height above ground was determined with a weighted measuring tape lowered to the ground from the gondola. Vegetation and light environment were denoted following Endler (1993), as well as the position of the fruits on the plant to assess important background structures and illumination conditions.

Measurements of reflectance

For all measurements, a portable Ocean optics S2000 diode-array spectrometer and a Top Sensor System Deuterium-Halogen DH-2000 as a standardised light source were used. The spectrometer yielded reliable readings in the range between 350 and 900nm, while the lamp supplied a continuous spectrum between 215 and 1500nm. The sensor consisted of a bundle of six 200 μm illuminating fibres, surrounding a seventh fibre, which transferred the reflected light into the spectrometer with an acceptance angel of 28°. A DAQ-Card-700 was used for transferring the data into a laptop, where they were processed with SpectraWin version 4.0 software. Reflectance was measured as the proportion of a standard white reference tile. Before measuring the sample, the reference data of the standard white tile were taken for a 100% reflectance and of black felt for 0% reflectance. To maintain constant measurement conditions, the probe was sheathed with a black plastic tube, such that light could only enter through a quartz-glass lamina at the open end of the tube right in front of the sensor. The tube was cut at a 45° angle, and the illuminated oval spot had an area of 3 x 3.5mm to reduce the object's glare (Endler 1990). The calculation of spectra into 5nm intervals between 350 and 700nm was done with the unpublished software package ColorMaster (Hans Winkler, KLIVV, Vienna, Austria).

Measurements of ambient light

Ambient light spectra were taken from the gondola with a CC3 cosine-corrected irradiance sensor with a measuring surface of 6mm in diameter, measuring the incoming light over a solid angle of 180°. The probe was connected with a 200 μm optical fibre or a 50 μm optical fibre, depending on light intensity. The sensor was held vertically above the measuring person to avoid any influence of reflecting light from clothes on the spectra. Light falling into the sensor from low angles produces a weaker signal than identical light striking the sensor from steeper angles. The cosine correction adjusts for these signal differences resulting from differing angles of the incoming light. 15 vertical transects were randomly selected in the study plot, and measurements were taken in 4m intervals, starting at 2m above the ground. The last measurement was always taken above the canopy varying between 22m and 30m. In all heights, all occurring light habitats (for description see below) were measured, though in the understory, woodland shade and large gaps could not often be found, while complementary canopy habitat not always yielded forest shade. ColorMaster transformed irradiance spectra into photon flux per unit area (moles m^{-2} s^{-1} or, for more convenience, micromoles μM) after the sensor had been calibrated accordingly. This procedure is necessary because the photoreceptors of vertebrates and invertebrates respond directly to the number of photons striking the photoreceptors rather than the photons' energy (Endler 1990). The spectra of each light habitat were summarised to mean spectra in every height.

Light habitat and light environment

Endler (1993) classified five major light habitats in forests with characteristic ambient light spectra. These irradiance spectra are also called light environments. Light habitats differ in the relative proportions of light arriving from the sun, blue sky, clouds and vegetation, with each having a different spectral composition. Forest shade is characteristic for places with a complete or nearly complete canopy cover above, with no direct sunlight or light from the open sky striking the spot (Fig. 4). The ambient light spectra is characterised by light transmitted through leaves and reflected by vegetation and is thus rich in middle wavelengths (yellow-green). Objects in woodland shade are mainly illuminated by light coming from the open blue sky, but not by direct sun light (Fig. 4). Reflected light from the vegetation only adds a small proportion to the ambient light spectrum, which is therefore rich in short wavelengths (blue) due to the light coming from the open sky. Small gap light is characteristic of sun flecks in places with broken canopy. Nearly all incoming light is direct sunlight, with only a small amount from reflectance of vegetation (Fig. 4). The ambient light spectrum is

therefore dominated by longer wavelengths (orange-reddish). Light in large gaps comes from the sun and the open blue sky (Fig. 4) and is hence rich in almost all wavelengths (nearly whitish). In overcast weather the ambient light spectra in all four light habitats become whitish due to the diffusion by clouds, converging on that of large gaps. The fifth light habitat, which will not be addressed in this study but shall be listed for completion, is determined by low sun angles at dawn and dusk. The ambient light spectrum is rich in both, short and long wavelengths (purplish) and gradually darkens, until colour vision is no longer possible. Furthermore, light habitats change with the moving sun, as woodland shade might turn into large gap sites or *vice versa*, and small gaps might change into forest shade throughout the day. These major light environments are inherent to all forests independent of tree species composition, latitude or continent (Endler 1993).
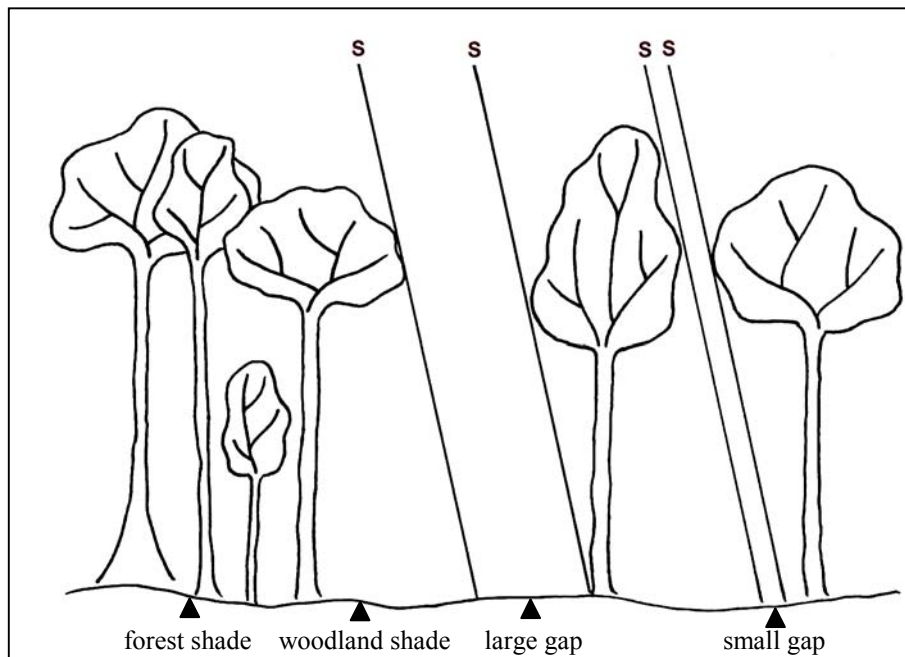
Fig. 2.4: Different light habitats in a forest under sunny conditions. Forest shade with no direct sunlight and most light reflected by or transmitted through vegetation, woodland shade with light mainly coming from blue sky, large gap with most light contributed directly by the sun, and small gap, where direct sunlight falls on a spot through small canopy holes. Sunlight represented by S. (after Endler 1993).

Cited literature

Anhuf, D. & Winkler, H. (1999): Geographical settings of the Surumoni-Crane-Project (Upper Orinoco, Estado Amazonas, Venezuela). Anzeiger Abt I Österreich, AKA 135: 3-23.

Bennett, A.T.D., Cuthill, I.C. & Norris, K.J. (1994): Sexual selection and the mismeasure of color. Am. Nat. 144: 848-860.

Coomes, D.A. & Grubb, P.J. (1996): Amazonian caatinga and related communities at La Esmeralda, Venezuela: Forest structure, physiognomy and floristics and control by soil factors. Vegetation 122: 167-191.

Endler, J.A. (1990): On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41: 315-352.

Endler. J.A. (1993): The color of light in forests and its implications. Ecol. Monogr. 63: 1-27.

Huber, O. (1982). Significance of savannah vegetation in the Amazon Territory of Venezuela. In Prance, G.T. [ed.]: Biological diversification in the tropics. Columbia University Press, New York: 221-244.

Seltmann, P. (2000): Untersuchungen zur Ökologie der *Loranthaceae* und *Viscaceae* am oberen Orinoco, Venezuela. Master thesis, University of Leipzig, Germany.

Winkler, H. & Preleuthner, M. (1999): The ecomorphology of neotropical frugivores. Acta Ornithologica 34: 141-147.

Fruit colour and the eye of the observer - an approach to objective colour assessment

Abstract

A number of studies have investigated the global fruit colour distribution and found a prevalence of red and black fruits and associated avian dispersers with the commonness of these colours. However, colour classification usually refers to human vision. The spectral raw data used for colour assessment in this study are analysed in a PCA, resulting in three principal components (PC) explaining 98% of the total variance among spectra. PC1 contributing 70,2% represents brightness, PC2 adding 23,9% reflects the relation between short- and long-wave range, while PC3 represents the relation between medium- and both, short- and long-wave range. Each spectrum is thus individually characterised by three values. The comparison with colour classification based on human vision reveals, that spectra with very different PC scores and spectral curves are grouped into one colour category, hereby loosing information. Thus, PCA is currently the most appropriate method for objective colour assessment. Fruit colour distribution in this study also exhibits a prevalence of humanly classified red and black fruits. Poor colour vision in mammals and the superior visual system of birds led to the hypothesis, that a potential influence on fruit colour evolution is likely to be due to avian frugivores in these hues. Red and black fruits were smaller than fruits of other colours, as also found in other studies, which supports the hypothesis due to different gape widths in birds and mammals.

Introduction

In the last 20 years, many studies tried to explain global patterns of fruit colours. Hypotheses on selective pressures leading to a dominance of red and black hues in mature fruits in both, temperate and tropical zones (e.g. Turcek 1963; Wheelwright & Janson 1985) have been reviewed by Willson and Whelan (1990). Apart from physiological and phylogenetic approaches, the impact of frugivores as seed dispersers on the evolution of colour in fleshy fruits is discussed. Major seed dispersers are birds, mammals (e.g. monkeys, tree rats or fruit bats, but also ground mammals consuming fallen fruits) and insects such as ants as secondary dispersers (Gautier-Hion et al. 1985; Levey & Byrne 1993; Dalling & Wirth 1998; Korine et al. 2000). Based on different colour and size, fruits have been divided into bird- and mammal-dispersed fruits (Janson 1983; Knight & Siegfried 1983; Gautier-Hion et al. 1985; Korine et

al. 2000), with the latter including mainly orange, yellow, brown or green fruits. The dichotomy of black and red fruits has been associated, not exclusively though, with avian foragers (Willson & Whelan 1990). Also, the evolution of fruit colour is more likely to be correlated with diurnal consumers (i.e. mainly birds) than with nocturnal foragers, such as bats and other mammals, when colour vision is restricted. Visual systems of frugivores differ to a large extent. Colour is a property of the receiving visual system (Endler 1978, 1990; Zeki 1993) resulting in different colour perception by animals with different visual abilities. Thus information on the visual system of frugivores is needed to test, whether selective pressures on fruit colour evolution have been imposed by frugivores. The visual system of mammals is well known, but information on the perceptual and neural processes in the visual system of birds is restricted. The two main differences in avian colour perception are the extension of the visible spectral range of birds into the UV (Burkhardt 1982, 1996; Burkhardt & Maier 1989), and the existence of at least four cones types (Chen & Goldsmith 1986; Goldsmith 1990; Vorobyev et al. 1998), which probably leads to the perception of a number of hues unknown to trichromates (Bennett et al. 1994). Therefore, no conclusions can be drawn from mammalian to avian perception. Nevertheless, most studies have applied colour classification based on human vision to investigate the avian impact on the evolution of fruit colour. Cuthill et al. (1999) proposed a principal component analysis with the original physical data, which clearly shows the advantage of maintaining independence of any visual system. In this chapter I will investigate, which information a PCA on reflectance spectra yields and elucidate differences to the methods used in previous studies on fruit colour. I will apply human based colour classification to compare fruit colour frequencies to previous studies.

Methods

The sample comprises fruits from a lowland rainforest in Venezuela and one savannah location about 12km south from the study plot (for further information on the site see chapter 2). 40 fruit species were collected in the forest at every vegetation height (ground species to canopy species in 26m height), and 10 species were gathered in the savannah. Reflectance measurements of fruits were taken immediately after collection with a portable spectrometer and a deuterium-halogen light source to prevent colour change due to deterioration (for details see chapter 2). If fruit crop size was large enough, 20 ripe fruits of each species were sampled. Reflectance spectra were processed through the software package ColorMaster (Hans Winkler, KLIVV, Vienna, Austria) which produces a table of 5nm intervals in a range from

350 to 700nm for each spectrum taken. To obtain a single spectrum for each species, the mean of all spectra taken from one species was calculated.

For the principal component analysis the number of variables (5nm intervals) was reduced. Intervals of 20nm were obtained by taking the median of all 5nm intervals included. Medians have the advantage of being insensitive to occasional artifactual spikes in recordings (Cuthill et al. 1999). Since a spectrum consists of many variables, and the variables of adjacent wavebands are highly correlated, PCA is a natural approach in the analysis of reflectance spectra, and often over 95% of the variation between spectra can be summarised in only two or three principal components (Endler 1990; Cuthill et al. 1999). Statistical analyses were performed with SPSS (SPSS. Inc. & Norusis 1986). PCA was done with the correlation matrix. The use of the covariance matrix instead did not yield different results.

For the comparison with the findings of other studies, fruits were independently classified by three human observers. 11 colour categories were defined: white, yellow, orange, pink, red, green, blue, brownish yellow, brown, bluish black and black. All fruits were consistently categorised. A Mann-Whitney-Test was performed to investigate the relation between fruit diameter and colour.

Results

The principal component analysis of all reflectance data of 50 fruit species yielded three principal components, explaining 98.6% of the total variance in spectral shape. PC1 accounted for 70.2% and yielded positive coefficients of similar magnitude (Fig. 3.1). PC1 therefore captures variance in achromatic properties of the spectra, representing brightness rather than aspects of hue or chroma. PC2 and PC3 capture variation in spectral shape in terms of relations between different segments of the spectrum. The second component explained 23.9%. Coefficients were negative for the variables in the short-wave range of the spectra, and positive for variables in the long-wave section. The third PC explained 4.5% of the total variance and had positive values for both, variables in the short-wave and the long-wave range, but negative coefficients for variables in the medium-wave section (Fig. 3.1). 94% of the variation can be explained through the first two components, which will be referred to as *brightness* and *short-wave to long-wave ratio*. In the following, distinction will be made between *short-wave to long-wave ratio* and *human colour* as a synonym for perceived colour by human vision.
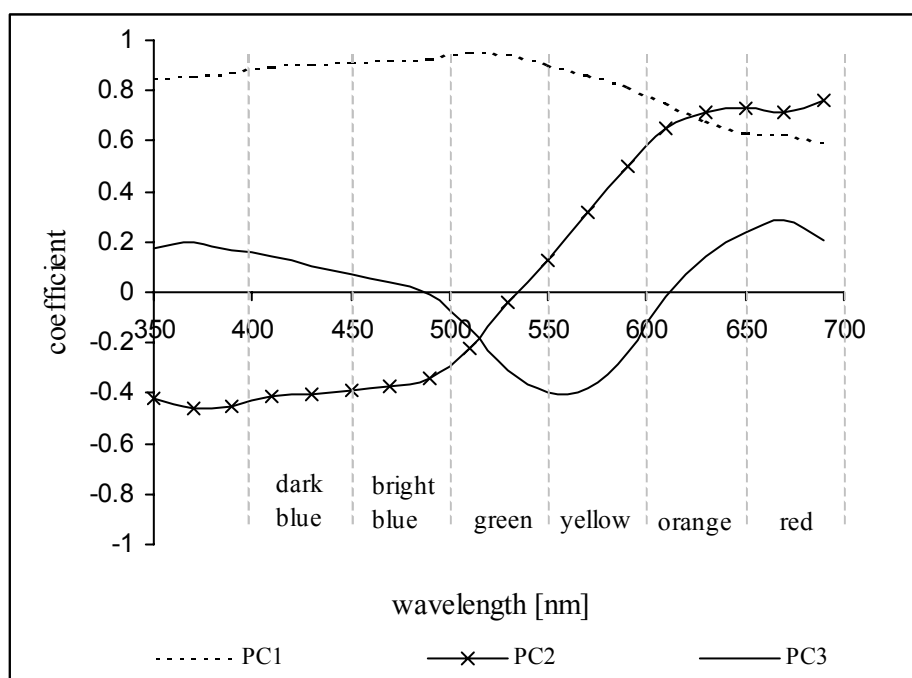
Fig. 3.1: Graphical representation of the factor loadings of the PC's. For illustration, the major colour sensations for humans correlating with wavelength segments are enclosed, but this does not apply for avian vision.

The PC scores characterise the geometrical shape of the spectra. The comparison with the *human colour* shows, that fruits perceived by humans as the same colour like the yellow fruits of *Bactris bidentula* and *Nepometia sp.* have distinct PC2 scores (Table. 3.1).
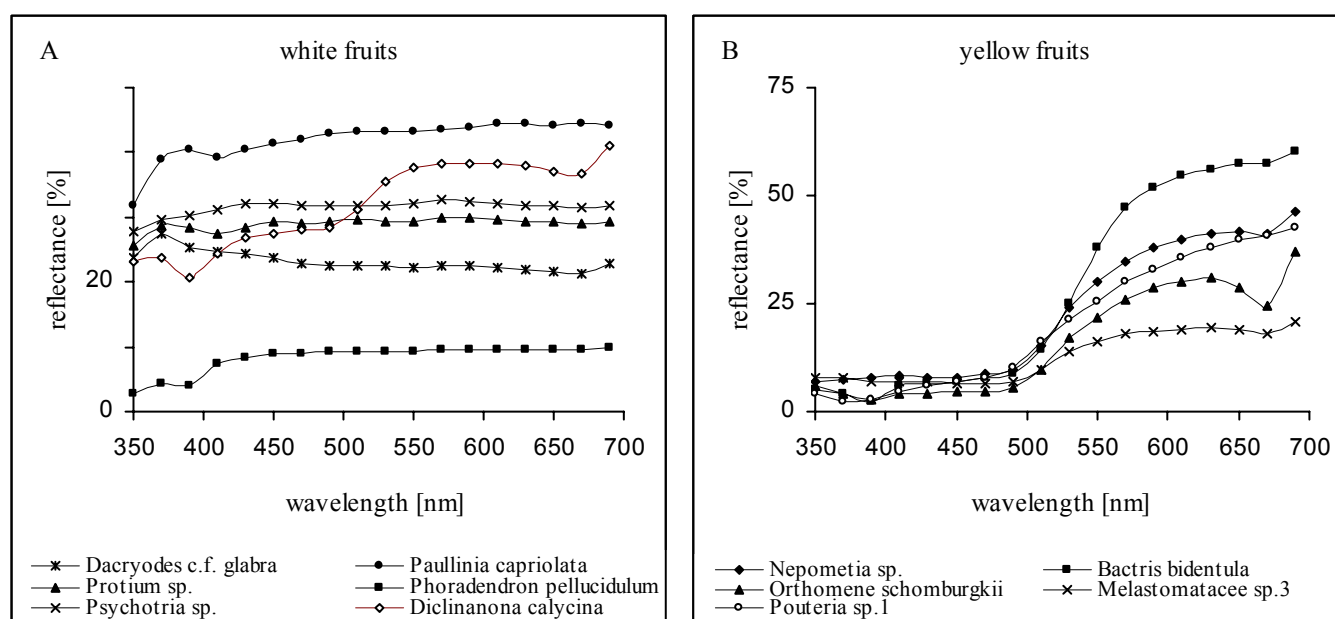
Fig. 3.2 A-F: Reflectance spectra of different fruit species assigned into categories of *human colour*. Depicted are the categories of the most common fruit colours. Note the different scaling in the y-axis. For C-F, see next page.
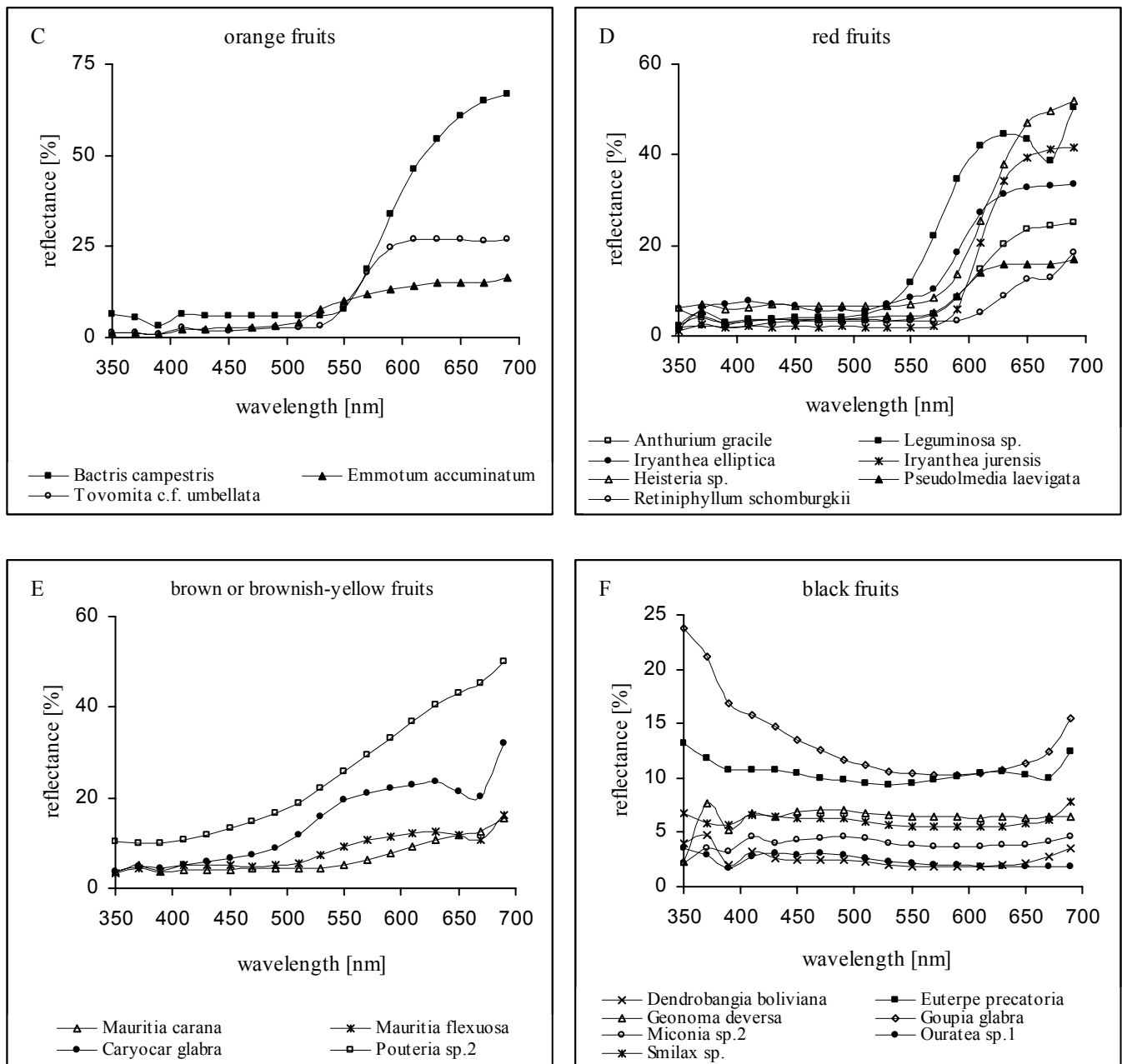
Fig. 3.2 C-F: Reflectance spectra of different fruit species assigned into categories of *human colour*. Depicted are the categories of the most common fruit colours. Note the different scaling in the y-axis.

This is further elucidated, when reflectance spectra are grouped into categories according to *human colour* (Fig. 3.2 A-F).

Spectra in the same group can vary considerably in their reflectance curve. The PC1 and PC2 scores exhibit a separation between black and white fruits and all "coloured" fruits (Fig. 3.3). Black and white fruits, as expected, only vary in the achromatic component of colour and are scattered along the PC1 axis.
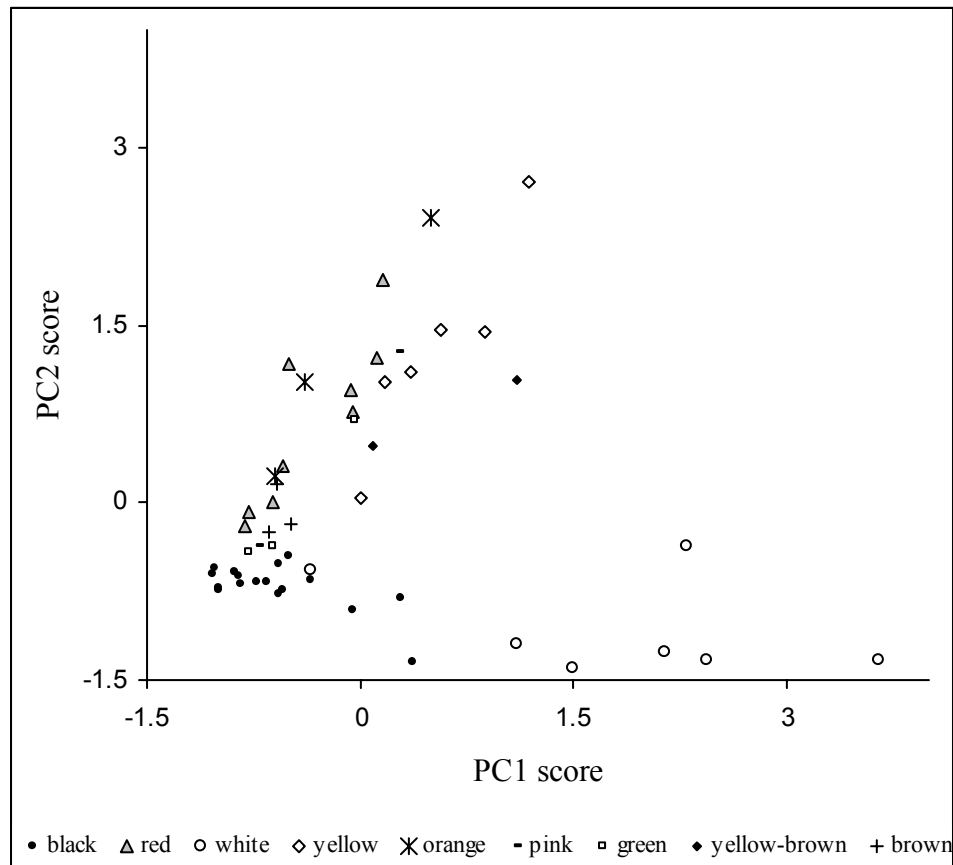
Fig. 3.3: PC1 scores versus PC2 scores of all fruit species. Note, that PC2 scores are
"inflated" due to the differences in explained variance between the two
components.

All "coloured" fruits on the contrary show a large variation in PC2 values. But fruits of the same *human colour* do not cluster together, as one might expect. They rather form an ellipse with variation in both, PC1 and PC2 scores. The reflectance curves of fruits of the same *human colour* show, that peaks within a graph vary between fruits (Fig. 3.2 A-F).

Fruits like *Retiniphyllum schomburgkii*, *Anthurium gracile* and *Heisteria sp.* exhibit differing spectra, but all appear bright red to humans. Also *Melastomataceae sp.4* and *Bactris bidentula* look both yellow to humans. The PC scores for both, *brightness* and *short-wave to long-wave ratio*, and also the reflectance curves differ considerably, though. Since brightness is the integral over the area covered by the curve, a difference in peak magnitude is always correlated with a difference in brightness, if spectra are otherwise similar. The only *human white* fruit with a PC1 score as low as black fruits is *Phoradendron pellucidulum*, with a very pale transparent reddish tint to human eyes, but with a PC1 score as low as black fruits. The brightness of the black fruit of e.g. *Euterpe precatoria* (Fig. 3.2 F) with a higher PC1 score is increased through higher values in the UV and blue range, where *Phoradendron pellucidulum*

clearly reflects less light than at all other wavelengths (Fig. 3.2 A). This indicates, that *Phoradendron pellucidulum*, although appearing nearly white for the human visual system looks different for avian eyes. White objects reflect light over all wavelengths of the visible spectrum, but *Phoradendron pellucidulum* clearly lacks reflectance in the short-wave range, perceivable for birds with a visible range extending to at least 350nm. Due to low intensity in short wavelengths, this fruit has a higher PC2 value than other white fruits. Also *Diclinanona calycina*, bearing a white cover, which does not fully conceal the underlying green skin, exhibits therefore the highest PC2 value of all white fruits.

Goupia glabra, the other black fruit with a high PC1 score for black fruits, is the only fruit of the whole sample strongly reflecting in the UV range (Fig. 3.2 F), without a noticeable waxy bloom and has therefore a very negative *short-wave to long-wave ratio* due to the decline in reflectance from short-wave to long-wave section.

The majority of fruits is either black (17 out of 51) or red (9 out of 51) in mammalian vision, adding to 51% of the total sample. To compare the *human colour* of fruits with other tropical forest locations, fruits from the savannah (marked with S) are excluded. Still black (12 out of 41) and red (7 out of 41) dominate the sample to 46.3%. In the savannah, black (5 out of 10) is the most widespread colour with 50%.

The majority of smaller fruits has a red or black *human colour*, while larger fruits exhibit a broader colour range (Table 3.1, Mann-Whitney-Test; U= 173.0; z= -2.864; p< 0.01).

Discussion

The differences in PC scores and humanly defined colour categories show the need for objective colour assessment. Spectra grouped together into one category can be of rather different shape. Most studies classify colours in groups of white, yellow, orange, red (sometimes combining the last two), green, blue, brown and black fruits (Herrera 1987; Knight & Siegfried 1983; Gautier-Hion et al. 1985; Lee et al. 1988; Willson et al. 1990) and deliberately lose information for the benefit of summarising a complex data set to a clear number of categories. Also fruit colours which show no variation in the *human colour*, can still have different spectral shapes. Information contained in reflectance curves is lost during perceptual processes in any visual system, but the loss of information presumably differs between systems. Hence human colour classification (including devices such as the Munsell Colour System) is biased towards trichromats.

Table 3.1: PC scores of all collected fruit species with fruit width and the *human colour* for comparison.
Savannah fruits are marked with (S). Fruits are assorted according to colour categories.

family		species	PC1	PC2	PC3	fruit width	*human colour*
Myrsinaceae	(S)	Cybianthus spicatus	-0.5000	-0.4563	0.0387	6.33	black
Burseraceae	(S)	Dacryodes microcarpa	-0.8803	-0.5834	-0.1834	7.66	black
Icacinaceae		Dendrobangia boliviana	-0.9897	-0.7230	-0.0342	12.32	black
Arecaceae		Euterpe precatoria	-0.0480	-0.9113	0.2789	8.30	black
Arecaceae		Geonoma deversa	-0.5495	-0.7404	-0.2396	7.02	black
Goupiaceae		Goupia glabra	0.3691	-1.3542	1.1777	5.1	black
Annonaceae		Guatteria schomburgkiana	-0.7329	-0.6751	-0.0876	9.14	black
Melastomataceae		Miconia sp. 2	-0.8376	-0.6885	-0.2425	10.10	black
Lauraceae		Ocotea aff. Amazonica	-0.8632	-0.6230	-0.1581	12.57	black
Arecaceae		Oenocarpus bacaba	0.2853	-0.8018	0.3705	15.76	black
Ochnaceae		Ouratea sp. 1	-0.9985	-0.7376	-0.1898	6.69	black
Ochnaceae	(S)	Ouratea sp. 2	-1.0353	-0.6023	-0.2417	6.95	black
Liliaceae	(S)	Smilax sp.	-0.5768	-0.7803	-0.0239	5.18	black
Burseraceae	(S)	Trattinickia bursereaefolia	-0.6612	-0.6739	-0.2651	9.07	black
Melastomataceae	(S)	Miconia sp.1	-0.5757	-0.5255	-0.3876	9.05	bluish black
Melastomataceae		Melastomataceae Genus sp.1	-1.0183	-0.5543	-0.3035	3.03	bluish black
Melastomataceae		Melastomataceae Genus sp. 2	-0.3435	-0.6578	-0.2422	8.69	bluish black
Araceae		Anthurium gracile	-0.5400	0.3073	1.0283	4.88	red
Clusiaceae		Clusia columnaris	-0.7765	-0.0790	0.4078	25.27	red
Myristicaceae		Iryanthea elliptica	-0.0582	0.7751	0.9722	17.13	red
Myristicaceae		Iryanthea jurensis	-0.4975	1.1701	2.1281	16.24	red
Leguminosaceae		Fabaceae genus sp.	0.1533	1.8846	0.3816	9.20	red
Olacaceae		Heisteria scandens	0.1141	1.2176	2.2756	8.69	red
Moraceae		Pseudolmedia laevigata	-0.6176	0.0078	0.3505	10.42	red
Rubiaceae	(S)	Retiniphyllum schomburgkii	-0.8069	-0.1892	0.2970	9.35	red
Meliaceae		Trichilia sp.	-0.0599	0.9562	2.0475	7.82	red
Burseraceae		Dacryodes c.f. glabra	1.4963	-1.4032	0.6508	13.83	white
Annonaceae		Diclinanona calycina	2.3031	-0.3729	-0.8515	29.50	white
Sapindaceae		Paullinia capriollata	3.6462	-1.3381	0.3276	21.75	white
Santalaceae		Phoradendron pellucidulum	-0.3475	-0.5683	-0.5466	5.91	white
Burseraceae		Protium sp.	2.1421	-1.2662	0.2704	14.13	white
Rubiaceae		Psychotria sp.	2.4434	-1.3333	0.3144	8.40	white
Arecaceae		Bactris bidentula	1.1830	2.7092	-2.0050	23.20	yellow
Melastomataceae		Melastomataceae Genus sp. 3	0.0043	0.0423	-0.7507	8.93	yellow
Sapotaceae		Nepometia sp.	0.8780	1.4467	-1.4526	27.67	yellow
Menispermaceae		Orthomene schomburgkii	0.1808	1.0280	-1.3775	17.66	yellow
Simaroubaceae		Picramnia sp.	0.3574	1.1040	-2.0482	6.51	yellow
Sapotaceae		Pouteria sp.1	0.5667	1.4598	-1.4701	18.55	yellow
Arecaceae		Bactris campestris	0.4942	2.4071	2.2585	9.12	orange
Icacinaceae		Emmotum acuminatum	-0.6041	0.2270	-0.7353	17.91	orange
Clusiaceae		Tovomita c.f. umbellata	-0.3828	1.0134	-0.2096	8.78	orange
Apocynaceae		Couma utilis	-0.6182	-0.3731	-0.9022	18.19	green
Rubiaceae		Kutchubaea sp.	-0.7864	-0.4116	-0.5038	36.85	green
Annonaceae		Xylopia venezuelana	-0.0310	0.6973	-0.8731	8.46	green
Arecaceae	(S)	Mauritia carana	-0.6390	-0.2468	0.1128	39.89	brown
Arecaceae	(S)	Mauritia flexuosa	-0.4897	-0.1762	-0.4366	32.50	brown
Arecaceae		Iriantella setigera	-0.5790	0.1633	-0.4413	7.06	brown
Caryocaceae		Caryocar glabrum	0.0897	0.4718	-1.2489	50.61	brownish-yellow
Sapotaceae		Pouteria sp.2	1.1011	1.0367	-0.3401	51.80	brownish-yellow
Marcgraviaceae		Marcgravia sp.	0.2519	1.2799	2.4057	13.83	pink
Marcgraviaceae		Noranthea sp.	-0.7241	-0.3699	0.2321	17.01	pink

Strictly speaking, hypotheses involving sensory abilities of species should only be addressed with enough information on these abilities in the target species (Bennett et al. 1994). But until then, a PCA is a good compromise. The PCA captured 98% of the total variance in the spectra and condenses a large number of variables to (in this case) three variables, maintaining also minor differences between spectra. The three PC scores of each spectrum can be entered into subsequent analyses and apply to the visual abilities of all taxa. This is especially useful in systems involving different colour vision, such as *Goupia glabra* being used by birds, mammals and ants (pers. observation). Once sufficient information has been collected on the addressed visual systems, the obtained data can be processed in appropriate analyses.

Principal components depend on the spectra entered in the PCA, and for different samples separate PCA's have to be performed. PC scores cannot be compared between different samples (Endler 1990; Cuthill et a. 1999). But still the PCA is the best approach for objective colour assessment, that is currently possible.

The colour distribution in this sample reveals a dominance of black and red in ripe fruits, similar to the reports from Wheelwright & Janson (1985) for different tropical forests. Just over 50% of all collected fruits are either red or black in maturity. Less frequent colours are white and yellow, while brown, brownish-yellow, orange, green and pink are rare. If fruits from the savannah location are removed from the sample to scrutinise forest species (Table 3.1), black and red still dominate the colour range to 46%, but the prevalence of black fruits is less evident than in the study of Wheelwright & Janson. Fruits in the savannah are mainly black in this study, but the sample size was limited.

The results of this study corroborate the findings of previous investigations, that fruits with red and black *human colours* are usually small, contrary to fruits with colours associated with mammalian dispersers (Table 3.1). This supports the assumption, that if frugivores put selective pressures on the evolution of fruit colours, the commonness of red and black has been established by avian dispersers.

Cited literature

Bennett, A.T.D., Cuthill, I.C. & Norris, K.J. (1994): Sexual selection and the mismeasure of color. Am. Nat. 144: 848-860.

Burkhardt, D. (1982): Birds, berries and UV: A note on some consequences of UV vision in birds. Naturwiss. 69: 153-157.

Burkhardt, D. (1996): Die Ultraviolett-Tüchtigkeit des Vogelauges und einige Konsequenzen. Naturwiss. 83: 492-497.

Burkhardt, D. & Maier, E. (1989): The spectral sensitivity of a passerine bird is highest in the UV. Naturwiss. 76: 82-83.

Chen, D.-M. & Goldsmith, T.M. (1986): Four spectral classes of cone in the retinas of birds. J. Comp. Physiol., A 159: 473-479.

Cuthill, I.C., Bennett, A.T.D., Partridge, J.C. & Maier, E.J. (1999): Plumage reflectance and the objective assessment of avian sexual dichromatism. Am. Nat. 153: 183-200.

Dalling, J.W. & Wirth, R. (1998): Dispersal of *Miconia argenta* seeds by the leaf-cutting ant *Atta colombica*. J. of Tropical Ecology 14: 705-710.

Endler, J.A. (1978): A predator's view of animal colour patterns. Evolutionary Biology 11: 319-364.

Endler, J.A. (1990): On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41: 315-352.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, P., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J.-M. (1985): Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324-337.

Goldsmith, T.H. (1990): Optimization, constraint, and history in the evolution of eyes. Quarterly Review of Biology 65: 281-322.

Herrera, C.M. (1987): Vertebrate-dispersed plants on the Iberian peninsula: A study of fruit characteristics. Ecological Monographs 57: 305-331.

Janson, C.H. (1983): Adaptation of fruit morphology to dispersal agents in a neotropical forest. Science 219: 187-189.

Knight, R.S. & Siegfried, W.R. (1983): Inter-relationships between type, size and colour of fruits and dispersal in Southern African trees. Oecologia 56: 405-412

Korine, C., Kalko, E.K.V. & Herre, E.A. (2000): Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. Oecologia 123: 560-568.

Lee, W.G., Wilson, J.B. & Johnson, P.N. (1988): Fruit colour in relation to the ecology and habitat of *Coprosma* (Rubiaceae) species in New Zealand. Oikos 53: 325-331.

Levey, D.J. & Byrne, M.M. (1993): Complex ant-plant interactions: Rain forest ants as secondary dispersers and post-dispersal seed predators. Ecology 74: 1802-1812.

SPSS Inc. &. Norusis, M.J. (1986): SPSS/PC +. SPSS Inc., Chicago.

Turcek, F.J. (1963): Color preference in fruit- and seed-eating birds. Proc. XIII Intern. Ornithol. Congr., 285-292.

Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J. & Cuthill, I.C. (1998): Tetrachromacy, oil droplets and bird plumage colours. J. Comp. Physiol. A 183: 621-633.

Wheelwright, N.T. & Janson, C.H. (1985): Colors of fruit displays of bird dispersed plants in two tropical forests. Am. Nat. 126: 777-799.

Willson, M.F. & Whelan, C.J. (1990): The evolution of fruit color in fleshy-fruited plants. Am. Nat. 136: 790-809.

Willson, M.F., Graff, D.A. & Whelan, C.J. (1990): Color preferences of frugivorous birds in relation to the colors of fleshy fruits. Condor 92: 545-555.

Zeki, S. (1993): A vision of the brain. Blackwell Scientific, Oxford.

Fruit colours - how much information do they convey?

Abstract

Among the adaptive hypotheses on the evolution of fruit colour, this fruit trait has been assumed to either announce ripeness or even convey information on the chemical compounds of the fruits. An ANOVA followed by a Tamhane-test revealed, that ripe fruits in general are conspicuous to their background, which forms the basis for both hypotheses. A simultaneous study analysed chemical contents of fruit species. A multiple regression with the PC2 scores of the spectral data of the fruits included and the chemical compounds resulted in 37% explained variance. Fruits with a low PC2 value, black and some white fruits, are high in tannins, while fruits with a high PC2 score, some yellow, orange and red fruits, have a high protein content. In ripe fruits, tannins often form complexes with anthocyanins, resulting in a dark fruit colour. The dark colour could announce the binding of tannins and thereby probably their inactivation, indicating palatability to birds. However, the heterogenous group of tannins is yet scarcely studied. Effects on birds are diverse. For a closer investigation, tannin composition of the fruits as well as bioactivity and effects on consumers should be known. Protein is limited in fruits. Frugivorous birds would thus benefit from information on high protein contents. Fruits with high PC2 values are diversely coloured to the human eye, but might have a common component perceivable by the avian visual system. However, only knowledge on the avian perception will elucidate the correlation between protein content and fruit colour for birds' eyes. Fruit colour has the potential to reveal information on fruit chemistry, and birds are endowed with very fine-tuned discrimination abilities. The data on fruit chemistry and spectral curves should be reanalysed, when colour assessment adequate for the avian eye is available.

Introduction

Conspicuousness

In a mutual system, in which plants depend on frugivores for seed dispersal, fruit traits might have evolved, which enhance fruit removal and thus the possibility of dispersal (e.g. Snow 1971; Wheelwright & Janson 1985). Fruit colour has often been documented as one of the factors influencing fruit choice (e.g. Willson 1994; Gautier-Hion et al. 1985), but its function is yet not fully understood. Conspicuous displays may facilitate fruit detection and have been discussed and reported to increase fruit removal (e.g. Willson & Thompson 1982; Willson and Melampy 1983; Willson & Hoppes 1986). Conspicuousness has been tackled only in a few

further investigations (Lee et al. 1988, 1994). Most studies have concentrated on fruit colour itself, and conspicuousness has rarely been quantified. Lee et al. (1994) defined conspicuousness as the magnitude of the colour difference between a fruit and adjoining plant structures, which form the background pattern of a fruit. The adjoining structures can be the top and back side of leaves, stem, capsules, the infructescence or the exocarp, which can be diversely coloured and add different proportions to the background pattern (Endler 1990). Conspicuousness of fruit against the background can vary between these structures (Endler 1990). Often a part of adjoining structures contribute most of the background pattern and can be called the main background. Assuming strong selective pressures on the conspicuousness of fruits, colour contrast to the main background could be greater than to other adjoining structures. This chapter investigates in a first step, whether ripe fruits in general are conspicuous against their background pattern, and whether the conspicuousness of fruits varies towards different background structures.

Information content of fruit colours

Fruit colour develops during ripening (Rhodes 1970; Ballinger & Kushman 1970). The consumption of unripe fruits is disadvantageous for the plant because seeds might not be fully developed (Cipollini & Levey 1997). To prevent removal of unripe fruits, these can be cryptic and inconspicuous or contain unpalatable compounds. The colour of unripe fruits is usually green or distinct from the colour in maturity (McPhearson 1987; García et al 1999). The coloration process might therefore increase detectability and also function as a signal of ripeness and palatability for dispersers (Willson & Thompson 1982). But the variation in fruit colours and the number of different shades have also led to the assumption, that fruit colour announces more than just maturity to dispersers. It has been discussed, that the coloration of mature fruits could provide information for a certain chemical compound, but only few correlations have yet been found (Greig-Smith 1986; Herrera 1987; but see Wheelwright & Janson 1985). The co-operation with a complementary study on chemical analyses of fruit species (Schaefer 2002) allows the presentation of 45 fruit species with information on colour and nutritional components. To investigate, whether fruit colours indicate chemical contents or related fruit traits, PC scores from reflectance spectra as objective colour assessment and multiple regression on fruit nutrients and secondary compounds are used.

Methods

Conspicuousness

To investigate conspicuousness in ripe fruits, a PCA was performed for reflectance spectra of each paired fruit and background sample (for details see chapter 2), and the first two PC's were tested in a one-way ANOVA for differences between fruits and each background structure. To compare group means, the posthoc Tamhane T^2-test was used. Conspicuous fruits should exhibit a significant difference in mean values, while inconspicuous fruits should lack such a difference. A greater conspicuousness against the main background should be evident in the comparison of mean differences between fruit and the various background structures. In a χ^2-test, observed and expected frequencies of greater conspicuousness against the main background and other structures were compared. Fruits with no specific main background and fruits with secondary structures were excluded from the test.

Information content of fruit colours

For fruit colour assessment, all reflectance spectra of fruits contained in the chemical analysis were processed through a PCA. Fruits were chemically analysed for the following compounds: water, energy yield, protein (Kjeldahl analysis), lipid (Soxleth analysis), sugar (glucose and fructose, photometric analysis with Boehringer analysis kit), tannin, and overall phenol contents (proanthocyanidin and Price & Butler analysis; for further details see Schaefer 2002). A multiple regression was performed with the PC scores of each principal component for all fruit species and nutrient contents to detect potential correlations. Tannin and phenol concentrations were log-transformed. For the comparative analyses, I employed generalised linear methods outlined in Dobson (1990). Models of this kind can be extended to include errors due to the evolutionary process to weigh data accordingly (Martins & Hansen 1997). The response variable was treated as a trait with an evolution which can be characterised with a continuous-time Markov model (Pagel 1994). This was incorporated in the parameter estimates as outlined by Martins & Hansen (1997). The phylogeny used was derived from Soltis et al. (2000) with additional information from Asmussen & Chase (2001).

Results

Conspicuousness

The results show a clear difference between fruit and background in all plant species (Table 4.1). Fruits are not always conspicuous against all parts of the background pattern, but all (except *Ocotea amazonica*) are conspicuous against their main background. Some fruits like

Caryocar glabrum could not be assigned to a particular main background. Mean differences between fruits and main background were not greater than between fruits and other parts of the background (χ^2= 0.242; df= 1; p= 0.622). Brightly coloured secondary structures will be treated in chapter 5 to estimate their contribution to the conspicuousness.

Table 4.1: Differences in PC scores between fruit and different background structures for each species. PC scores result from PCA for each fruit species separately. Significance is given as * indicating p< 0.05 and ** for p< 0.01. Main background is marked with (M). Different signs indicate higher or lower PC values of fruits than of background. For significance of PC1 and PC2, see further below.

species	background	PC1 signif.	PC1 diff.aver.	PC2 signif.	PC2 diff.aver.
Caryocar glabrum	top side	**	2.444	**	1.353
	back side	−	0.837	**	2.687
Couma utilis	top side	**	1.345	*	-0.949
Cybianthus spicatus	top side (M)	**	0.602	**	2.084
	back side	**	-1.689	**	1.416
Dacryodes c.f. glabra	top side (M)	**	3.703	**	-1.943
	back side	**	2.782	**	-2.728
	capsule (M)	**	3.685	**	-0.928
Dacryodes microcarpa	top side (M)	**	-0.426	**	1.775
	back side	**	-2.424	−	0.543
Dendrobangia boliviana	top side	**	-0.642	**	1.157
	back side (M)	**	-2.611	−	0.134
Diclinanona calycina	top side (M)	**	2.252		anova n. s.
	back side	**	1.846		anova n. s.
Emmotum accuminatum	top side (M)	**	1.551	**	1.601
	back side	**	-0.951	**	2.225
Euterpe precatoria	top side	**	-1.756	−	0.713
Fabaceae sp.	top side (M)	**	2.113	**	-0.831
	back side	−	0.267	**	-2.229
Geonoma deversa	top side	**	1.264	**	-0.529
	back side	−	-0.236	−	0.185
	racimo (M)	−	-0.939	*	-2.541
Goupia glabra	top side (M)	**	1.996	*	-0.345
	back side	*	0.881	**	-2.153
Guatteria schomburgkiana	top side (M)	−	0.119	*	1.976
	back side	*	-1.745	*	1.702
Heisteria sp.	top side (M)	*	0.513	**	2.501
	back side	**	-1.957	**	1.336
Iriantella setigera	top side	**	1.886	−	-0.561
	back side (M)	−	0.420	**	-1.764
Iryanthea elliptica	capsule	*	1.668	−	-1.095
Iryanthea jurensis	capsule (M)	**	-0.616	**	2.310
	stem	**	-1.964	*	1.210
Kutchubaea sp.	top side	−	-0.134	*	-1.178
	back side (M)	**	-2.042	−	-0.766

species	background	PC1 signif.	PC1 diff.aver.	PC2 signif.	PC2 diff.aver.
Miconia sp. 1	top side (M)	-	-0.405	**	-0.579
	back side	**	-1.936	**	-0.994
	stem (M)	-	-0.136	**	-3.044
Miconia sp. 2	top side (M)	**	-0.296	**	-1.548
	back side	**	-2.538	-	0.022
Melastomataceae Genus sp.1	top side	**	-0.707	-	0.654
	back side	**	-2.257	-	0.571
Melastomataceae Genus sp.2	top side (M)	*	0.550	**	2.022
	back side	**	-1.622	**	1.592
Melastomataceae Genus sp.3	top side (M)	-	1.292	**	2.199
	back side	-	-0.325	**	2.377
Ocotea aff. Amazonica	top side (M)	-	0.021		anova n. s.
	back side	**	-1.951		anova n. s.
Oenocarpus bacaba	top side	*	0.875	**	-2.065
	racimo (M)	**	1.942	*	0.544
Orthomene schomburgkii	top side (M)	**	2.056	**	-1.235
	back side	-	0.184	**	-2.425
Ouratea sp. 1	top side (M)	*	-1.540		anova n. s.
	back side	**	-2.062		anova n. s.
Ouratea sp.2	top side (M)	*	-1.012	-	0.118
	back side	**	-2.526	-	0.069
	stem (M)	-	-2.062	**	-2.287
Paullinia capriolata	top side (M)	**	2.501	**	0.325
	back side	**	2.068	-	-0.162
	capsule (M)	**	1.718	**	-2.165
Phoradendron pellucidulum	top side (M)	-	-0.253	**	1.737
	back side	*	-1.106	**	1.628
Picramnia sp.	top side (M)	**	2.317	-	0.129
	back side	**	1.133	**	-1.960
Pouteria sp.1	top side (M)	**	2.237	**	-0.734
	back side	-	0.201	**	-2.311
Pouteria sp.2	top side	**	2.503	-	-0.204
	back side (M)	**	1.219	**	-2.078
Protium sp.	top side (M)	**	2.333	**	0.545
	back side	**	1.928	-	0.151
	capsule (M)	**	1.500	**	-1.910
Pseudolmedia laevigata	top side	**	2.028	-	-0.152
Psychotria sp.	top side (M)	*	2.700		anova n. s.
	back side	*	2.108		anova n. s.
Retiniphyllum schomburgkii	top side (M)	-	-0.145	**	2.474
	back side	**	-1.867	**	1.430
Tovomita c.f. umbellata	top side (M)	**	-1.624	**	1.644
	back side	**	-2.689	*	-0.561
	exocarp (M)	**	-0.762	**	1.431
Trattinickia bursereaefolia	top side (M)	**	-0.773	**	1.732
	back side	**	-2.573	-	0.370
Trichilia sp.	top side (M)	*	1.452	**	-1.089
	back side	-	-0.112	**	-2.160
Xylopia venezuelana	top side (M)	**	2.077	**	-1.052
	back side	-	0.194	**	-2.056

Information content of fruit colours

The first 3 principal components explain 98.5% of the variance in the reflectance spectra of this sample (Fig. 4.1). PC1 accounts for 69.8%, PC 2 for a further 24.4%, and PC 3 for 4.3% of the explained variance. As in chapter 3, the first PC represent brightness, while PC 2 and PC 3 capture variance in geometrical shape. PC 2 accounts for the relation between short-wave and long-wave range, whereas PC 3 explains variance in the relation between medium-wave and both, short-wave and long-wave range.
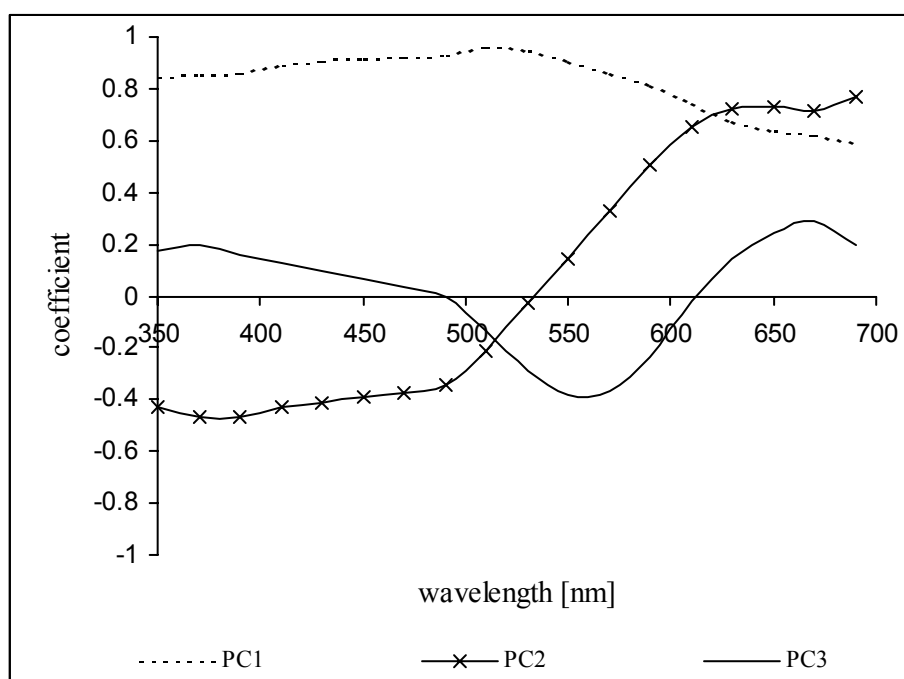
Fig. 4.1: Graphical presentation of the factor loadings of the PC's. Differences to the coefficients in chapter 3 are hardly noticeable in the graph, but exist.

In a stepwise multiple regression, PC 1 showed no correlation to any chemical compound. PC 2 exhibited a negative correlation with the log-transformed tannin concentration, and a positive correlation with protein content (p<0.001; r^2= 0.3696/ Fig. 4.2 A-B). The correction for phylogeny with the Brownian motion did not alter the results (Table 4.2). The correlation explains 37% of the total variance. PC 3 did not exhibit a significant correlation to any chemical fruit trait. The inclusion of protein lipid ratio and energetic equivalents of protein (17.2 kJ/g), lipid (38.9 kJ/g) and sugars (17.2 kJ/g; Karlson 1972) did not alter the results. PC scores and chemical traits of all fruits are presented in Table 4.3.
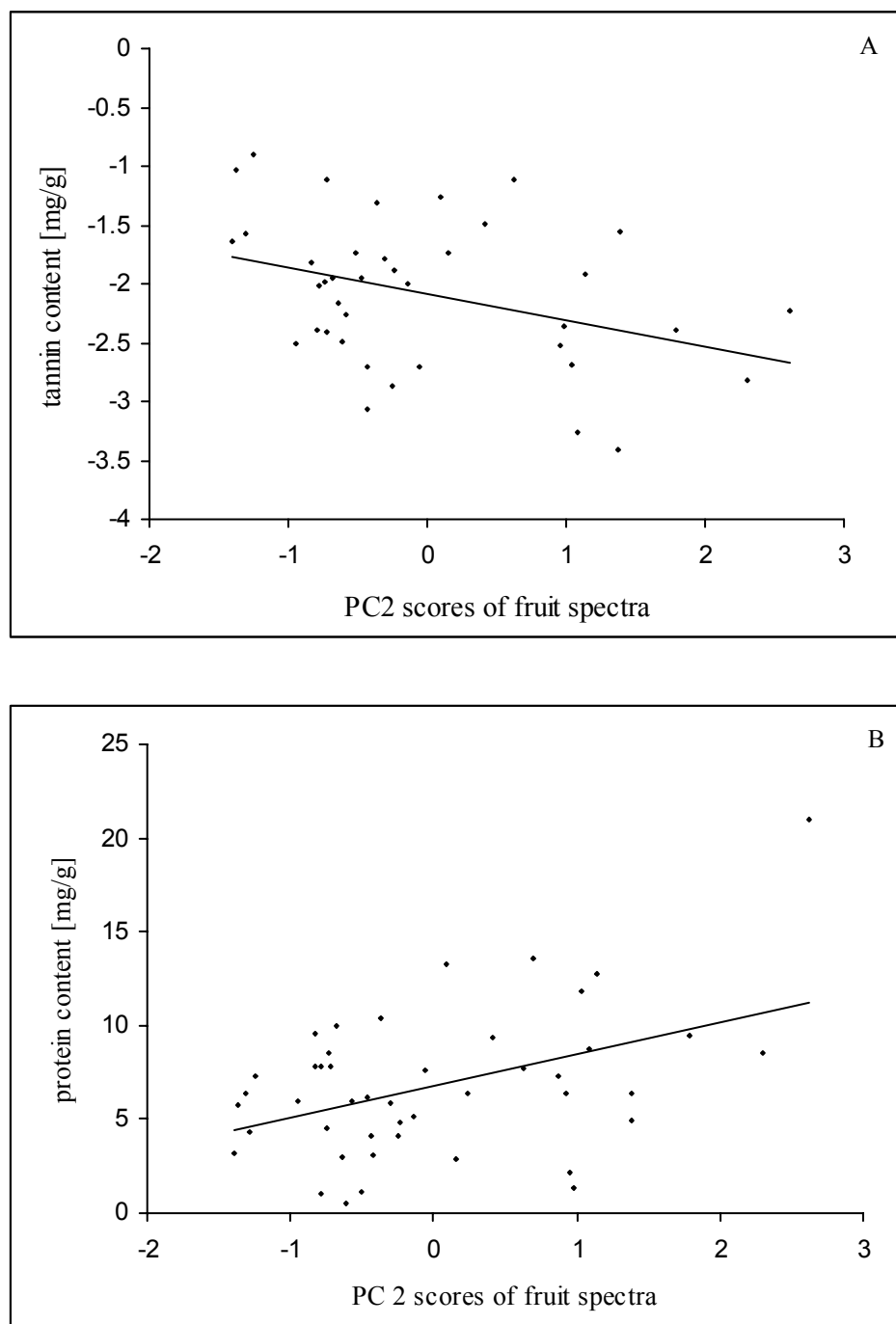
Fig. 4.2 A-B: Correlation between PC2 values and two chemical components in fruits, tannins (Fig. 4.2 A, log-transformed) and protein (Fig. 4.2 B).

Table 4.2: Results of the used multiple regression model with and without correction for phylogeny.

Method	p-value	r²-value	β-value for tannin	β-value for protein
without correction	< 0.001	0.3696	-0.6989	0.1234
corrected for phylogeny	< 0.001	0.3665	-0.6385	0.1332

Table 4.3: PC scores as colour assessment and contents of major nutrient components and secondary metabolites of all 45 fruit species included in chemical analyses. PC1 scores represent brightness, PC2 scores exhibit the ratio between short- and long-wave segment (high scores indicate peaks in the long-wave segment).

species	PC1	PC2	energy	water	sugar	protein	lipid	phenol	tannin
Anthurium gracile	-0.567	0.234	0.04	95.40	33.13	6.42	2.90		
Bactris bidentula	0.454	2.302	21.27	59.45	5.73	8.52	24.40	0.0124	0.0015
Bactris campestris	1.122	2.617	0.54	73.29	0.19	21.02	30.59	0.0241	0.0059
Caryocar glabrum	0.045	0.413	87.33	78.40	0.28	9.32	15.50	0.2677	0.0326
Clusia columnaris	-0.800	-0.145	25.09	77.51	0.36	5.19	17.88	0.0109	0.0099
Couma utilis	-0.650	-0.428	15.67	66.61	15.66	3.06	27.07	0.0030	0.0009
Cybianthus spicatus	-0.534	-0.509	0.12	67.67	26.03	1.11	1.54	0.0286	0.0184
Dacryodes c.f. glabra	1.405	-1.396	0.61	78.49	0.43	3.18	3.44	0.0326	0.0227
Dacryodes microcarpa	-0.906	-0.640	0.33	79.67	13.63	2.99	2.81	0.0070	0.0068
Dendrobangia boliviana	-1.013	-0.780	0.51	75.15	6.63	1.03	1.64	0.0592	0.0095
Diclinanona calycina	2.196	-0.367	7.49	76.54	0.27	10.34	1.66	0.5002	0.0492
Emmotum acuminatum	-0.632	0.156	1.53	61.38	2.64	2.90	2.53	0.0209	0.0185
Euterpe precatoria	-0.096	-0.946	0.62	32.95	0.11	5.96	5.59	0.0069	0.0031
Fabaceae sp.	0.116	1.785	1.07	69.76	0.33	9.42	6.27	0.0067	0.0040
Geonoma deversa	-0.585	-0.787	0.46	50.95	0.39	7.83	13.44	0.0708	0.0041
Goupia glabra	0.309	-1.373	0.12	79.19	13.43	5.72	20.95	0.0959	0.0931
Guatteria schomburgkiana	-0.762	-0.727	0.73	78.85	5.15	8.55	13.45	0.0901	0.0754
Heisteria sp.	0.078	1.139	0.30	63.76	1.12	12.73	8.76	0.3468	0.0121
Iriantella setigera	-0.608	0.093	0.44	59.73	0.26	13.30	4.36	0.3399	0.0552
Iryanthea elliptica	-0.095	0.699	9.23	52.95	0.66	13.62	50.27		
Iryanthea jurensis	-0.518	1.080	25.88	51.62	0.99	8.77	54.30	0.0562	0.0005
Kutchubaea sp.	-0.813	-0.470	24.63	83.12	0.75	6.14	3.08	0.0127	0.0111
Mauritia carana	-0.668	-0.308	16.33	72.54	4.14	5.89	1.95	0.0172	0.0164
Mauritia flexuosa	-0.523	-0.235	55.49	74.26	1.06	4.81	18.90	0.0168	0.0128
Miconia sp.1	-0.865	-0.743	1.31	82.40	37.26	4.55	1.57	0.0103	0.0105
Miconia sp.2	-0.609	-0.577	1.52	84.63	32.71	5.96	3.86	0.2991	0.0055
Nepometia sp.	0.818	1.379	34.96	70.74	3.88	6.34	14.30	0.0007	0.0004
Noranthea sp.	-0.752	-0.431	1.64	92.24	31.62	4.16	9.37	0.0050	0.0019
Ocotea aff. Amazonica	-0.889	-0.679	10.07	59.95	0.26	9.99	61.16	0.0303	0.0111
Oenocarpus bacaba	0.229	-0.830	20.47	70.37	0.27	9.60	45.34	0.0172	0.0154
Orthomene schomburgkii	0.137	0.955	1.20	61.86	2.63	2.21	3.23	0.0151	0.0030
Paullinia capriolata	3.499	-1.285	0.39	87.11	2.06	4.32	3.95	0.0059	0.0000
Phoradendron pellucidulum	-0.387	-0.614	0.03	84.65	5.52	0.49	2.10	0.0600	0.0032
Picramnia sp.	0.308	1.036	0.44	69.52	2.18	11.83	5.06	0.0065	0.0020
Pouteria sp.1	0.516	1.388	6.74	74.02	0.23	4.97	3.76	0.1072	0.0276
Pouteria sp.2	1.035	0.985	17.12	72.77	3.42	1.31	5.47	0.0067	0.0044
Protium sp.	2.035	-1.247	1.97	70.01	13.69	7.29	4.16	0.1230	0.1234
Pseudolmedia laevigata	-0.646	-0.059	0.63	80.26	8.01	7.58	5.94	0.0209	0.0019
Psychotria sp.	2.328	-1.306	0.38	89.87	23.34	6.37	3.94	0.0400	0.0267
Retiniphyllum schomburgkii	-0.831	-0.252	0.26	85.13	8.86	4.12	8.08	0.0033	0.0014
Smilax sp.	-0.611	-0.828	0.22	86.75	10.37	7.87	15.33		
Tovomita c.f. umbellata	-0.412	0.924	0.24	75.32	18.18	6.41	1.93	0.0028	0.0000
Trattinickia bursereaefolia	-0.693	-0.724	0.73	82.04	0.30	7.84	45.75	0.0185	0.0039
Trichilia sp.	-0.094	0.877	0.48	53.15	7.38	7.32	9.14		
Xylopia venezuelana	-0.071	0.628	1.79	58.21	0.17	7.76	12.02	0.0770	0.0769

Discussion

Conspicuousness

All mature fruits exhibit differences in colour against their background structures, and ripe fruits are therefore generally conspicuous. The hypothesis, that the colour difference to the main background is most striking, could not be supported. Apart from secondary structures, background colours are mainly dull, and often only top and back sides of leaves form the background. Usually both sides of the leaves are green, differing in brightness or the shade of green, with similar reflectance spectra. Thus, foliage background can be summarised by a spectrum averaged over the different proportions of top and backsides in the overall pattern. The conspicuousness of ripe fruits forms the basis for the hypothesis that fruit colours convey information on fruit chemistry or function as a long-range signal advertising ripe fruit crop to avian frugivores (chapter 5).The occurrence of brightly coloured secondary structures has often been interpreted as enhancing fruit conspicuousness (Willson & Thompson 1982). Willson & Melampy (1983) have shown, that bi-coloured fruit displays were more attractive to birds than uni-coloured displays and explained these findings with higher conspicuousness. This conclusion and the differences in conspicuousness between fruit colours will be stressed in chapter 5.

Information content of fruit colours

The three principal components representing brightness and colour in terms of wavelength ratio capture 98% of the total variance of fruit colours. Thus, correlations with chemical fruit traits are likely to be detected. The multiple regression revealed that fruits with low PC 2 values have a high tannin concentration, while fruits with a high PC2 value exhibit a high protein content. Fruits with a high PC 2 score are some yellow, orange and red fruits, while fruits with low PC2 values are black and white.

The principal fruit pigments belong to the group of anthocyanins, which are phenolic compounds (Brouillard et al 1997) and cause hues of orange and red as well as purple and dark blue to black. Black fruit colour is often achieved by a high concentration of anthocyanins (Harborne 1976), and their colouring ability especially for blue and black hues is enhanced by binding co-pigments such as tannins (van Buren 1970). Due to the anti-microbial activity of tannins (Provenza et al. 1990; Clark et al. 1991), they might prevent microbial or insect infestation as well as consumption of unripe fruits to ensure seed maturation. However, the biological activity of different tannins and their effects on the metabolism of consumers are yet poorly understood. Some tannins have been shown to be detrimental while others like catechin, known from different fruits like strawberry, apple and

pear (van Buren 1970; DiVenere et al. 1998; Tabak et al. 2001), have been documented to inactivate viruses (Selway 1986) and are discussed to counteract a number of human diseases (e.g. Arts et al. 2001; Tabak et al. 2001). Diets with small amounts of tannins can lead to a higher proteolysis reaction than tannin-free diets, but proteolysis is inhibited at a higher tannin level (Mole & Waterman 1985). High tannin concentrations in fruits may therefore have adverse effects on consumers, and the binding of tannins could therefore enhance fruit attractiveness and palatability, announced by the resulting dark fruit colour. However, birds have been shown to cope with high amounts of tannic acid (Bairlein 1996). Bairlein (1996) also estimated, that wild blackcaps (*Sylvia atricapilla*) feeding on black elder (*Sambucus nigra*) have a daily intake of nearly 1g of tannins. The biological activity of most tannins is still not understood, and the composition of tannins in most fruits, as well as the mechanisms birds might have evolved to neutralise these compounds are yet unknown. Willson & Whelan (1990) hypothesise that astringency as a potential adverse effect on consumers (Clifford 1997) could be reduced by the formation of complexes between tannins and anthocyanins with dark fruit colours as a by-product. For a better understanding of the correlation between tannin content and fruit colour, further information on tannin composition of fruits, as well as their effects on consumers is required.

Fruits with high PC 2 values have high protein contents. Proteins are generally known to be scarce in plants, and contents in fruits are low (Moermond & Denslow 1985; Izhaki 1998). Most frugivores supply their diet with insects to cover protein needs, and protein deficiency has often been suggested to explain body mass loss of frugivores in aviary experiments (e.g. Berthold 1976; Sedinger 1990). Protein rich fruits should therefore be attractive for birds, and the signalling of high protein contents should enhance fruit removal. Fruits with high PC 2 values all have maximum peaks in long wavelengths. For human eyes, though, differences in short-wave and long-wave ratio can not be perceived as such, and the fruits with high PC2 values belong to different colour categories. However, knowledge on the avian perception system is too scarce to exclude the possibility, that birds have the visual abilities to perceive differences in wavelength ratio and to extract information conveyed in this aspect of fruit colour. Only few studies investigated correlations between colour and nutrient content. Wheelwright & Janson (1985) did not find any correlation with nutritional compounds, but they only analysed few nutritional traits. Herrera (1987) analysed the major chemical compounds and found a decrease of non-structural carbohydrate and mineral content -in association with growth form- from black fruits over orange/red to fruits of different colours. He did not present a hypothesis for these correlations. In this study, non-structural carbohydrates showed no correlation with fruit colour. Mineral contents were not

investigated. Herrera found no correlation between fruit colour and protein content. Both studies, Wheelwright & Janson and Herrera, used human colour classification in their analyses, and both, tannin and protein content were not associated with distinct human colours in this study. Still, clear trends are missing. It is known, that crude protein might not be the relevant content, but rather certain essential amino acids (Izhaki 1998). Due to the birds' sophisticated discrimination abilities even on the level of single amino acids (Levey 1987; Murphy & Pearcy 1993), it cannot be excluded, that signalling takes place on a much finer level and has not yet been found due to only rough analyses of major nutrient compounds.

The multiple regression explains 37% of the variance, and other factors have to account for the remaining 64%. However, information provided by fruit colour is possible. A further analysis on the information about fruit chemistry conveyed by fruit colour requires more knowledge on micronutritional composition of fruits, the importance of specific micronutrients for consumers and on their visual system.

Cited literature

Asmussen, C.B. & Chase, M.W. (2001): Coding and noncoding plastid DNA in palm systematics. Am. J. Bot. 88: 1103-1117.

Arts, I.C.W., Hollmann, P.C.H., Feskens, E.J.M., Bueno de Mesquita, H.B. & Kromhout, D. (2001): Catechin intake might explain the inverse relation between tea consumption and ischemic heart disease: the Zutphen Elderly Study. Am. J.. Clin. Nutr. 74: 227-232.

Bairlein, F. (1996): Fruit-eating in birds and its nutritional consequences. Comp. Biochem. Physiol. 113A: 215-224.

Ballinger, W.E. & Kushman, L.J. (1970): Relationship of stage of ripeness to composition and keeping quality highbush blueberries. J. Amer. Soc. Hort. Sci 95: 239-242.

Berthold, P. (1976): Animalische und vegetabilische Ernährung omnivorer Singvogelarten: Nahrungsbevorzugung, Jahresperiodik der Nahrungswahl, physiologische und ökologische Bedeutung. J. Orn. 117: 145-209.

Brouillard, R., Figueiredo, P., Elhabiri, M. & Dangles, O. (1997): Molecular interactions of phenolic compounds in relation to the colour of fruit and vegetable. In Tomás-Barberán, F.A. & Robins, R.J. [eds.]: Phytochemistry of fruit and vegetables. Proceeding of the phytochemical society of Europe, Oxford Science Publications, 29-49.

Cipollini, M.L. & Levey, D.J. (1997): Secondary metabolites of fleshy vertebrate-dispersed fruits: Adaptive hypotheses and implications for seed dispersal. Am. Nat. 346-372.

Clark, L. Shah, P.S. & Mason, J.R. (1991): Chemical repellency in birds; Relationship between chemical structure and avoidance response. J. Exp. Zool. 260: 310-322.

Clifford, M.N. (1997): Astringency. In Tomás-Barberán, F.A. & Robins, R.J. [eds.]: Phytochemistry of fruit and vegetables. Proceeding of the Phytochemical Society of Europe, Oxford Science Publications: 87-107.

DiVenere, D., Linsalata, V., Ippolito, A., Nigro, F., Arcuti, P. & Lattanzio, V. (1998): Endogenous phenolics, ripening and susceptibility of strawberry fruits (Fragaria x ananassa Duch.) to post-harvest diseases. Proc. 2nd Internat. Electronic Conference on Synthetic Organic Chemistry: 224

Dobson, A.J. (1990): An introduction to generalized linear models. Chapman and Hall.

Endler, J.A. (1990): On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41: 315-352.

García, D., Zamora, R., Gómez, J.M. & Hódar J.A. (1999): Bird rejection of unhealthy fruits reinforces the mutualism between juniper and its avian dispersers. Oikos 85: 536-544.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, P., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J.-M. (1985): Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324-337.

Greig-Smith, P.W. (1986): Bicolored fruit displays and frugivorous birds: the importance of fruit quality to dispersers and seed predators. Am. Nat. 127: 246-251.

Harborne, J.B. (1976): Function of flavonoids in plants. In Goodwin, T.W. [ed.]: Chemistry and biochemistry of plant pigments. 2nd ed. Academic Press, New York: pp 736-778.

Herrera, C.M. (1985): Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44: 132-141.

Herrera, C.M. (1987): Vertebrate-dispersed plants on the Iberian peninsula: A study of fruit characteristics. Ecological Monographs 57: 305-331.

Izhaki, I. (1998): Essential amino acid composition of fleshy fruits versus maintenance requirements of passerine birds. J. Chem. Ecol. 24: 1333-1345.

Karlson, P. (1972): Biochemie, 8th ed. Thieme Verlag, Stuttgart, Germany.

Lee, W.G., Wilson, J.B. & Johnson, P.N. (1988): Fruit colour in relation to the ecology and habitat of *Coprosma* (Rubiaceae) species in New Zealand. Oikos 53: 325-331.

Lee, W.G., Weatherall, I.L. & Wilson, J.B. (1994): Fruit conspicuousness in some New Zealand *Coprosma* (Rubiaceae) species. Oikos 69: 87-94.

Levey, D. J. (1987): Sugar-tasting ability and fruit selection in tropical fruit-eating birds. Auk 104: 173-179.

Martins, E.P. & Hansen, T.F. (1997): Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am. Nat. 149: 646-667.

McPhearson, J.M (1987): A field study of winter fruit preferences of Cedar Waxwings. Condor 89: 293-306.

Moermond, T.C. & Denslow, J.S. (1985): Neotropical avian frugivores: patterns of behaviour, morphology and nutrition, with consequences for fruit selection. In Buckley, P.A., Foster, M.S., Morton, E.W., Ridgley, R.S. & Buckley, F.G. [eds.]: Neotropical Ornithology. Ornith. Monogr. 36, 865-897.

Mole, S. & Waterman, P.G. (1985): Stimulatory effects of tannins and cholic acid on tryptic hydrolysis of proteins: Ecological implications. J. Chem. Ecol. 11: 1323-1332.

Murphy, M.E. & Pearcy, S.D. (1993): Dietary amino acid complementation as a foraging strategy for wild birds. Physiology and Behavior 53: 689-698.

Pagel, M. (1994): Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proc. R. Soc. Lond. B 255: 37-45.

Provenza, F.D., Burritt, E.A., Clausen, T.P., Byrant, J.P., Reichardt P.B. & Distel R.A. (1990): Conditioned flavor aversion: a mechanism for goats to avoid condensed tannins in blackbrush. Am. Nat. 136: 801-826.

Rhodes, M.J.C. (1970): The climacteric and ripening of fruits. In Hulme, A.D. [ed.]: The biochemistry of fruits and their products. Academic Press, New York: 521-533.

Schaefer, H.M. (2002): The influence of fruit pulp chemistry on avian fruit choice. PhD thesis, University of Oldenburg, Germany.

Sedinger, J.S. (1990): Are plant secondary compounds responsible for negative apparent metabolizability of fruits by passerine birds? A comment on Izhaki and Safriel. Oikos 57: 138-140.

Selway, J.W.T. (1986): Antiviral activity of flavones and flavans. In Cody, V., Middleton, E. Jr. & Harborne, J.B. [eds.]: Plant flavonoids in biology and medicine. Allan R. Liss, Inc. New York: 521-536.

Snow, D.W. (1971): Evolutionary aspects of fruit-eating by birds. Ibis 113: 194-202.

Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D., Zanis, M., Savolainen, V., Hahn, W.H., Hoot, S.B., Fay, M.F., Axtell, M., Swensen, S.M., Prince, L.M., Kress, W.J., Nixon, K.C. & Farris-Soltis, D. (2000): Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. Bot. J. Linn. Soc. 133: 381-461.

Tabak, C., Arts, I.C.W., Smit, H.A., Heederik, D. & Kromhout, D. (2001): Chronic Obstructive Pulmonary Disease and Intake of Catechins, Flavonols, and Flavones. Am. J. Respir. Crit. Care Med. 164: 61-64.

van Buren, J. (1970): Fruit Phenolics. In Hulme, A.D. [ed.]: The biochemistry of fruits and their products. Academic Press, London: 269-304.

Wheelwright, N.T. & Janson, C.H. (1985): Colors of fruit displays of bird dispersed plants in two tropical forests. Am. Nat. 126: 777-799.

Willson, M.F. (1994): Fruit choices by captive American robins. Condor 96: 494-502.

Willson, M.F. & Hoppes, W.G. (1986): Foliar "flags" for avian frugivores: signal or serendipity? In Estrada, A. & Fleming T.H. [eds.]: Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht: 55-69.

Willson, M.F. & Melampy, M.N. (1983): The effect of bicolored fruit displays on fruit removal by avian frugivores. Oikos 41: 27-31.

Willson, M.F. & Thompson, J.N. (1982): Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are 'green'. Can. J. Bot. 60: 701-713.

Willson, M.F. & Whelan, C.J. (1990): The evolution of fruit color in fleshy-fruited plants. Am. Nat. 136: 790-809.

Red and black fruits - can their prevalence be explained?

Abstract

The signal hypothesis postulates, that fruit colours act as long-range signals to attract frugivores. Red and black fruits as the most common should then be more conspicuous than others. Conspicuousness is defined as the contrast between fruit and background. Contrast calculations between colour spectra were done using the Euclidean distance. Red and black fruits exhibit greater colour contrasts than fruits of other colours, regardless of habitat and environmental light. Brightness differences were disregarded due to the light-dark-adaptation abilities of birds. In most multi-coloured displays, secondary structures or pre-mature fruits enhance the conspicuousness of displays in comparison to the contrast between ripe fruits and background only. These findings strongly support the signal hypothesis. The influence of conspicuousness on fruit choice in birds should be investigated.

Introduction

Conspicuousness of fruit colours

The patterns of fruit colour have been investigated for plant species in tropical, neotropical and temperate zones, and the dominance of red and black fruits has been documented in most studies (Willson & Whelan 1990, and references therein). One hypothesis on the evolution of fruit colour is that it serves as a conspicuous advertising long-distance signal. According to this signal hypothesis, red and black fruits should exhibit greater contrast to their natural background than other fruit colours, leading to enhanced conspicuousness and increased fruit removal and seed dispersal (Wheelwright & Janson 1985; Willson & Whelan 1990). The perceived colour of an object is influenced by illumination, and a change in the spectral composition of the ambient light can severely change the perceived colour and therefore conspicuousness (Endler 1990). Illumination varies among habitats. In a forest, illumination in the understory is usually less intense than in the canopy, and a broken leave cover or a treefall gap allows more light to reach the understory than an intact canopy, and spectral composition of the light in these habitats differs (Endler 1993). The perception of colour contrasts also depends on the discrimination abilities of a visual system. In the avian visual system, little is yet known about the neural processing leading to the perception of different hues or the ability of colour discrimination. In mammalian vision, colour discrimination abilities differ between wavelength segments in the visible spectrum. Primates e.g. have the

finest tuning in red and green contrasts, and this may also be the case in birds (Neumeyer 1991). To objectively assess the conspicuousness of fruit colours, I compared the contrasts of the spectral curves of different fruit species against their natural background under natural illumination conditions.

Consumer composition and conspicuousness

It has been discussed that fruit colours facilitate quick food recognition, and that this might be important for migrating bird species (Grant 1966; Grant & Grant 1968; see Willson & Whelan 1990 for discussion). It could also be argued, that specialised frugivores, which need to cover all their nutritional requirements by fruit consumption, respond more readily to a conspicuous signal than opportunistic omnivorous species with a more flexible diet. I tested this hypothesis by investigating, whether specialised frugivores were more abundant in plant species with conspicuous fruits than opportunistic birds.

Contrast optimisation

If conspicuousness of fruits has been favoured in evolution, certain fruit colours could be associated with specific habitats or illumination conditions, i.e. light environments (Willson and Whelan 1990). To test this hypothesis, I first compared the fruit colour distribution in all habitats and light environments. Then I examined, whether fruits found in a certain light habitat are adapted to that habitat by having maximised the contrast. According to this hypothesis, fruits typical for a certain locality should exhibit greater contrasts to their background under the specific light conditions than fruits from other habitats.

Multi-coloured fruit displays

The existence of brightly coloured secondary structures and the colour changes of adjacent plant structures during fruit ripening, as well as the simultaneous presentation of differently coloured mature and pre-ripe fruits has led to the assumption that multi-coloured fruit displays have evolved in favour of enhanced conspicuousness and to attract frugivores (Morden-Moore & Willson 1982; Willson & Melampy 1983; see also Greig-Smith 1986). To assess the contribution of accessory structures to fruit display conspicuousness, I compared the contrast between all involved plant structures.

Methods

Conspicuousness of fruit colours

Reflectance spectra of fruit and background, as well as ambient light spectra were taken as described in chapter 2. To measure the contrasts between fruit and background pattern, I took the average reflectance spectrum of the fruit sample. For the background I calculated an average spectrum consisting of the estimated proportion contributed by each structure (such as top side and backside of leaves and bark, without brightly coloured secondary structures) to the overall background pattern. Additionally, I measured ambient light spectra of all light environments in different vegetation heights of the forest. I then multiplied the mean reflectance spectra of both, fruit and background sample, with the mean ambient light spectrum of the corresponding height and light environment (see Endler 1990 for details). This yielded the photon flux (μmol m^{-2} s^{-1} nm^{-1}) that reaches a receiver. Brightnesses were calculated as photon flux per unit area (μmol $\cdot$ m^{-2} $\cdot$ s^{-1}).

Contrast is usually calculated as the Euclidean Distance. But due to different discrimination abilities between wavelength segments, colour space is usually distorted to some extent, and the Euclidean Distance is therefore only a generalised estimate of contrast. It can be assumed, however that in general, greater Euclidean Distances between spectra will also represent greater colour contrasts, even if this might not hold for all specific perceivers.

To investigate colour contrast as well as differences in brightness, I normalised spectra to the same brightness (similar to Endler 1990) and considered both aspects separately. Brightness contrast Δ_T was obtained by the difference between total brightness Q_T of both, fruit and background spectra after multiplication with the ambient light:

$$Q_T \equiv \int Q(\lambda)d\lambda \ \text{ and } \ \Delta_T \equiv \sqrt{(Q_Tf - Q_Tb)^2}$$

with Qf and Qb representing the products of fruit and background reflectance spectra and ambient light spectrum and Q_Tf and Q_Tb as measures of their brightness. Then fruit spectra were normalised to the brightness of background spectra. To obtain a value for colour contrast, the Euclidean Distance D was calculated for the normalised spectra as:

$$D = \sqrt{\sum [Qf(\lambda) - Qb(\lambda)]^2}$$

To test, whether red and black fruits are more conspicuous than fruits of other colours, I used a Mann-Whitney U-Test.

Consumer composition and conspicuousness

To investigate, if plant species with differently conspicuous fruits vary in their consumer composition, I noted all fruit-consuming birds occurring at seven plant species. I then calculated the ratio of mainly frugivorous birds versus more opportunistic species and correlated the proportion with the values of fruit colour contrast. I categorised frugivores according to the extent of fruits in their diet. Species with a diet of more than 80% of fruits were regarded as specialised, all others as opportunistic species. Data are based on own observations and Ertan (1999).

Contrast Optimisation

The hypothesis on habitat correlated fruit colour distribution was tested by assigning the PC2 scores of all fruits (see chapter 3) to combined categories of habitat (i.e. understory, midstory, canopy and savannah) and light environment (i.e. forest shade, small gap, woodland shade and large gap), depending on their locality and the light environment in which they mainly occur. I then performed a Kruskal-Wallis test to detect differences among these categories. I also used this method to test effects of light environment and habitat separately. For the further investigation of contrast optimisation in relation to habitat, fruits and background from the understory were multiplied with irradiance spectra from the canopy and *vice versa*. I chose two very contrasting localities, forest shade in the understory and a large gap in the canopy, and "illuminated" fruits of both localities with both irradiance spectra. I tested with a Mann-Whitney Test, whether fruits show greater contrast values in their specific habitat than fruits of other habitats. I combined fruits from 2m and 6m growing in forest shade into one group as well as fruit species from 22m and 26m growing under large gap conditions into the other group.

Multi-coloured fruit displays

I measured the reflectance spectra of all accessory structures, i.e. brightly non-green coloured secondary structures adjacent to the fruit, and pre-ripe stadiums of *Goupia glabra* and calculated the contrasts of these structures to the leafy background and the ripe fruit. If contrasts between an accessory structure to the fruit or to the background were greater than the contrast between mature fruit and background, the secondary structures or pre-ripe fruits were regarded to enhance conspicuousness.

Results

Conspicuousness of fruit colours

Brightness contrasts were positively correlated with the total brightness Q_T of the ambient light spectrum in the corresponding light environment (r= 0.625; p< 0.001; Fig. 5.1). The Euclidean Distances of brightness-normalised spectra showed differences between certain fruit colours. Red and black fruits contrasted more with their background than fruits of other colours (Table 5.1; Mann-Whitney-Test; U= 130.0; z= -2.435; n= 43; p= 0.015). There was no difference in colour contrast between red and black fruits (U= 52.0; z= -0.693; n= 23; p= 0.488).
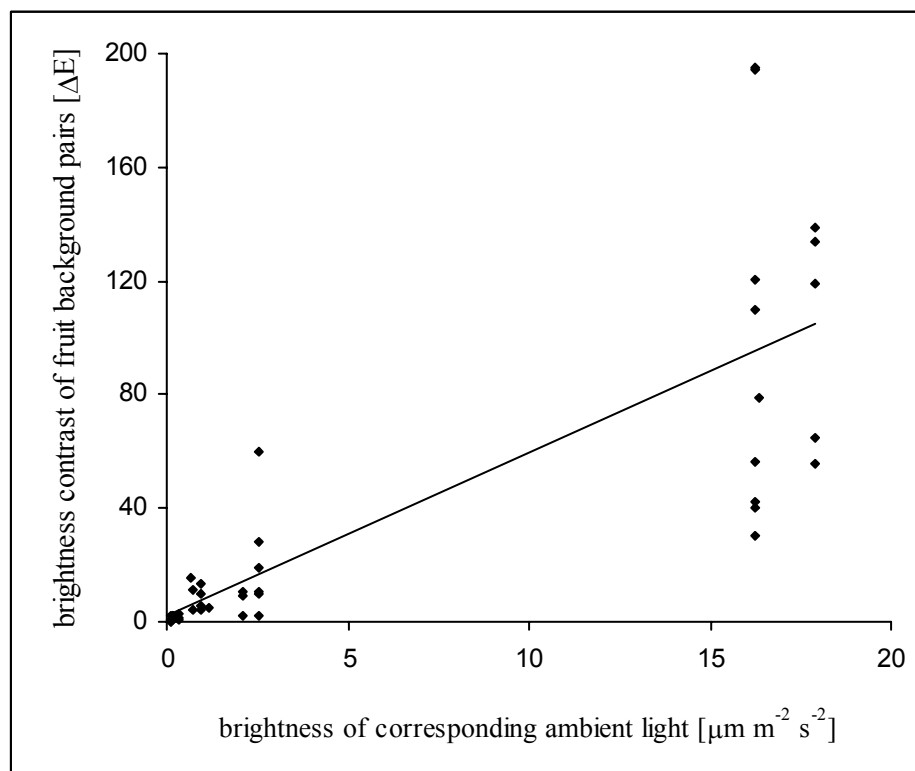

Fig. 5.1: Correlation of brightness contrast between fruits and background with the total brightness of ambient light. Since no fruits occurred mainly in small gaps, the ambient light of this light environment is missing.

Contrast optimisation

In the investigation of ecological correlations of locality and fruit colour (represented as PC2 scores), I found neither effects on fruit colour of the combined habitat/light environment categories (Kruskal-Wallis-Test, χ^2= 4.036; n= 40; df= 5; p= 0.544), nor for each of these factors alone (habitat: χ^2= 1.528; df= 3; p= 0.676; light environment: χ^2= 3.153; df= 2; p= 0.207).

Table 5.1: Brightness contrast under natural illumination and colour contrast of brightness-normalised spectra with colour in human perception for comparison. Colours are assigned into colour categories. Contrasts are measured as the Euclidean Distance.

species	brightness contrast	colour contrast	*human colour*
Dacryodes microcarpa	133.726	303.606	black
Trattinickia bursereaefolia	139.029	212.525	black
Goupia glabra	78.527	211.947	black
Ouratea sp.2	119.078	199.009	black
Ocotea aff. Amazonica	109.761	190.860	black
Miconia sp.1	55.308	141.323	black
Oenocarpus bacaba	2.386	56.712	black
Euterpe precatoria	28.007	53.439	black
Cybianthus spicatus	10.382	42.395	black
Guatteria schomburgkiana	10.561	26.018	black
Dendrobangia boliviana	5.828	11.546	black
Geonoma deversa	0.398	1.600	black
Ouratea sp.1	0.403	0.652	black
Melastomataceae Genus sp. 1	4.571	7.077	bluish black
Miconia sp.2	5.174	6.009	bluish black
Melastomataceae Genus sp. 2	0.170	0.785	bluish black
Clusia columnaris	64.746	437.402	red
Heisteria scandens	194.093	354.009	red
Pseudolmedia laevigata	42.521	213.282	red
Xylopia venezuelana	120.469	188.011	red
Iryanthea elliptica	9.853	55.231	red
Retiniphyllum schomburgkii	9.500	43.772	red
Iryanthea jurensis	2.741	19.204	red
Trichilia sp.	9.530	12.625	red
Fabaceae sp.	2.052	2.032	red
Paullinia capriollata	517.624	211.830	white
Phoradendron pellucidulum	2.329	26.568	white
Protium sp.	60.101	14.523	white
Dacryodes c.f. glabra	13.421	9.790	white
Diclinanona calycina	15.792	5.051	white
Psychotria sp.	2.183	0.610	white
Orthomene schomburgkii	195.111	182.743	yellow
Melastomataceae Genus sp. 3	0.873	2.889	yellow
Pouteria sp.1	2.028	1.902	yellow
Picramnia sp.	1.981	1.434	yellow
Kutchubaea sp.	4.091	7.694	brown
Iriantella setigera	0.393	1.364	brown
Caryocar glabrum	18.938	22.371	brownish-yellow
Pouteria sp.2	10.977	10.638	brownish-yellow
Emmotum acuminatum	56.091	137.539	orange
Tovomita c.f. umbellata	1.543	5.300	orange
Noranthea sp.	30.616	125.852	pink
Couma utilis	40.096	68.203	green

The "illumination" of fruit spectra with irradiance spectra from both, forest shade in the understory and large gap in the canopy, showed no differences in contrasts between fruits belonging or not belonging to these habitats, neither in the understory (Mann-Whitney Test; U= 33.0; Z= -0.622; n= 18; p= 0.534), nor in the canopy (U= 37.0; Z= -0.267; n= 18; p= 0.79).

Consumer composition and conspicuousness

The estimated consumer compositions among plant species differed, but this was not associated with differences in the conspicuousness of fruits (Pearson coeff.= -0.268; n= 7; p= 0.562).

Multi-coloured fruit displays

The sample comprised eight plant species with brightly coloured structures associated with the ripe fruit, including capsules (5) , stems (2) and exocarp (1). In all plants except one (*Dacryodes c.f. glabra*), secondary structures enhance the contrast, either due to greater contrast to the fruit or to the leafy background (Table 5.2). The differences in the contrast values of particular species are due to the different natural illumination conditions.

Table 5.2: Species with bi-coloured displays due to adjacent plant structures. The differences in the Euclidean Distances show, that most secondary structures contribute to conspicuousness.

species	type of structure	fruit vs. leaves	sec. structures vs. leaves	sec. structures vs. fruit
Noranthea spec.	capsule	125.852	175.726	67.626
Dacryodes c.f. glabra	capsule	**9.790**	8.168	6.991
Ouratea sp. 2	stem	199.009	351.072	305.600
Miconia sp. 1	stem	141.323	359.169	308.109
Paullinia capriolata	capsule	211.830	521.186	464.033
Tovomita c.f. umbellata	exocarp	5.300	8.444	5.613
Protium spec.	capsule	14.523	63.793	61.665
Geonoma deversa	racimo	0.430	0.912	1.600

Even though many other fruit species have bi-coloured displays due to the simultaneous presentation of pre-ripe and ripe stadiums, I only found few during the field season. I restricted the study to ripe fruits, except for *Goupia glabra*, which exhibits several pre-ripe stadiums with distinct colours. While green and yellow ripening stages have smaller contrasts to the leafy background, bright red and dark red fruits show greater contrasts than black ripe

fruits (Table 5.3). The multi-coloured fruit display also enhances contrast due to greater colour differences between pre-ripe and mature fruits than between black fruits and green leaves.

Table 5.3: Contrasts of colour stages (in ripening order) of *Goupia glabra* towards leafy background or ripe black fruits. Note the contrast between black and green fruits.

colour stage	fruit vs. leaves	ripe black fruit vs. unripe fruit
green	92.342	244.478
yellow	159.668	211.194
bright red	235.338	227.801
dark red	224.365	138.502
black	211.947	--

Discussion

Conspicuousness of fruit colours

Brightness contrast is correlated with brightness changes in the ambient light. Ambient light differs also in spectral composition, but by far most of the changes in illumination between habitats are due to differences in brightness. Contrasts increase with the intensity of illuminating light numerically, but this might not reflect, how birds perceive these contrasts. The Weber-Fechner Law states that the absolute change in sensation is proportional to the relative change in the stimulus. It applies to human perception (Wyszecki & Stiles 1982), and is also assumed to operate in birds (Vorobyev et al. 1998). Furthermore, the light-dark-adaptation mechanisms of the vertebrate eyes suggests, that contrasts in bright sunlight are not necessarily perceived as being greater than in less illuminated habitats. Sensitivity to the achromatic component of colour is low in bright illumination, at least for static targets subtending a large visual angle for both, humans and bees (Backhaus 1991; King-Smith & Carden 1976; Thornton & Pugh 1983; Vorobyev & Osorio 1998). The light-dark-adaptation abilities of birds have not yet been thoroughly investigated, but it can be assumed, that they at least match the abilities of the human eye, which can adapt to light intensity changes of roughly 10^{10} (Sauermost 1994). Colour contrasts are probably not modified to a great extent in the visual system and are therefore a better approach to investigate conspicuousness. Moreover, it has been shown, that birds choose hue, rather than brightness in both, mate choice and fruit selection (Puckey et al. 1996; Pearn et al. 2001). The results show, that red and black, the most common ripe fruit colours in neotropical and temperate zones, are also the

most conspicuous ones. Conspicuousness is a trait applying to the visual abilities of the observer. Therefore, selection for conspicuous fruit displays will only be exerted by frugivores with good colour vision. Most fruit-eating mammals are known to have poor colour vision and to be night-active, when colour vision is not possible (e.g. Willson & Thompson 1982; Knight & Siegfried 1983). Birds on the contrary are endowed with a highly developed visual system, with four receptor types and vision extending into the UV (e.g. Burkhardt 1996; Chen & Goldsmith 1986). Mainly mammal- and mainly bird-dispersed fruits have often been distinguished. Red and black fruits are usually small and have been associated with avian dispersers (e.g. Snow 1971; Knight & Siegfried 1983; Fischer & Chapman 1993; Gautier-Hion et al. 1985; Korine et al. 2000). Red and black fruits were smaller than fruits of other colours in my study site, too (see chapter 3). The evolution of colours in fruit species consumed mainly by birds might be driven by selection for conspicuousness, while in species mainly dispersed by night-active mammals, other traits might influence selection. To concentrate on the role of conspicuousness, a study should thus be limited to bird-dispersed species, since ignoring this dichotomy might confound the results. In this sample, fruit species are comprised independently of their consumer spectra, fruits were mainly eaten from birds, but also night-active mammals (pers. obs.). Lee et al. (1988, 1994) have also investigated the conspicuousness of different fruit colours in *Coprosma* species in New Zealand. Mainly birds and some small lizards and one frugivorous bat consume these fruits. However, they based their study on the human chromaticity diagram of the CIE standard observer and used the CIE standard illuminants for ambient light, which does not adequately account for all different light habitats. But they also found that red and black (though only 2 species were available) exhibit greater contrasts to their natural background than other colours. The present study, using a more objective colour assessment and based on a large data set including a high proportion of black and red fruits, corroborates their results. Lee et al (1994) suggest, that their findings support the hypothesis of Poston & Middendorf (1988), that red and black fruits can be considered as equivalents due to similar energy yield. This is doubtful for two reasons. First, Poston & Middendorf (1988) limited their analysis to pre-ripe and ripe stadiums of one fruit species and did not assume that red and black fruits are generally equivalent. Second, they did not analyse major nutrients such as lipids, protein or sugar, nor secondary compounds, which are abundant in pre-ripe fruits (e.g. van Buren 1970; Häkkinen 2000). Schaefer (2002) showed that pre-ripe fruits generally yield less energy and possess higher concentrations of phenolic compounds than ripe fruits. Though birds can cope with a high amount of secondary metabolites (Bairlein 1996), it has also been

shown, that they do limit food intake and protein digestion (Guglielmo & Karasov 1996; Provenza et al. 1990). Aviary experiments showed that birds prefer mature to unripe fruits (e.g. Moermond & Denslow 1983; Garcia et al. 1999). In fact, red and black fruits are equally conspicuous against their background, but analyses showed, that mature red and black fruits differ well in energy yield, also within colours (see chapter 4), as well as between ripening stadiums in the same species (e.g. *Goupia glabra*, Schaefer 2002).

Black fruit colour can be achieved by high concentrations of colour pigments, and also through co-pigmentation with e.g. tannins, which might occur in fruits with high tannin concentrations in order to reduce astringency (Willson & Whelan 1990, see also chapter 4). It is remarkable that one of the most conspicuous colours, red, appears in ripe as well as in pre-ripe fruits. Since I did not measure enough red pre-ripe stadiums, I cannot compare colour contrasts between red pre-ripe and red ripe fruits. Conspicuous pre-ripe fruits may have the function to announce the ripening process for resident frugivores, but prevent consumption through higher levels of secondary metabolites. Birds are known to remember localities after previous visits (e.g. Hitchcock & Sherry 1990; Hurley & Healy 1996), and several frugivorous bird species were observed flying long distances straight to a certain fruit species (*Noranthea sp.*) as soon as fruits were ripe, or even removed the capsule of not yet open fruits (pers. observation).Therefore, the announcement of the ripening process could lead to enhanced fruit consumption of ripe fruits and thus improved seed dispersal.

Consumer composition and conspicuousness

Mainly frugivorous species are dependent on fruiting plants and need to cover their nutritional needs by fruit consumption. Red fruits have been shown to have generally high protein contents (chapter 4) and might be an important protein source for frugivores, whereas omnivorous birds may cover their protein requirements with insect food. However, I found no correlation between consumer composition and conspicuousness of fruit colour in seven plant species with high consumer diversity.

Contrast optimisation

I did not find, that plants optimise the contrast of their fruits with respect to particular habitats. Wheelwright & Janson (1985) report that bright fruit colours (red, orange, yellow and white) were more abundant in the understory than in higher forest levels. In the canopy, they found more black fruit species than expected, but this applied only to one neotropical site and could not be documented in the other studied neotropical location or in temperate zones

(Wheelwright & Janson 1985). Willson & O'Dowd (1989) found no correlation with habitat in the polymorphic fruits of *Rhagodia parabolica*. The results of the present study are consistent with their findings. Forest shade in the understory is the habitat with the lowest illumination, while a large gap in the canopy is very bright. If contrast optimisation has evolved, it should be noticeable in the comparison between these two localities. But there were no differences between the contrasts of habitat specific and foreign fruit species. However, it must be kept in mind that the Euclidean Distance constitutes only an estimate of contrast, and furthermore that contrasts between physical spectra may not adequately reflect contrasts as perceived by birds.

Multi-coloured fruit displays

It has often been discussed, that bi-coloured displays enhance conspicuousness, but this has never been quantified. This study demonstrates that brightly coloured secondary structures associated with the ripe fruit increase conspicuousness. In the multi-coloured display of *Goupia glabra*, colours simultaneously displayed with ripe fruits partly show greater contrasts to the leafy background or to the black fruit than the ripe fruit alone to the leafy background. Structures such as stems, that change colour during the ripening process, might have evolved to favour conspicuousness. Brightly coloured structures such as the red capsule of *Protium sp*. could also serve to announce maturing fruits before dehiscence.

In conclusion, this study has documented that the dominant fruit colours red and black are also the most conspicuous ones with respect to their natural background. Multi-coloured fruit displays can enhance conspicuousness, either by adjacent plant structures or by the simultaneous presentation of pre-ripe and mature fruits. Many factors influence the evolution of fruit colour, but this study shows, that being conspicuous may be important for bird-dispersed fruits.

Cited literature

Backhaus, W. (1991): Color opponent coding in the visual system of the honeybee. Vision Res. 31: 1381-1397.

Bairlein, F. (1996): Fruit-eating in birds and its nutritional consequences. Comp. Biochem. Physiol. 113A: 215-224.

Burkhardt, D. (1996): Die Ultraviolett-Tüchtigkeit des Vogelauges und einige Konsequenzen. Naturwiss. 83: 492-497.

Chen, D.-M. & Goldsmith, T.M. (1986): Four spectral classes of cone in the retinas of birds. J. Comp. Physiol., A 159: 473-479.

Endler, J.A. (1990): On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41: 315-352.

Endler. J.A. (1993): The color of light in forests and its implications. Ecol. Monogr. 63: 1-27.

Ertan, A. (1999): Spezialisation und Koevolution von fruchtfressenden Vögeln. Master thesis, Universität Konstanz, Germany.

Fischer, K.E. & Chapman, C.A. (1993): Frugivores and fruit syndromes: differences in patterns at the genus and species level. Oikos 66: 472-482.

García, D., Zamora, R., Gómez, J.M. & Hódar J.A. (1999): Bird rejection of unhealthy fruits reinforces the mutualism between juniper and its avian dispersers. Oikos 85: 536-544.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, P., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J.-M. (1985): Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324-337.

Grant, K.A. (1966): A hypothesis concerning the prevalence of red coloration in California hummingbird flowers. Am. Nat. 100: 85-97.

Grant, K.A. & Grant, V. (1968): Hummingbirds and their flowers. Columbia University Press, New York.

Greig-Smith, P.W. (1986): Bicolored fruit displays and frugivorous birds: the importance of fruit quality to dispersers and seed predators. Am. Nat. 127: 246-251.

Guglielmo, C.G., Jakubas, W.J. & Karasov, W.H. (1996): Nutritional costs of a plant secondary metabolite explain the selective foraging by ruffed grouse. Ecology 77: 1103-1115.

Häkkinen, S. (2000): Flavonols and phenolic acids in berries and berry products. Doctoral Thesis. Kuopio University Publications D. Medical Sciences 221.

Hitchcock, C.L. & Sherry, D.F. (1990): Long-term memory for cache sites in the blackcapped chickadee. Anim. Behav. 40: 701-712.

Hurly T.A. & Healy, S.D. (1996): Memory for flowers in rufous hummingbirds: location or local visual cues? Animal Behaviour 51: 1149-1157.

King-Smith, P.E. & Carden, D. (1976): Luminance and opponent color contributions to visual detection and adaptation and to temporal and spatial integration. J. Opt. Soc. Am. 66: 709-717.

Knight, R.S. & Siegfried, W.R. (1983): Inter-relationships between type, size and colour of fruits and dispersal in Southern African trees. Oecologia 56: 405-412

Korine, C., Kalko, E.K.V. & Herre, E.A. (2000): Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. Oecologia 123: 560-568.

Lee, W.G., Wilson, J.B. & Johnson, P.N. (1988): Fruit colour in relation to the ecology and habitat of *Coprosma* (Rubiaceae) species in New Zealand. Oikos 53: 325-331.

Lee, W.G., Weatherall, I.L. & Wilson, J.B. (1994): Fruit conspicuousness in some New Zealand *Coprosma* (Rubiaceae) species. Oikos 69: 87-94.

Moermond, T.C. & Denslow, J.S. (1983): Fruit choice in neotropical birds: Effects of fruit type and accessibility on selectivity. J. Anim. Ecol. 52: 407-420.

Morden-Moore, A.L. & Willson, M.F. (1982): On the ecological significance of fruit color in *Prunus serotina* and *Rubus occidentalis*: Field experiments. Can. J. Bot. 60: 1554-1560.

Neumeyer, C. (1991): Evolution of colour vision. In Cronly-Dillon. R.J. & Gregory, R.L. [eds.]: Vision and visual dysfunction Vol. 2 Evolution of the eye and visual system. Macmillan Press, Basingstoke: 285-305.

Pearn, S.M., Bennett, A.T.D. & Cuthill, I.C. (2001): Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. Proc. R. Soc. Lond. B 286: 2273-2279.

Poston, M.E. & Middendorf III, G.A. (1988): Maturation characteristics of *Rubus pennsylvanicus* fruit: are red and black the same? Oecologia 77: 69-72.

Provenza, F.D., Burritt, E.A., Clausen, T.P., Byrant, J.P., Reichardt P.B. & Distel R.A. (1990): Conditioned flavor aversion: a mechanism for goats to avoid condensed tannins in blackbrush. Am. Nat. 136: 801-826.

Puckey, H.L., Lill, A. & O'Dowd, D.J. (1996): Fruit color choices of captive silvereyes (*Zosterops lateralis*). Condor 98: 780-790.

Sauermost, R. [ed] (1994): Lexikon der Biologie. Spektrum-Verlag Heidelberg, Berlin, Oxford.

Schaefer, H.M. (2002): The influence of fruit pulp chemistry on avian fruit choice. PhD thesis, University of Oldenburg, Germany.

Snow, D.W. (1971): Evolutionary aspects of fruit-eating by birds. Ibis 113: 194-202.

Thornton, J.E. & Pugh, E.N. (1983): Red-green color opponency at detection threshold. Science 219: 191-193.

van Buren, J. (1970): Fruit Phenolics. In Hulme, A.D. [ed.]: The biochemistry of fruits and their products. Academic Press, London: 269-304.

Vorobyev, M. & Osorio, D. (1998): Receptor noise as a determinant of colour thresholds. Proc. R. Soc. Lond. B 265: 351-358.

Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J. & Cuthill, I.C. (1998): Tetrachromacy, oil droplets and bird plumage colours. J. Comp. Physiol. A 183: 621-633.

Wheelwright, N.T. & Janson, C.H. (1985): Colors of fruit displays of bird dispersed plants in two tropical forests. Am. Nat. 126: 777-799.

Willson, M.F. & Melampy, M.N. (1983): The effect of bicolored fruit displays on fruit removal by avian frugivores. Oikos 41: 27-31.

Willson, M.F. & O'Dowd, D.J. (1989): Fruit color polymorphism in a bird-dispersed shrub (*Rhagodia parabolica*) in Australia. Evol. Ecol. 3: 40-50.

Willson, M.F. & Thompson, J.N. (1982): Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are 'green'. Can. J. Bot. 60: 701-713.

Willson, M.F. & Whelan, C.J. (1990): The evolution of fruit color in fleshy-fruited plants. Am. Nat. 136: 790-809.

Wyszecki, G. & Stiles, W.S. (1982): Color science, concepts and methods, quantitative data and formulae, 2nd ed. John Wiley, New York.

Colour and conspicuousness - how to get chosen by a bird

Abstract

To explain the commonness of red and black fruits, birds have been suggested to exhibit a general colour preference for these hues. Furthermore, migrant species could use red as a cue for quick food recognition in unknown areas with unfamiliar fruit species. This could also be the case in juveniles after fledging. In central Europe, red fruits are very dominant in early summer, when juveniles leave the nest. A genetic predisposition to associate red with edible fruits could facilitate food search. These hypotheses were tested in cafeteria choice experiments. I found no general preference for any colour in all species. However, there were indicated preferences for specific colours among bird species. The hypothesis on colour cues in migrant species was not supported. Adult Blackcaps consumed fruits randomly, while juvenile Blackcaps strongly favoured red fruits. Hence, a genetic predisposition seems to exist, which gets then overridden by learning and experience resulting in random food choice in adult Blackcaps. This should further be tested in other European migratory species. The influence of conspicuousness on fruit choice was tested in choice experiments with uni-coloured and contrasting displays. Birds consistently chose the contrasting display, disregarding of fruit colour. Hence, conspicuousness plays a great role in fruit choice, corroborating the findings of chapter 5 and the signal hypothesis.

Introduction

Fruit selection by avian frugivores has often been regarded as an explanation for the current fruit colour distribution. A number of both, field and aviary experiments have been conducted to test, whether birds choose fruits on the basis of colour (e.g. McPhearson 1987, 1988; Willson 1994; Willson & Comet 1993; Willson et al. 1990; Gervais et al. 1999). But most of these experiments failed to provide strong evidence for consistent colour choices (Willson et al. 1990), and the question remains yet unsolved. The studies are difficult to compare due to different species and methods and also due to the inherent complexity of fruit colour choice (Whelan & Willson 1994). The complexity lies in the different natural contexts, in which fruit colour is presented, the abundance and diversity of frugivorous species, and the different experience of tested individuals. It is therefore necessary to address different aspects separately. First, the prevalence of red and black fruits leads to the question, whether these

colours are genuinely preferred by avian frugivores, or whether birds exhibit a ranking between different fruit colours at all. If red and black fruits are favoured by birds, their colour choice might have led to the present colour distribution in fleshy fruits (Willson & Whelan 1990). A second hypothesis presented by Willson and Whelan (1990) postulates that fruit colours act as a signal for quick food recognition in migrant birds. Moreover, quick food recognition is important for juveniles, which could benefit from the association of colour with "good" food in their learning process after fledging. In Central Europe, there is a very pronounced dominance of red fruits in early summer, when juveniles fledge and start searching for food (Snow & Snow 1988). This prevalence is less distinct in late summer and autumn. Therefore, a genetically embodied predisposition for red fruits to facilitate quick food recognition and the prevalence of red fruits in that time span could have co-evolved (Bairlein pers. comm.). This has yet not been investigated, since experiments often include birds caught in the wild of different age and experience which can differ in their colour preference due to the consumption of fruit species in the wild prior to the experiments, and this impedes the interpretation of the results. A third hypothesis addressed in the paper of Willson & Whelan (1990) states, that fruit colour serves as a long-range signal advertising fruit crop, and that the most conspicuous fruits are more readily seen and eaten than inconspicuous fruits. This hypothesis has already been approached in chapter 5, demonstrating that red and black fruits are more conspicuous against their natural background than fruits of other colours. Hence, since the most common colours are also the most conspicuous ones, conspicuousness rather than colour itself might be responsible for fruit choice. Fruits are always presented in a certain visual context. Background and fruit often show a distinct colour contrast, and fruits of different maturity stages or other accessory structures can enhance fruit conspicuousness (chapter 5).

The aim of the aviary experiments presented here was therefore to investigate, whether i) birds exhibit a colour preference for red fruits or otherwise show a fine-tuned ranking between fruit colours, ii) migrant species show a predilection of red fruits, or a genetic predisposition in juveniles for the preference of red fruits exists, and iii) the conspicuousness of fruit displays, either due to contrasting background or by simultaneously presenting pre-mature fruits, influences fruit choice.

Methods

For the experiments on the general preference of red fruits and the colour ranking (i), as well as the influence of conspicuousness on colour choice (iii), I used three species of neotropical tanagers, Green Honeycreepers (GH, *Chlorophanes spiza*), Blue Dacnis (BD, *Dacnis cayana*) and Short-billed Honeycreepers (SH, *Cyanerpes nitidus*), all available in trade. These species were very common at the study plot in Venezuela. For the investigation of a genetically embodied predisposition for red fruits (ii), I chose European Blackcaps (*Sylvia atricapilla*). Adult Blackcaps were mist netted in the Wilhelmshaven area, North Germany, juveniles were taken from nests on app. the third day after hatching. All birds were fed on a standard maintenance diet (see Bairlein 1986) and mealworms (*Tenebrio molitor* larvae). Water was always available *ad libitum*. Birds were held individually in Joko-cages 62 x 40 x 40 cm under constant conditions (GH, BD, SH: LD 12:12; 25°C ± 1°C; app. 70% r.h., Blackcaps: LD 14:10; 20°C ± 1°C; app. 60% r.h.). The experimental trials lasted for 45min and were conducted at the beginning of the light phase to ensure appetitive behaviour in birds.

Artificial fruits

I used artificial fruits for most of the experiments, since natural fruits usually differ in more traits than just colour. Even though they might not resemble natural fruits, they are readily eaten, and their main advantage is the possibility to precisely test one variable, while keeping all other traits constant. Fruits were produced following the recipe of Levey and Grajal (1991). The fruit mass consisted of 100ml H_2O mixed with 1.5g of agar and was heated up to 85°C. Under permanent stirring, 7.5g of glucose and 7.5g of fructose were added. To make fruits opaque, I also added 2.5g of indigestible cellulose. As food dye I used „Crazy colours" by Brauns Heitmann GmbH, Germany, which are absolutely tasteless, and titanium white for white fruits (Puckey et al. 1996). After the mass had cooled down, I portioned it in slices and froze them separately to be able to use the same sample for all consecutive trials to ensure the same colour shade. The colour shade was controlled by measuring and comparing reflectance spectra of slices of the same colour after defrosting. For the experiment fruits were cut into small cubes of the same weight and shape and were presented in petri dishes.

Preference of red fruits

In a first approach I investigated, whether birds exhibit a general colour preference for red fruits. I restricted the experiments to red rather than red and black fruits because the colour

shade of natural black fruits was not possible to obtain with food dye. The trials were done on four consecutive days with the neotropical species (n= 12; GH n= 4; BD n= 5; SH n= 3). In a cafeteria-design, the species were simultaneously exposed to five fruit cubes of different colours. Each of the cubes weighed 5g, which exceeded the birds' consumption within the exposure time. The fruits were presented in petri dishes on a tray at the lattice side of the cage for equal light conditions, and the colour positions were changed between experiments on consecutive days during the four day course. After 45min of exposure to the birds, I collected the unconsumed fruits and food spills and determined the amount eaten of each colour. With a permutation test (Good 1994) I analysed, whether red fruits were preferred over fruits of other colours. Since the design was hierarchical (treatments, species, individuals) and repeated over individuals, permutations were carried out on values centred at zero within individuals (Mundry 1999). The results were statistically evaluated in 10,000 permutations as between treatments variance versus within treatments variance. The permutation tests were performed using unpublished software (H. Winkler, KLIVV, Vienna, Austria). The permutation test yielded both, general choice and preferences among species.

Colour ranking

To analyse colour ranking, I conducted choice experiments with pair-wise colour presentation. These experiments yielded finer tuned preferences and a ranking between colours, which could not be shown in the cafeteria-design experiments. Black artificial fruits were included in these experiments with the constraint of an only rough matching between spectral curves of artificial and natural black fruits. For each colour, I counted the wins and losses over all experiments including that colour and calculated a linear preference from that matrix (analogous to calculations used for social hierarchies, Lehner 1979). The trials were conducted with the three neotropical species (n= 12; GH n= 4; BD n= 5; SH n= 3). I tested with a Kendall test of concordance, whether colour ranking differed among the tanager species.

Genetic predisposition

Since the neotropical species were of different and partly unknown age, I used Blackcaps to investigate, whether a genetic predisposition influences colour choice. Both groups (juveniles n= 10; adults n= 10) were held in different rooms to prevent imitation of feeding behaviour by

juveniles. The experimental design and the statistical analysis were identical to the cafeteria trials explained above.

Influence of contrasting background

To test, whether conspicuousness plays a role in food choice, green fruits were simultaneously presented on a red and a green dish on three consecutive days. The position of both cups were switched daily. In a second trial, red artificial fruits differing from green fruits only in colour were presented on the dishes to eliminate the possibility, that food choice in the first trial had been influenced by the colour red in just one display. The experiment was conducted with the tanager species (n= 14; GH n= 5; BD n= 5; SH n= 4). Birds were held in indoor aviaries of app. 1,20 x 1,20 x 2,40 m. All perches were located above the food cups in a minimum distance of 50 cm.

The influence of simultaneously presented pre-mature fruits of different colour on fruit choice was tested in Venezuela with birds caught in the wild (BD n= 6; SH n= 5; Purple Honeycreeper (*C. caeruleus*) PH n= 3). They were presented two food cups with either 20 black, ripe fruits of *Goupia glabra*, or with 7 additional green unripe fruits of the same species. *G. glabra* fruits were the major food source in the birds' natural diet and were readily eaten during caging. Birds were kept in cages for two weeks before the experiment for habituation and released after the trials, spending a maximum of four weeks in cages. For both experiments, a χ^2-test revealed, if birds preferred one type of display.

Results

Preference of red fruits

When offered a choice of five differently coloured food cubes, the three tanager species exhibited a general preference for red fruits over fruits of other colours ($p<0.001$; red: 0.142 ± 0.055 ($\overline{X}$ ± SD), other: -0.142 ± 0.029). When reanalysed on species level, only Green and Short-billed Honeycreepers selected red fruits, while Blue Dacnis individuals did not prefer any specific colour (GH n= 4, p= 0.0024; BD n=5, p> 0.05; SH n=3, p< 0.001; see Fig. 6.1 A-B).
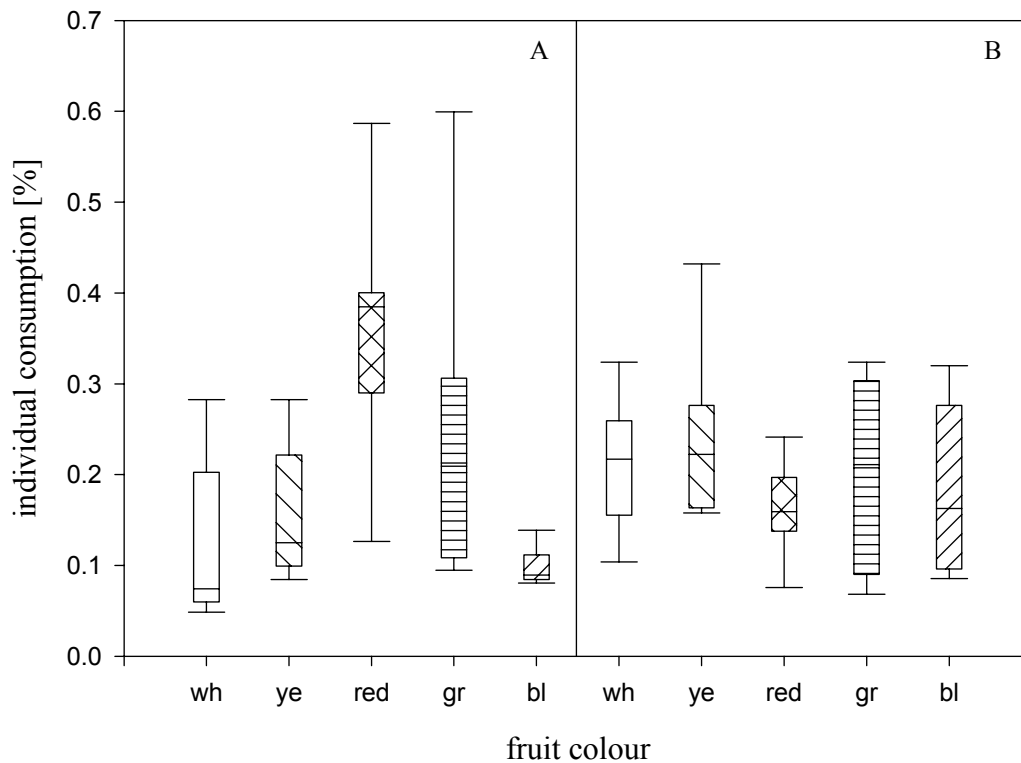
Fig. 6.1 A-B: Colour preferences of Green and Short-billed Honeycreepers (A) and Blue
Dacnis (B) in cafeteria designed experiments. Colour abbreviations as follows: wh
(white), ye (yellow), red (red), gr (green), bl (blue).

Colour ranking

Colour ranking differed in the three tanager species. Green and Short-billed Honeycreepers
showed similar colour predilection (r = 0.964; GH n= 4, SH n= 3; p< 0.001) and preferred red
and green fruits, rejecting white and black. Contrasting to the cafeteria trials, Blue Dacnis
individuals selected blue and white food colours, but showed aversion against red and orange
fruits (Fig. 6.1 B, 6.2). In 66.7% and 72.2% respectively, of all trials including red, Green and
Short-billed Honeycreepers favoured red over the other colour, while Blue Dacnis chose red
in only 33.3% of all cases including red artificial fruits (Fig. 6.2).

Genetic predisposition

Blackcaps did not show a consistent choice of fruit colour (n= 20; p> 0.05; red: $\overline{X} \pm SD$ =
0.0549, 0.049; other: $\overline{X} \pm SD$ = -0.0549, 0.029). But there was a marked difference between
adults and juveniles. While adult birds did not select food by colour, but seemed to consume
differently coloured fruits at random (n= 10; p> 0.05), juveniles preferred red fruits over all
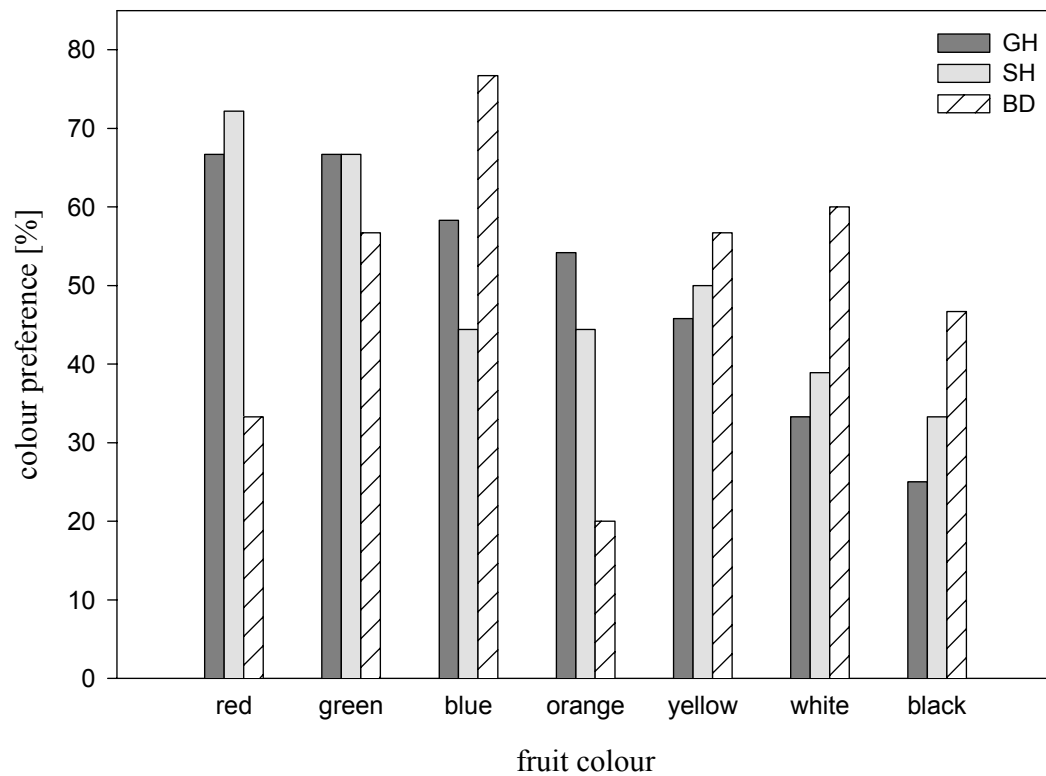other colours (n= 10; p= 0.0029; Fig. 6.3 A-B).

Fig. 6.2: Colour ranking of the three tanager species. Both Honeycreepers show similar preferences, while Blue Dacnis clearly ranks colours differently.
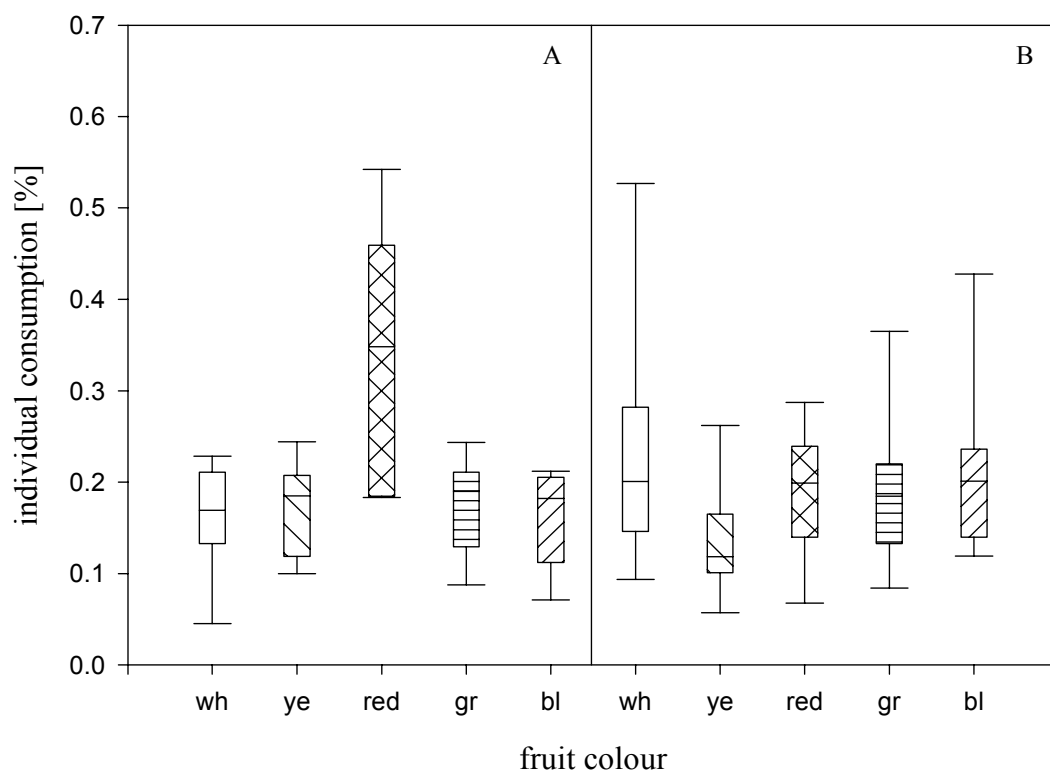

Fig. 6.3 A-B: Colour preference of juvenile (A) and adult (B) Blackcaps in cafeteria-design experiments. Colour abbreviations as in Fig. 6.1.

Influence of background contrast

When green fruits were simultaneously presented in front of a red or a green background, birds strongly preferred the contrasting food display over three consecutive days (χ^2= 7.143; df= 1; n= 14; p= 0.008/ Fig. 6.4 A). A second trial with red fruits presented in front of a red or green background yielded the same result (χ^2= 10.286; df= 1; p= 0.001/ Fig. 6.4 B).

Wild caught birds in Venezuela also favoured the contrasting display, when given the choice between a single colour display of black ripe fruits and a two colour display including the same amount of ripe fruits but with additional green unripe fruits. Only ripe fruits were consumed, and birds strongly preferred the contrasting display (χ^2= 7.118; df= 1; n= 14; p= 0.008/ Fig. 6.4 C).
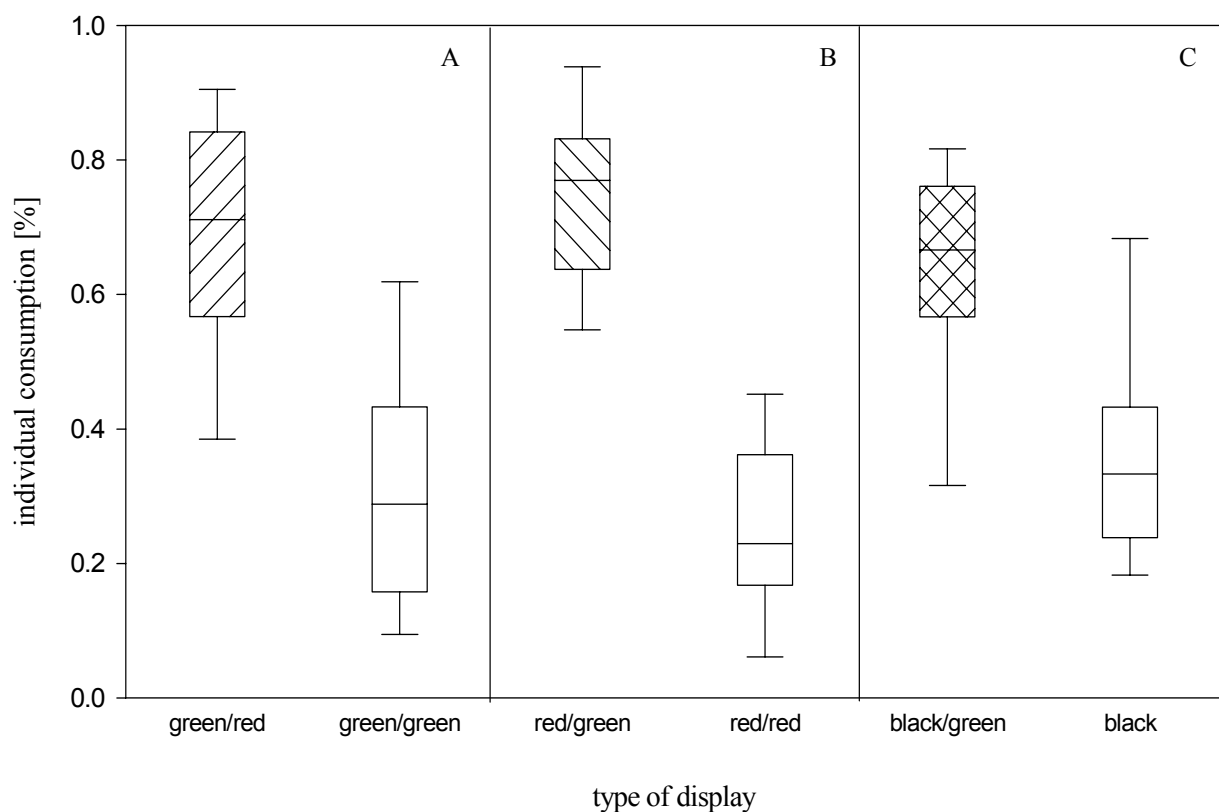

Fig. 6.4 A-C: Choice experiments with contrasting (barred) and uni-coloured (plain) food displays. Trials were conducted with artificial green (A) and red (B) fruits, and with natural ripe black and unripe fruits (C).

Discussion

Beside black, red is the most common fruit colour in nature. A possible explanation for this dominance is, that birds inherently prefer red fruits over fruits of other colours, which could be due to e.g. visual sensitivity (Willson & Whelan 1990). This hypothesis was tested with the cafeteria-design trials. In these experiments with all three tanager species, I found indeed a

preference for red fruits. Yet, on species level it became clear, that Green and Short-billed Honeycreepers preferred red fruits, and that Blue Dacnis individuals exhibited no colour-based food selection. Therefore, no general colour preference for red fruits could be shown. Winkel (1969) conducted similar experiments with congeners, he tested five Red-legged Honeycreepers (*Cyanerpes cyaneus*), of which four exhibited a preference for red, while one favoured blue. However, in a similar test, four individuals of the closely related Purple Honeycreeper (*C. caeruleus*) showed no preference for any colour. Winkel (1969) also investigated the Black-faced Dacnis (*D. lineata*), which showed a tendency to favour green, but individuals differed in their preferences. In this study, the pair-wise colour choice experiments revealed a similar colour ranking to the cafeteria trials in Green and Short-billed Honeycreeper, and again, the Blue Dacnis selected very differently. The first two favoured red and green fruits, while Dacnis individuals preferred blue and white fruits, in contrast to the cafeteria trials, where this species did not reveal any particular colour choice. This individual variation and inconsistency is known for many species (Willson 1994; Willson & Comet 1993; Willson et al. 1990) and has led to the assumption that colour choice by avian frugivores has not influenced the evolution of fruit colour (Murray et al. 1993). I will not discuss the clear avoidance of artificial black fruits, since their spectral curves did not closely match the curves of natural black fruits. Green and Short-billed Honeycreepers are closer related to each other than to the Blue Dacnis (Ridgely & Greenfield 2001), but observations in the field and a study on feeding ecology of these species and congeners (Snow & Snow 1971) did not reveal any differences in fruit consumption. All have been observed consuming a variety of fruits and taking nectar from flowering trees (Snow & Snow 1971; pers. obs.). Since age and experience of the tested individuals are unknown, the observed differences in colour preference might as well be due to different individual biography rather than species-specific choice. This applies also to Winkel's study (1969). All results on species level in both, colour ranking experiments as well as cafeteria-design trials, can only be regarded as preliminary due to small numbers of birds. Further experiments with a larger sample size and birds of known age should be conducted to investigate, why interspecific differences in colour preferences exist between these tanager species.

Willson and Whelan (1990) hypothesised, that red fruit colour acts as a signal for quick food recognition in migratory species often being confronted with new environments and fruit species (Whelan & Willson 1994). But migratory adult Blackcaps did not choose red fruits, when presented previously unknown food, and fed randomly on fruits of all colours. It can be

argued that artificial fruits are not presented in a natural environment. Since the significance of colour is context dependent, the lack of the right context might invalidate the association of colour with appropriate food, but following the hypothesis, red should have triggered fruit choice under these unusual circumstances. The assumption that red is a signal for migratory species to facilitate food recognition can therefore not be supported by this study. Instead it was found, that juvenile Blackcaps without any experience with fruit consumption showed an *a priori* preference for red fruits. In early summer in Europe, when juveniles start searching for food, the majority of ripe fruits is red, and Blackcaps prefer to feed on these fruits (Bairlein 1978; Snow & Snow 1988). A food search image for red fruits would therefore be advantageous for fledglings. Juveniles in this study were hand-raised and kept on a maintenance diet without former experience with dyed food, natural or artificial fruits. Adults were kept on the same diet. However, they were caught from the wild, and since Blackcaps switch from being mainly insectivorous during spring and summer to a mostly frugivorous diet in autumn, they may already have eaten wild fruits before capture. The results indicate, that a predisposition in juvenile birds exists, which then becomes overridden by the experience with differently coloured wild fruits in late summer and autumn. This has yet only been proposed for European bird species, since fruit supply in the tropics is not as seasonal, and breeding seasons among species are not as synchronised (Stutchbury & Morton 2001), and to my knowledge, no period with only ripe red fruits exists.

Experience has also been shown to influence feeding behaviour in other bird species. Roper (1990) found an unlearned avoidance against red insect prey in domestic chicks, which then got overruled by experience. Blackbirds (*Turdus merula*) were able to develop a search image for cryptic prey (Lawrence 1985). In contrast to adult Blackcaps, wild caught adult Silvereyes (*Zosterops lateralis*) consistently preferred red fruits, even after the exposure to white, yellow or red maintenance diet and were thus not biased by the colour of the previous maintenance diet (Puckey et al. 1996). This might be due to the type of fruit display. Puckey et al. (1996) placed the glass dishes containing the fruits upon green cardboard to create a contrasting display resembling natural conditions. On a green background, red (besides black) is the most conspicuous colour (chapter 5), and therefore, adult experienced Silvereyes might have preferred red over all other fruit colours due to conspicuousness. Also Blackbirds have been observed to strongly favour red berries, while simultaneously white fruits differing only in colour and thus conspicuousness were present (Disselhorst 1972).

To further investigate the aspect of conspicuousness in food choice, I conducted separate experiments. I first tested the influence of contrast on fruit choice. In the background experiments subsequently including red and green fruits in front of both, red and green backgrounds, birds strongly preferred food from the more contrasting display regardless of fruit colour, and there was no indicated difference among species. In trials with caught birds in Venezuela, which were simultaneously presented single colour displays with ripe black fruit only and bi-coloured displays with additional green unripe fruits, birds also clearly favoured the contrasting display without differences among species. This is strong evidence that conspicuousness plays a role in fruit choice. Also, Willson & Melampy (1993) report that birds favoured black fruits mixed with unripe red fruits over displays with ripe fruits alone. The presence of unripe fruits might yield additional information. If in the wild, fruits of one infructescence do not mature simultaneously, an overall black display could mean that part of the fruits are already deteriorating, while displays combining ripe with unripe fruits might indicate that ripe fruits are still fresh (Greig-Smith 1986). This hypothesis is yet to be tested. Overall, the choice experiments in this study show that the conspicuousness of fruit presentation enhances the attractiveness for avian frugivores, regardless of age and experience. Conspicuousness, the colour contrast between fruit and background, might therefore be a more general trait influencing fruit choice than colour itself, as predicted by the signal hypothesis which posits that fruit colour serves as a long distance signal for dispersers to advertise ripe fruit. The strongest signal will be the most conspicuous contrast between fruit and background. This has been shown for red and black fruits in chapter 5. This and the fact that conspicuousness influences fruit choice in birds strongly supports the signal hypothesis. Of course, fruit choice is not based on single factor decisions, and fruits in the wild are always presented within a larger context than just colour. A number of influencing factors has been found, such as accessibility, nutrient contents, seed load, size and shape or different digestive strategies of consumers (e.g. McPhearson 1988; Willson 1994; Levey & Grajal 1991; Whelan & Willson 1994; Witmer & van Soest 1998; Stanley & Lill 2001; Johnson et al. 1985; Murray et al. 1993). And colour itself can convey different information. Red fruits indicate maturity in one species, but belong to a pre-ripe fruit stage in another. Thus, the complex relations between frugivores and fruits cannot be explained by one interaction alone. But the role of conspicuousness seems to contribute one piece to the mosaic eventually elucidating the different motives influencing the process of fruit choice by avian frugivores and explaining the current fruit colour pattern.

Cited literature

Bairlein, F. (1978): Über die Biologie einer südwestdeutschen Population der Mönchsgrasmücke (*Sylvia atricapilla*). J. Orn. 119: 14-51.

Bairlein, F. (1986): Ein standardisiertes Futter für Ernährungsuntersuchungen an Singvögeln. J. Ornithol. 127: 338-340.

Disselhorst, G. (1972): Beeren und Farbwahl durch Vögel. J. Orn. 113: 448-449.

Gervais, J.A., Noon, B.R. & Willson, M.F. (1999): Avian selection of the color-dimorphic fruits of salmonberry, *Rubus spectabilis*: a field experiment. Oikos 84: 77-86.

Good, P.A. (1994): Permutation Tests, a practical guide to resampling methods for testing hypotheses. Springer Verlag, New York.

Greig-Smith, P.W. (1986): Bicolored fruit displays and frugivorous birds: the importance of fruit quality to dispersers and seed predators. Am. Nat. 127: 246-251.

Johnson, R.A., Willson, M.F., Thompson J.N. & Bertin, R.I. (1985): Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66: 819-827.

Lawrence, E.S. (1985): Evidence for search image in blackbirds (*Turdus merula* L.): short-term learning. Anim. Behav. 33: 929-937.

Lehner, P.N. (1979): Handbook of ethological methods. 1st ed. Cambridge, University Press.

Levey, D.J. & Grajal, A. (1991): Evolutionary implications of fruit processing limitations in cedar waxwings. Am. Nat. 138: 171-189.

McPhearson, J.M (1987): A field study of winter fruit preferences of Cedar Waxwings. Condor 89: 293-306.

McPherson, J.M. (1988): Preferences of cedar waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. Anim. Behav. 36: 961-969.

Mundry, R. (1999): Testing related samples with missing values: a permutation approach. Anim. Behav. 58: 1143-1153.

Murray, K.G., Winnett-Murray, K., Cromie, E.A., Minor, M. & Meyers, E. (1993): The influence of seed packaging and fruit color on feeding preferences of American robins. In Fleming, T.H. & Estrada, A. [eds.]: Frugivory and seed dispersal: Ecological and evolutionary aspects. Vegetatio 107/108: 217-226.

Puckey, H.L., Lill, A. & O'Dowd, D.J. (1996): Fruit color choices of captive silvereyes (*Zosterops lateralis*). Condor 98: 780-790.

Roper, T.J. (1990): Responses of domestic chicks to artificially coloured insect prey: effects of previous experience and background colour. Anim. Behav. 39: 466-473.

Ridgely, R.S. & Greenfield, P.J. (2001): The birds of Ecuador. Status, distribution, and taxonomy. A & C Black Publishers Ltd., London.

Snow, B.K. & Snow, D.W. (1971): The feeding ecology of tanagers and honeycreepers in Trinidad. Auk 88: 291-322.

Snow, B.K. & Snow, D.W. (1988): Birds and berries. A study of an ecological interaction. Butler & Tanner Ltd, Frome and London.

Stanley, M.C. & Lill, A. (2001): Accessibility as a factor influencing frugivory by silvereyes (*Zosterops lateralis*): field comparisons with aviary experiments. Aust. J. Zool. 49: 171-182.

Stutchbury, B.J.M. & Morton, E.S. (2001): Behavioral ecology of tropical birds. Academic Press London and San Diego.

Whelan, C.J. & Willson, M.F. (1994): Fruit choice in migrating North American birds: field and aviary experiments. Oikos 71: 137-151.

Willson, M.F. (1994): Fruit choices by captive American robins. Condor 96: 494-502.

Willson, M.F. & Comet, T.C. (1993): Food choices by northwestern crows: experiments with captive, free-ranging and handraised birds. Condor 95: 596-615.

Willson, M.F. & Melampy, M.N. (1983): The effect of bicolored fruit displays on fruit removal by avian frugivores. Oikos 41: 27-31.

Willson, M.F. & Whelan, C.J. (1990): The evolution of fruit color in fleshy-fruited plants. Am. Nat. 136: 790-809.

Willson, M.F., Graff, D.A. & Whelan, C.J. (1990): Color preferences of frugivorous birds in relation to the colors of fleshy fruits. Condor 92: 545-555.

Winkel, W. (1969): Experimentelle Untersuchungen an Zuckervögeln (*Coerebidae*) im Funktionskreis der Nahrungssuche: Über die Bedeutung von Farben, Formen und Zuckerkonzentrationen. Z. f. Tierpsychol. 26: 573-608.

Witmer, M.C.& Van Soest, P.J. (1998): Contrasting digestive strategies of fruit-eating birds. Functional Ecology 12: 728-741.

Zusammenfassung

Frugivorie ist eine mutualistische Beziehung zwischen früchtetragenden Pflanzen und frugivoren Tierarten. Die Pflanze profitiert von dieser Beziehung durch Samenverbreitung in Form von Endozoochorie, während die Tiere durch die Verdauung des Fruchtfleisches Energie und Nährstoffe erhalten. Viele Faktoren, z.B. Fruchtgröße, Erreichbarkeit, Inhaltsstoffe etc. beeinflussen die Fruchtwahl der Verbreiter. Bevor diese Faktoren die Wahl bestimmen, muss die Frucht entdeckt werden. Die Fruchtfarbe ist daher ein entscheidender Faktor der Fruchtwahl. Über 50% der Früchte sind rot oder schwarz, unabhängig von Kontinent und Habitat. Unter den adaptiven Hypothesen zu der Entstehung dieser ungleichen Verteilung stehen Interaktionen mit Samenverbreitern im Vordergrund. Als Samenverbreiter fungieren vor allem Säuger und Vögel. Aufgrund des meist schlecht ausgeprägten Farbsehvermögen der Säuger und ihrer häufig nachtaktiven Lebensweise, sowie des hervorragend ausgebildeten Sehsystems der meist tagaktiven Vögel beziehen sich diese Hypothesen auf Vögel als Verbreiter. Wegen der unterschiedlichen Farbwahrnehmung wird die Fruchtfarbeneinschätzung durch das menschliche Sehsystem den Diskriminierungsfähig-keiten der Vögel nicht gerecht. Das Wissen über die rezeptorischen und neuronalen Prozesse im Vogelauge und Hirn ist limitiert, sodass eine angemessene Farbdefinition nicht angewendet werden kann. Das Ziel dieser Arbeit ist es daher, eine objektive Methode der Farbeinschätzung auszuwählen und mit dieser Methode verschiedene Hypothesen zum Einfluss frugivorer Vogelarten auf die Evolution der Fruchtfarbenverteilung zu untersuchen. Aufgrund des hohen Anteils an frugivoren Vogelarten, des großen Fruchtvorkommens in den Tropen und der geringen Saisonalität im Fruchtangebot wurden die Freilandarbeiten im Tieflandregenwald Venezuelas durchgeführt. Dort wurde ebenfalls eine Dominanz roter und schwarzer Früchte von über 50% des Fruchtangebotes gefunden. Für eine objektive Farbeinschätzung wurden die Reflektionsspektren reifer Früchte und die spektrale Zusammensetzung des Umweltlichtes mit einem Spektroradiometer vermessen. Die Beschränkung auf die Spektralkurven, bevor die Informationen im jeweiligen spezifischen Sehsystem zu Farbwahrnehmungen verarbeitet werden, stellt zur Zeit die einzige Möglichkeit einer objektiven Farbeinschätzung und damit einer der Wahrnehmung des Vogels angemessenen Methode dar. Eine Hauptkomponentenanalyse ermöglicht die Zusammenfassung der Spektren in die Werte von drei Hauptkomponenten. Statt in Farbkategorien nach menschlichem Sehvermögen gruppiert, wird in dieser Methode jedes Spektrum individuell durch drei Werte charakterisiert.

Einige adaptive Hypothesen zum Einfluss frugivorer Vogelarten auf die bestehende Fruchtfarbenverteilung gehen von Farbbevorzugungen durch Vögel aus. Die Dominanz roter und schwarzer Früchte könnte durch eine generelle Farbpräferenz frugivorer Vögel entstanden sein. Eine weitere Hypothese postuliert, dass eine angeborene Präferenz für rot Zugvögeln die Futtersuche in unbekannten Gebieten mit fremden Früchten während des Zuges erleichtert.

Dies könnte auch für Jungvögel gelten, die nach Verlassen des Nestes erstmals eigenständig auf Nahrungssuche gehen. Dafür spricht die Dominanz roter Früchte im Frühsommer in Zentraleuropa. In Käfigexperimenten mit Kunstfrüchten zeigten Vögel keine generelle Präferenz für rot. Adulte Mönchsgrasmücken, die als Zugvögel eine Assoziation zwischen der Farbe rot und essbarer Nahrung ausgebildet haben könnten, wählten keine spezielle Fruchtfarbe, handaufgezogene Jungvögel dieser Art hingegen präferierten deutlich rote Früchte. Dies spricht für eine genetische Prädisposition bei juvenilen Vögeln, die später durch Erfahrung und Lernprozesse überlagert wird.

Die Informationshypothese postuliert, dass Fruchtfarben bestimmte chemische Inhaltsstoffe anzeigen. Dies wurde in einer Korrelation der Spektraldaten mit Fruchtinhaltsstoffen aus einer Parallelstudie untersucht. Schwarze und einige weiße Früchte haben einen hohen Tanningehalt, während stark im langwelligen Bereich reflektierende (gelbe, orange und rote) Früchte einen hohen Proteingehalt aufweisen. Schwarze Fruchtfarbe kommt häufig durch Komplexbildung zwischen Anthocyaninen und Tanninen zustande und könnte dem Vogel die biologische Inaktivität der Tannine und damit die Reife der Frucht anzeigen. Das Anzeigen eines hohen Proteingehalts käme frugivoren Vögeln aufgrund des generell geringen Proteinanteils in Früchten zugute. Der hohe Proteingehalt ist mit einem großen Unterschied zwischen den Bereichen kurzwelligen und langwelligen Lichts in der Spektren korreliert. Für das menschliche Auge ist dieses Verhältnis nicht definierbar sondern findet sich in verschiedenen Fruchtfarben. Inwieweit Vögel diesen Unterschied wahrnimmt, ist noch unklar.

Der Signalhypothese folgend dienen Fruchtfarben als Fernsignal, um Vögel auf reife Früchte aufmerksam zu machen. Die Dominanz schwarzer und rote Früchte wäre dann durch ihre besondere Auffälligkeit entstanden. Tatsächlich sind schwarze und rote Früchte kontrastreicher zu ihrem Hintergrund als Früchte anderer Farben, unabhängig vom Habitat. Auch die farbigen Sekundärstrukturen in manchen Fruchtständen wirken kontrastverstärkend. In Käfigexperimenten wurde gezeigt, dass Vögel kontrastreichere Displays bevorzugen und Auffälligkeit daher Fruchtwahl beeinflusst.

Zusammenfassend stellt diese Studie die erste objektive Fruchtfarbeneinschätzung vor und ermöglicht durch die Kontrastberechnung ein neutrales Maß für die Auffälligkeit von Fruchtfarben. Mit dem Aufzeigen der größeren Auffälligkeit roter und schwarzer Früchte, sowie der Wahl kontrastreicher Displays durch Vögel unterstützen die Ergebnisse dieser Studie die Signalhypothese, während die Hypothesen zur generellen Farbpräferenz und der Assoziation der Farbe rot mit Nahrung in Zugvogelarten nicht bestätigt wurden. Die Existenz einer generell bestehenden genetischen Prädisposition bei Jungvögeln, sowie die Informationshypothese bedürfen noch weiterer Untersuchung.

Erklärung:

Hiermit erkläre ich, dass ich die Dissertation selbständig verfasst und nur die angegebenen Hilfsmittel benutzt habe.

Oldenburg, im Februar 2002

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Curriculum Vitae

Name: Schmidt, Veronika
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Education

09/98 start of PhD thesis on the influence of frugivorous birds on the evolution of fruit colour (Prof. F.Bairlein, University of Oldenburg, Germany, Prof. H. Winkler, Konrad-Lorenz- Institute, Vienna, Austria)
01/98 diploma of Biology (M.S.) on the globally threatened AquaticWarbler *Acrocephalus paludicola* (University of Freiburg, Germany, Dr. PD B. Leisler, Max-Planck-Institute for Ornithology, Radolfzell)
10/94 B.S. in Biology at Bonn University, Germany

Scientific research

03/02   start of conservation projects on both, the critically endangered Pale-headed Brushfinch as well as the endangered El Oro Parakeet in Ecuador
10 - 12/98 and
09/99 - 02/00   field work in a lowland rainforest in Venezuela for the PhD
05/99   study on the contamination of eggs of the Herring Gull (*Larus argentatus*) by pollutants
04/98 – 07/98 telemetry study on the home range size of female Aquatic Warblers (in co-operation with Dr. PD B. Leisler, Max-Planck-Institute for Ornithology, Radolfzell, Germany), Northeast Poland
01/98 – 04/98 ornithological trip to Bolivia and Peru
04/97 - 07/97 field work for a song study on the Aquatic Warbler in NE Poland for the M.S.
09/96   bird banding of a variety of native bird species, Germany
01/95 – 04/95 field and laboratory assistant in projects on juvenile dispersal of koalas and on bandicoots with Prof. Dr. I. Hume, University of Sydney, Australia

Technical skills

- trapping and handling of birds, banding, taking biometric parameters and spectrometric measurements
- tree climbing for the study and collection of fruits
- use of spectrometric device and experience with data analysis
- application of radio transmitters and use of telemetry equipment, design and conduction of telemetry studies
- conduction of choice experiments with caged birds
- computer experience with SPSS, Word-Programs, Excel, Sigma Plot

teaching experiences

05/95 - 08/96 teaching of undergraduate students in anatomy of vertebrates and invertebrates
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Language skills

German (native), English (fluent), Spanish (good), French (basic), Italian (basic), Polish (basic)

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