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Relations entre la visibilité du plumage et la complexité du chant chez des Passeriformes nord-américains

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a été évaluée par un jury composé des personnes suivantes:

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"Que vous êtes joli! que vous me semblez beau!

Sans mentir, si votre ramage

Se rapporte à votre plumage,

Vous êtes le phénix des hôtes de ces bois."

Jean de La Fontaine (1668)

Sommaire

Chez les Passeriformes, le chant et le plumage peuvent souvent remplir des rôles semblables. On considère que la sélection sexuelle favorise généralement l'évolution de chants plus complexes et de plumages plus voyants. Cependant, d'autres pressions sélectives peuvent limiter cette évolution. Darwin a émis l'hypothèse selon laquelle il existe une corrélation négative entre la complexité du chant et la visibilité du plumage. Bien que ce raisonnement se retrouve assez fréquemment dans la littérature scientifique, peu de chercheurs ont cherché à le vérifier. Cette étude visait donc à éprouver l'hypothèse de Darwin et 123 espèces nord-américaines d'oiseaux chanteurs ont été sélectionnées à cet effet.

Si la quantification de la complexité du chant pose peu de problèmes, il en va autrement pour celle de la visibilité du plumage. En premier lieu, nous avons mis au point une méthode d'évaluation quantitative de la visibilité du plumage fondée sur le système des couleurs de Munsell qui est plus facile à utiliser que les techniques de spectroradiométrie. Cette méthode se base sur des données mesurables et que l'on peut obtenir de façon répetée, fournit des indices de dimorphisme sexuel et unit les aspects de visibilité "à courte portée" et "à longue portée". Dix espèces de Passeriformes furent choisies pour illustrer cette procédure et des observateurs "naïfs" ont servi à la vérifier. Un degré élevé de concordance entre ces observateurs apparaît et les valeurs obtenues à partir de planches de guides d'identification ne diffèrent pas significativement de celles obtenues à partir de spécimens naturalisés.

Par la suite, nous avons corrigé les données tenir compte de l'autocorrélation phylogénétique, puis effectué une analyse des corrélations canoniques afin d'évaluer la corrélation entre un ensemble de variables mesurant la visibilité du plumage et un autre ensemble mesurant la complexité du chant. Cette analyse permit de démontrer l'existence d'une faible corrélation positive entre la visibilité du plumage et la complexité du chant. Il se peut que ces traits aient évolué de concert au sein du groupe d'espèces étudié pour permettre aux mâles de ces espèces, qui se reproduisent dans des régions où la période de nidification est courte, de se trouver une partenaire le plus rapidement possible.

Enfin, pour examiner l'influence possible de la structure de l'habitat sur la complexité du chant et la visibilité du plumage, nous avons réparti les 123 espèces sélectionnées en plusieurs groupes selon leur habitat général. Des analyses de variance, dont les tables de distribution de la statistique F tenaient compte de la parenté phylogénétique entre espèces, ne révélèrent aucune différence entre les habitats en ce qui a trait à la complexité du chant et la visibilité du plumage des espèces qui y vivent. Cependant, d'autres facteurs environnementaux, éthologiques, morphologiques et expérimentaux pourraient expliquer en partie l'absence de corrélation négative entre la complexité du chant et la visibilité du plumage. Des études plus approfondies, comprenant notamment des espèces tropicales, devront être effectuées avant que l'on puisse confirmer ou infirmer les idées de Darwin de façon décisive.

Mots-clefs: complexité du chant, visibilité du plumage, Passeriformes, Amérique du Nord, habitat, phylogénie, évolution.

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Liste des sigles et abréviations

B_C:	Contrast of a bird with its background in chroma
B_V:	Contrast of a bird with its background in value
$B_{V \bullet C}$:	Contrast of a bird with its background in Munsell power
C:	Total plumage chroma
COLOUR1:	First canonical variable of plumage
COLOUR2:	Second canonical variable of plumage
D_C:	Sexual dichromatism in chroma
D_V:	Sexual dichromatism in value
$D_{V \bullet C}$:	Sexual dichromatism in Munsell power
DUR:	Song duration
FMAX:	Maximum frequency
FMIN:	Minimum frequency
INDEX:	Syllable-type versatility index
RANGE:	Frequency range
SONG1:	First canonical variable of song
SONG2:	Second canonical variable of song
SYLL:	Number of syllable types in the song
TOT:	Total number of syllables, different or not, in the song
TRANS:	Number of transitions from one syllable type to another in the song
V:	Total plumage value
$V \bullet C$:	Total plumage Munsell power
W_C:	Within-plumage in chroma
W_V:	Within-plumage contrast in value
$W_{V \bullet C}$:	Within-plumage contrast in Munsell power

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À mes parents

Introduction

La grande variété de plumages et de chants que l'on retrouve chez les oiseaux a toujours fasciné l'homme (Catchpole 1979, Rowland 1979). Les rôles de ces attributs et les causes probables de leur évolution ont été étudiés en détail (pour une synthèse, voir Armstrong 1973, Rowland 1979, Kroodsma et Miller 1982, Burtt 1986, Searcy et Andersson 1986, Butcher et Rohwer 1989, Kroodsma et Miller 1996). Cependant, une des théories les plus populaires pour expliquer l'apparition de plumages voyants, du dimorphisme sexuel du plumage entre les mâles et les femelles et de chants élaborés demeure sans conteste celle de la sélection sexuelle (Darwin 1871). Selon cette théorie, les caractères sexuels secondaires auraient évolué de façon à donner un avantage à leurs porteurs dans la reproduction, que ce soit par l'entremise de la compétition entre mâles pour l'accès aux femelles ou par celle du choix d'un partenaire par celles-ci (Searcy et Yasukawa 1983). Il semble que l'on retrouve effectivement ces deux formes de sélection chez les oiseaux et qu'elles agissent sur le plumage et le chant des mâles (Catchpole 1979, Searcy et Andersson 1986, Butcher et Rohwer 1989).

La sélection sexuelle aurait donc favorisé l'évolution de chants plus complexes et de plumages plus voyants. Des corrélations entre le succès dans l'acquisition d'une partenaire sexuelle et certains paramètres du chant (voir Catchpole 1980, 1987, Hiebert et al. 1989, Horn et al. 1993, Lampe et Saetre 1995, Mountjoy et Lemon 1996) ou de la couleur du plumage (voir Saetre et al. 1994, Sundberg 1995, Sundberg et Dixon 1996 pour des exemples) ont d'ailleurs été trouvées chez certaines espèces. Cependant, peu d'ornithologues ont cherché à établir de façon rigoureuse des liens entre le niveau de complexité du chant et la coloration du plumage chez les oiseaux. Puisque le chant et le plumage peuvent remplir des rôles semblables, et que dans certains cas l'évolution d'un de ces traits vers une forme plus élaborée peut être restreinte par d'autres pressions évolutives comme la prédation (Butcher et Rohwer 1989), on peut se demander si la façon dont s'est développé un de ces traits ne peut pas avoir influencé l'évolution de l'autre trait. En effet, si le mâle d'une espèce a un chant complexe, a-t-il besoin d'un plumage voyant? Inversement, si le mâle a un plumage très marqué, a-t-il besoin d'un chant complexe? Autrement dit, y a-t-il une corrélation négative entre le caractère marqué du plumage et la complexité du chant chez les oiseaux? C'est ce que pensait Darwin (1871). En effet, celui-ci écrivait (p. 707): "It is... remarkable that birds which sing well are rarely decorated with brilliant colours or other ornaments. Of our British birds, excepting the bullfinch and the goldfinch, the best songsters are plain-colored. The king fisher, bee-eater, roller, hoopoe, woodpecker, & C., utter harsh cries; and the brilliant birds of the tropics are hardly ever songsters. Hence bright colours and the power of song seem to replace each other. We can perceive that if the plumage did not vary in brightness, or if bright colours were dangerous to the species, other means would be employed to charm the female; and melody of voice offers one such means". Darwin n'a cependant pas appuyé ses écrits par des observations plus systématiques. Pettingill (1985), suivant ses traces, nota: "Songs among different species vary tremendously, ranging from a repetition of one syllable to a highly complex series of sounds. The "best" songsters—i.e, those giving loud, extended song with a strong musical quality—are among songbirds in which the males are usually dull in color and closely resemble the females. Such males, it is believed, depend more on sounds than they do on appearance for the identification of their species and stimulation of mates". Pettingill n'a pas donné de références à ce sujet et n'a pas corroboré ses affirmations par des observations ou des données expérimentales.

D'autres chercheurs ont repris le raisonnement selon lequel les espèces au plumage peu voyant ont un chant plus élaboré sans vraiment chercher à le confirmer, et ce raisonnement se retrouve encore fréquemment dans la littérature scientifique (voir les références dans Read et Weary 1992). Selon Armstrong (1973), les oiseaux mettant l'accent sur le chant pour la communication devraient avoir un plumage peu voyant et vice versa. Kroodsma (1977), dans son étude sur la complexité du chant chez les troglodytes, suggéra que l'aspect relativement peu marqué du plumage des Troglodytidae et leur monomorphisme sexuel étaient sans doute des facteurs contribuant au degré élevé de développement du chant au sein de cette famille. D'après Catchpole (1980), le Phragmite des joncs (*Acrocephalus* *schenobaenus*) pourrait être classé parmi les espèces où le chant a une grande importance dans l'attraction d'une partenaire, vu sa petite taille et le caractère discret et monomorphe de son plumage. Stein (1958), enfin, estimait que tout groupe d'oiseaux favorisant les sons au détriment de l'aspect visuel comme moyen primaire de reconnaissance tendrait à posséder un plumage arborant une coloration protectrice et que le dimorphisme sexuel serait rare dans cette situation.

La plupart des chercheurs se sont donc contentés de récupérer l'hypothèse de Darwin sans chercher à la vérifier. Or, Hamilton et Barth (1962) ont observé une association entre un dimorphisme sexuel du plumage accentué et de courtes périodes pour la formation des couples en climat tempéré. Un dimorphisme sexuel du plumage plus intense permettrait aux oiseaux de s'apparier rapidement. Dans le même ordre d'idées, on peut présumer qu'un plumage plus voyant et un chant plus complexe chez les mâles pourraient jouer un rôle similaire.

Seuls Shutler et Weatherhead (1990) et Read et Weary (1992) se sont intéressés aux relations possibles entre la complexité du chant et le caractère voyant du plumage. Dans une étude sur les parulines nord-américaines, Shutler et Weatherhead (1990) sont arrivés à la conclusion que les mâles des espèces ayant le plus fort degré de dimorphisme sexuel du plumage émettaient des chants plus courts plus souvent, mais que ceux-ci n'étaient pas plus complexes. Toutefois, en excluant les espèces monomorphes, qui nichent généralement au sol et ont donc développé un plumage moins voyant à cause de la pression de prédation, ces chercheurs ont constaté une augmentation parallèle de la complexité du chant et du degré de dimorphisme sexuel, ce qui est contraire au postulat de Darwin. Dans une étude comparative portant sur l'évolution du chant des oiseaux, Read et Weary (1992), travaillant avec des espèces provenant de cinq taxons différents (Tyrannoidea, Corvoidea, Fringilloidea, Sylvioidea, Turdoidea), n'ont trouvé aucun lien entre le caractère marqué du plumage et la complexité du chant.

Les travaux mentionnés ci-haut sont intéressants, mais comportent des lacunes. Ainsi, les résultats de Shutler et Weatherhead (1990) se restreignent au Parulidae. De plus, le seul aspect de la coloration du plumage dont ces chercheurs se sont servis fut le dimorphisme sexuel. On n'y trouve rien quant au degré de visibilité ("conspicuousness") du plumage. Read et Weary (1992), de leur côté, ont utilisé une méthode de quantification de la visibilité du plumage basée uniquement sur des impressions. Les oiseaux étaient notés sur une échelle de 1 à 6 par un groupe d'ornithologues ignorant l'utilisation qui serait faite de cette classification, selon une procédure établie par Read et Harvey (1989). De plus, on n'y trouve rien quant au degré de dimorphisme sexuel des espèces.

Conséquemment, des recherches plus poussées doivent être effectuées avant qu'on ne puisse accepter ou rejeter les idées de Darwin (1871). Cette étude vise donc à vérifier l'exactitude de celles-ci, ainsi que de celles de Pettingill (1985). En termes clairs, il s'agit de vérifier s'il existe une corrélation entre la visibilité du plumage d'un oiseau chanteur et la complexité de son chant. Le terme chant est vague et sa signification quant aux vocalisations impliquées peut varier d'un auteur à l'autre (Spector 1994). De plus, ses fonctions n'ont souvent été démontrées que de façon indirecte (Kroodsma et Byers 1991). Il est donc très important de bien définir ce terme. Dans le cadre de cette étude, le chant se définit par les critères (iii) et (v) du Tableau 1 de Spector (1994). Il s'agit donc de sons émis exclusivement ou surtout par les mâles, exclusivement ou surtout en saison de reproduction, utilisés pour la communication sur de longues distances et l'annonce de la présence du mâle ("advertisement"), la défense du territoire, l'attraction d'une partenaire, la cour et le maintien d'un lien "conjugal". Cette définition s'applique principalement aux vocalisations des Passeriformes (voir cependant Spector 1994) vivant en milieu tempéré. Chez les espèces tropicales, tant les femelles que les mâles chantent, et le chant sert surtout à défendre le territoire toute l'année, que les oiseaux soient en période de nidification ou non. Dans ce cas, les rôles joués par le mâle et la femelle convergent (Morton 1996). En outre, il est possible que le dimorphisme sexuel du plumage exerce une plus grand influence sur la formation des couples chez les espèces des régions tempérées, où la saison de nidification est plus courte, qu'en milieu tropical, où les espèces sont souvent monomorphes (Hamilton et Barth 1962). La fertilisation de femelles par des mâles autres que leur partenaire au sein du couple ("extra-pair fertilization"), qui semble constituer un moteur important du processus de sélection sexuelle (Møller et Birkhead 1994), s'observe rarement chez les Passeriformes tropicaux (Morton 1996). Sur cette prémisse, on peut présumer que la sélection sexuelle est plus forte chez les espèces vivant en milieu tempéré. Pour ces raisons, et en tant que première étape d'un processus devant mener à une meilleure compréhension des relations entre la complexité du chant et la visibilité du plumage chez les oiseaux chanteurs, nous avons choisi de nous intéresser plus particulièrement aux représentants nord-américains de cinq familles présentant une grande diversité de plumages et de chants: les Emberizidae, Parulidae, Cardinalidae, Icteridae et Thraupidae (American Ornithologists' Union 1997). Cet échantillon comprend la plupart des membres de ces familles qui nichent au nord de la frontière mexicaine et pour lesquels des enregistrements de chants étaient disponibles. La question des relations possibles entre la complexité du chant et la visibilité du plumage est traitée de façon approfondie dans le deuxième chapitre de cet ouvrage.

Pour éprouver des hypothèses telles que celle émise par Darwin, il est nécessaire d'évaluer la complexité du chant et la visibilité du plumage de façon quantitative et le plus objectivement possible. Il n'existe pas de consensus quant à une définition de la complexité du chant. Cependant, plusieurs caractéristiques temporelles, spectrales et syntaxiques de celui-ci peuvent être mesurées sur une échelle quantitative où la valeur numérique obtenue ne dépend pas du seul jugement subjectif de l'observateur. Parmi ces caractéristiques, mentionnons la durée du chant (Kroodsma 1977, Shutler et Weatherhead 1990, Read et Weary 1992), le taux de répétitions par unité de temps (Shutler et Weatherhead 1990, Read et Weary 1992), le temps total passé à chanter pour une période donnée (Kroodsma 1977, Shutler et Weatherhead 1990), le nombre de syllabes différentes dans le chant (Staicer 1989, Shutler et Weatherhead 1990), le répertoire de syllabes ou de chants différents qu'un individu possède (Kroodsma 1977, Catchpole 1980, Catchpole et McGregor 1985, Shutler et Weatherhead 1990, Read et Weary 1992, Mountjoy et Lemon 1996), et les fréquences les plus élevées, les plus basses, ainsi que l'intervalle de fréquences (Shutler et Weatherhead 1990).

La situation s'avère différente dans le cas du plumage. Lorqu'on s'arrête plus longuement aux propos de Darwin (1871) et Pettingill (1985) quant au caractère voyant ou non du plumage des mâles, on peut voir que ces auteurs se sont intéressés non seulement à la visibilité de l'oiseau dans son milieu, mais également à la différence de plumage entre le mâle et la femelle, ou dimorphisme sexuel du plumage. Plusieurs auteurs ont mis au point des méthodes de quantification du dimorphisme sexuel, du caractère marqué du plumage ou des deux à la fois, mais la plupart de ces méthodes sont basées uniquement sur des impressions et non sur des données mesurables, en plus de ne pas tenir compte de l'arrière-plan de l'oiseau (Baker et Parker 1979, Rohwer et al. 1980, Hamilton et Zuk 1982, Read 1987, Read et Harvey 1989, Johnson 1991, Weatherhead et al. 1991, Götmark 1994, Martin et Badyaev 1996, Garvin et Remsen 1997). D'autres méthodes plus objectives, telles que celles basées sur des techniques spectroradiométriques (Burtt 1986, Endler 1990), exigent d'innombrables mesures sur le terrain et des calculs fort complexes, ce qui peut énormément compliquer la tâche d'un chercheur travaillant avec plusieurs espèces habitant une grande diversité de milieux. Dans le cadre de cette étude, nous avons élaboré une méthode, basée sur des données mesurables et que l'on peut obtenir de façon répétée, qui est plus facile à utiliser que les techniques spectroradiométriques. Cette méthode, fondée sur la spectrophotométrie et plus précisément sur le système de classification des couleurs de Munsell (Smithe 1975), est décrite en détail dans le premier chapitre de cet ouvrage.

Enfin, outre le processus de sélection sexuelle, des pressions sélectives dues à l'environnement peuvent intervenir dans le développement d'un chant plus moins complexe ou d'un plumage plus ou moins voyant. Par exemple, dans les milieux forestiers, la réverbération due à la végétation entraîne une dégradation rapide des signaux sonores avec une modulation de fréquence rapide et répétitive (trilles, bourdonnements) et favorise l'évolution de signaux formés de sifflements modulés de façon lente et non répétitive. En milieu ouvert, par contre, les fluctuations d'amplitude dues au vent favorisent l'apparition de signaux avec un taux de répétition élevé de modulations de fréquence, car elles peuvent provoquer une perte partielle de l'information contenue dans des sifflements non répétés

(Wiley et Richard 1982; Brenowitz 1986; Wiley 1991). Il est donc possible que les chants soient moins complexes (à cause de la répétition) en milieu ouvert. De plus, dans les milieux ouverts, les oiseaux peuvent se voir les uns les autres facilement en raison d'un couvert végétal réduit (Hailman 1977, Catchpole 1979, Lazarus et Symonds 1992). La coloration du plumage est peut-être moins importante dans de tels habitats. Le troisième chapitre de cet ouvrage porte sur l'influence possible de la structure de l'habitat sur la complexité du chant et la visibilité du plumage.

Les espèces utilisées dans le cadre de cette étude tirent leur origine d'ancêtres communs et ne peuvent donc pas être considérées comme des points tirés de façon indépendante d'une même distribution (Felsenstein 1985, Garland et al. 1993). Les deuxième et troisième chapitres de cette thèse présentent des résultats obtenus à partir de méthodes permettant de tenir compte de l'effet de l'autocorrélation phylogénétique (Garland et al. 1992, 1993) dans les analyses et les comparent à ceux obtenus à partir d'épreuves d'hypothèses classiques.

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Chapitre 1

Quantifying plumage conspicuousness and sexual dichromatism in birds: a new approach

Par

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Abstract: In studies of sexual selection in birds, plumage conspicuousness and sexual dichromatism must be quantified. We present a method, based on the Munsell colour system, that is easier to use than spectroradiometric techniques. It is based on measurable and repeatable data, but depends on human vision. The method provides indices of sexual dichromatism and incorporates aspects of close-range and long-distance conspicuousness. Ten species of Passeriformes were chosen to test the procedure with naive observers. The body of a bird is divided into regions and the colour of each region is matched to chips in a colour guide. The following indices based on the parameters of the Munsell system, were selected: value (V), chroma (C), and Munsell power ($V \bullet C$), which measure conspicuousness independently of the background; W_V, W_C, and $W_{V \bullet C}$, which measure the contrast between the colours in the plumage; B_V, B_C, and $B_{V \bullet C}$, which measure the contrast between the bird and its background; and D_V, D_C, and $D_{V \bullet C}$, which are the indices of sexual dichromatism of the plumage. The scores of naive observers were similar across observers and scores based on field guides did not differ significantly from those recorded on museum specimens. The dichromatism index $D_{V \bullet C}$ gave more information than the others. However, our results indicate that conspicuousness and dichromatism indices should not be used individually because they are interdependent, and that they should be used in conjunction with multivariate analyses.

Introduction

Conspicuousness and sexual dichromatism of avian plumage have been the subject of discussion since Darwin's (1871) writings on sexual selection. Some authors have related the evolution of conspicuous male plumage to female choice, while others have claimed that it is a consequence of competition between males (reviewed by Andersson 1994). Hamilton and Zuk (1982) hypothesized that the bright plumage of males is a signal of resistance to parasites, and their hypothesis has generated much debate (Read 1987, Read and Harvey 1989, Johnson 1991, Weatherhead et al. 1991). Another hypothesis states that conspicuous birds may be unpalatable to predators or hard to catch (Cott 1947, Baker and Parker 1979, Baker and Hounsome 1983, Johnson 1991). Quantification of plumage colours is fundamental to testing these and other hypotheses concerning the evolution of plumage conspicuousness and sexual dichromatism. The conspicuousness of a bird depends upon many factors, such as its environment, the visual system of the observer, light conditions throughout the day, and the movements performed by the bird (Baker and Parker 1979, Burtt 1986, Endler 1990, Götmark 1994, Götmark and Unger 1994).

Various approaches have been used to quantify dichromatism, conspicuousness, or both at the same time. Rohwer et al. (1980) classified 279 North American passerines into four categories according to both their conspicuousness and their degree of sexual dichromatism. This classification relies only on what the observers find to be more or less showy or dichromatic. The scales of conspicuousness used by Hamilton and Zuk (1982), Read (1987), Read and Harvey (1989), Weatherhead et al. (1991), Götmark (1994), and Martin and Badyaev (1996), rank birds on a numerical scale (e.g., 1–6 or 1–10) according to whether the observers found the birds conspicuous or not. Some rankings were made by birders or professional ornithologists who knew what the birds looked like in the wild (Read and Harvey 1989); nevertheless, their scores were still based on impressions rather on than quantifiable data. Others, like Baker and Parker (1979) and Johnson (1991), divided the body of the bird into parts and took into account the contrast between the parts, but the score given to each part was still based on subjective judgment. Finally, Shutler and Weatherhead (1990) based their evaluation of sexual dichromatism on the percentage of the body surface in which the coloration differs between males and females (e.g., 15 or 25% of the body is coloured differently), the body surface being divided into regions, as in Burtt (1986). Burtt (1986) ascribed a precise percentage of the body surface to each region. This method is interesting, but does not take into account the degree of differentiation between colours. For instance, the difference between a blue bird and a red bird is considered to be the same as the difference between birds of different shades of blue, and the difference between two pale blues is considered the same as that between a dark and a pale blue.

Subjectivity can cause problems when one needs to classify birds into groups according to their coloration. The assessment of plumage conspicuousness is a complex issue, avoided by a number of workers who consider only a limited number of colour parameters, for example intensity ("brightness"; Promislow et al. 1992). The way a colour is perceived varies according to a number of factors, and it is often assumed that birds perceive colours in the same way as humans (Johnson 1991). This assumption is known to be flawed (Bennett and Cuthill 1994, Bennett et al. 1994). While humans possess three types of retinal cones, birds have four types, perhaps five (e.g., chicken, *Gallus gallus;* Varela et al. 1993), and their visual system shows a complexity of which "our own sensory experience provides little intuitive understanding" (Varela et al. 1993). For instance, at least some birds can see in the UV range, whereas humans cannot (Burkhardt 1989, Bennett and Cuthill 1994, Bennett et al. 1994, Finger and Burkhardt 1994), and birds can see more hues, including some that are completely different from those perceived by humans (Burkhardt 1989, Finger and Burkhardt 1994). Therefore, an objective categorization of birds based on their coloration must be as independent as possible of criteria specific to human vision.

Endler (1990) proposed a method, relying on spectroradiometry, that permits one to assess the conspicuousness of an animal by measuring the hue, chroma (saturation), and brightness of the colours of different parts of the body, as well as their contrast with the background. Although this method is based on measurable data, it has the disadvantage of requiring that measurements be taken in the field for each species. While carrying a spectroradiometer into the field is possible, for studies involving many species found in areas far away from each other, the task quickly becomes unmanageable. Furthermore, Endler's technique requires calculations that researchers not proficient in mathematics and computer programming will find cumbersome.

Burtt (1986) presented a technique for quantifying the contrast between a coloured patch and its background . This technique consists of a three-dimensional colour space where the three parameters are the dominant wavelength (hue), the excitation purity (saturation), and the relative luminance (brightness). Scales are defined for the three perceptual parameters, and the shortest distance between two points within the colour space is the contrast distance. The longer the distance, the greater the contrast. The measurements are adjusted to ambient light conditions and the spectral sensitivity of birds is assumed to be the same as that of humans, but again, spectroradiometric measurements are required in order to quantify the ambient illumination, and one has to perform cumbersome calculations before obtaining the contrast distance.

Hill et al. (1994) subjectively assessed the plasma colour (representative of carotenoid concentration) of molting House Finches *(Carpodacus mexicanus)* and found it to correlate with plumage redness. Colour variation is likely caused by differences associated with the uptake of carotenoids. In subsequent research, Hill (1996) found that red carotenoid pigmentation is a more energetically costly form of ornamentation than orange or yellow, and concluded that brightness could be scored according to this hierarchy of carotenoid-based display. However, this method allows the assessment of the relative value of a colour as a signal, not its conspicuousness. This method works only with carotenoid-based colours, and there are colours resulting from other pigments (Burkhardt 1989). Clearly, a simpler method that makes measurements both quantifiable and easy to obtain could promote quantitative field studies of colour.

We developed a technique for quantifying the conspicuousness and sexual dichromatism of avian plumage that has the advantage of being easier to use than Endler's (1990) or

Burtt's (1986) techniques, is based on measurable and repeatable data, and is as independent as possible of human judgment and physical and biological limitations.

Materials and methods

Value, chroma, and Munsell power indices

The Munsell colour system defines a colour by three characteristics: the hue (the dominant wavelength of light), the value (degree of lightness or brightness) and the chroma (degree of saturation). An overview of this system is found in Smithe (1975). The value (V) is measured on a scale from 0 to 10 and is related to the visual sensation of light (Hailman 1977, Endler 1990). The scale for chroma (C) or saturation has no upper limit, although the highest chroma found in Smithe (1975) is 16.5. Hailman (1977) predicted that signal coloration should be highly saturated. Hue as a circular scale that consists of letters and numbers with no absolute lower and upper limits. Complementary hues and hue contrasts present conceptual problems (Hailman 1977, 1979). Burtt (1986) experienced difficulties when he chose to include hue in his colour space model. Firstly, he could not deal with nonspectral purples, and secondly, he treated colour as a dominant frequency, which is a physical measure, rather than as a hue, which is a perceptual property. For instance, his model implies that red and violet, which are at opposite ends of the scale, are easier to discriminate than red and green, but there is no perceptual basis for that implication, as Burtt (1986) acknowledges. Since V and C can easily be represented by numbers and given the many problems associated with hue, we decided to use only V and C in quantifying conspicuousness. Judd and Wyszecki (1963) stated that for an observer adapted to daylight, the product of V and C, called Munsell power, correlates with the power of a colour to attract attention in humans. We also used this parameter (hereafter referred to as $V \bullet C$) to quantify conspicuousness.

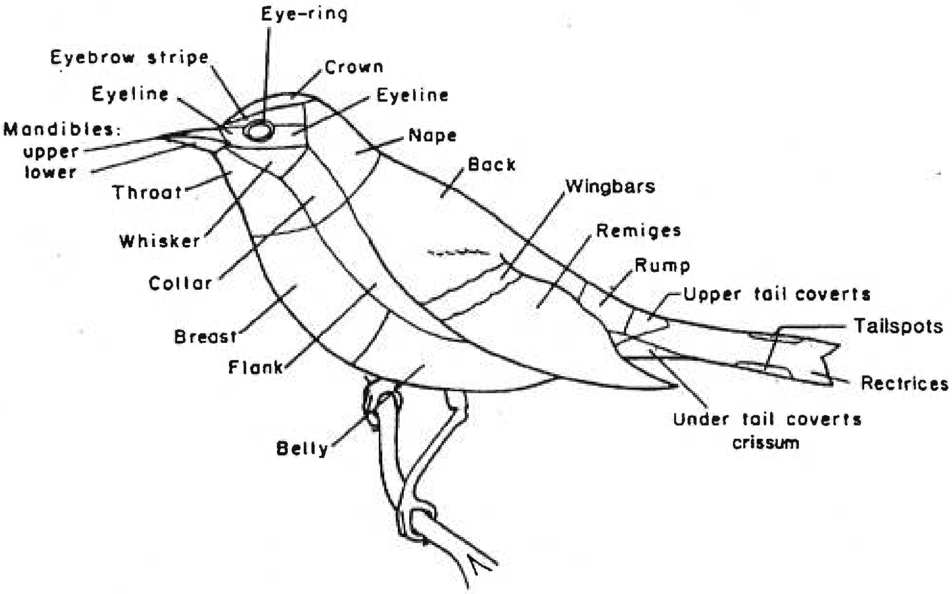
Our method can be described as follows. A bird's plumage is seldom a single, uniform colour, it usually has several colours. The V, C, and V • C indices of these colours differ, and mean indices for the entire body are calculated to take this into account. Burtt (1986) divided the plumage of wood warblers (Parulidae) into 19 regions, each occupying a percentage of the plumage (Fig. 1; see also Appendix II-1 in Burtt 1986). In this study, we also deal with other passerine from other families (buntings, blackbirds, cardinals, etc.). However, since their form resembles that of warblers, we assume that the percentages of the plumage occupied by the regions remain similar. Since the V and C for each colour are found in Smithe (1975), the numerical values of the colours that best match those depicted in the Peterson (1994) field guide are ascribed to each region. There are 182 colours in Smithe (1975), some differing only slightly from one another. For simplicity, those colours that seem to occur most frequently in the feathers of North American birds can be selected (see the Appendix), but any colour in Smithe (1975) can be used if necessary. If a region has more than one colour (e.g., a streaked patch, like the breast of the Yellow Warbler, *Dendroica petechia*), the fraction of the region occupied by each colour is estimated and the average V and C indices and the resulting average product, V • C, for that region are calculated. When some parts of the birds are not illustrated in Peterson (1994), their colours are checked in another field guide (e.g., National Geographic Society 1987). However, the colours used to match swatches in Smithe (1975) are the corresponding colours in Peterson (1994). In the next step of the procedure, the V, C, and V • C indices for each region are multiplied by the percentage of the plumage covered by that region. The results for each region are summed, giving total V, C, and V • C scores for the entire body:

[1] $V = \Sigma(V_i \times A_i)$,

[2] $C = \Sigma (C_i \times A_i)$,

[3] $V \bullet C = \Sigma ((V \bullet C)_i \times A_i)$

Figure 1. Topography of a wood warbler (taken from Burtt 1986).


Eye-ring
Eyebrow stripe
Crown
Eyeline
Eyeline
Mandibles:
upper
lower
Nape
Back
Throat
Wingbars
Whisker
Remiges
Collar
Rump
Upper tail coverts
Tailspots
Breast
Flank
Rectrices
Under tail coverts
crissum
Belly

where A_i is the percentage of the body surface represented by region i, and V_i, C_i, and $(V \bullet C)_i$ are the V, C, and V • C indices, respectively, for region i. To test our method, we selected the following 10 species of Emberizidae, Parulidae, Icteridae, Cardinalidae and Thraupidae (American Ornithologists' Union 1997), which are very diversified in terms of coloration and plumage pattern, to calculate the V, C, and V • C indices for males in definitive breeding plumage: Yellow Warbler, Black-throated Blue Warbler *(Dendroica caerulescens)*, Hooded Warbler *(Wilsonia citrina)*, Red-winged Blackbird *(Agelaius phoeniceus)*, Northern Oriole *(Icterus galbula)*, Scarlet Tanager *(Piranga olivacea)*, Lapland Longspur *(Calcarius lapponicus)*, Dark-eyed Junco *(Junco hyemalis)*, Indigo Bunting *(Passerina cyanea)*, and Song Sparrow *(Melospiza melodia)*. First, we calculated the conspicuousness indices (equations 1-3) for these species, following the method outlined above. We then asked 10 naive observers who were unaware of the aim of the study to follow the method outlined above, using the same species. They also matched colours in Smithe (1975) to colours depicted in the Peterson field guides (Peterson 1989, 1994), but the V and C indices were not available to them. We then performed the same calculations as above with the colours as determined for each region by the naive observers. To see if all birds were ranked in the same way by all observers, we then calculated Spearman's rank correlation coefficients between their rankings and ours for the three indices. However, when several comparisons are carried out simultaneously, the probability of a type 1 error becomes larger than the nominal significance level (e.g., 0.05). Therefore, we used Bonferroni correction to adjust our critical P values accordingly. Finally, as the colours in a field guide may differ from those of the real bird, we applied the same method to museum specimens of the same species and included the results in the multiple testing to determine whether the ranking would vary. If the rankings were the same, this would allow field guides to be used instead of museum specimens. The museum specimens, collected during the breeding season, were taken from the collections of Université de Montréal and the Canadian Museum of Nature. The location and tag numbers of the specimens are available from the authors upon request. For each species, we chose at random an individual from the most numerous group of birds that were alike in terms of overall coloration and, if relevant, number of streaks or stripes. Colour matching took place in the laboratory under fluorescent light but next to a window to provide indirect sunlight.

Within-plumage contrast indices

The colour of a patch affects the way an adjacent but differently coloured patch is perceived (Hailman 1977). Contrast in V is the difference in the amount of visible light reflected between two surfaces. The extreme contrast in V occurs between white, which reflects nearly all incident light, and black, which reflects almost none (Hailman 1977). Similarly, the contrast between two surfaces differing in C is greatest when the C scores differ by the maximum, the range being from achromatic to monochromatic (Hailman 1977). To take into account the fact that adjacent colours in a plumage can contrast with one another, we calculated V, C, and V • C within-plumage contrast indices. A strong contrast between adjacent colour patches often leads to the disruption of an animal's outline (Cott 1957, Hailman 1977), which reduces the probability of an observer's detecting the animal against its background (Hailman 1977). Consequently, within-plumage contrast indices quantify crypsis. A high within-plumage contrast index indicates a high degree of crypsis in the V, C, or V • C index, while a low within-plumage contrast index indicates a high degree of detectability, recognition, or conspicuousness. For male in breeding plumage of each of the 10 species, we determined the colour in the plumage with the highest V score, V_h, and that with the lowest V score, V_l. Then the within-plumage contrast in the V index, W_V, was defined as:

[4] $$W_V = (V_h/V_l) \times A_l$$

where A_l is the percentage of the plumage covered by the least abundant of the two colours. In the same way, we defined within-plumage contrast in the C index, W_C, and in Munsell power, $W_{V \bullet C}$:

[5] $W_C = (C_h/C_l) \times A_l$

[6] $W_{V \bullet C} = ((V \bullet C)_h/(V \bullet C)_l) \times A_l$.

In most cases, the colour with the highest V index also has the highest C and V • C indices, and the colour with the lowest V index also has the lowest C and V • C indices. Colours present only in wing bars or tail spots were not taken into account, since these colours are often hidden by other feathers (Burtt 1986).

Contrast with the background

Conspicuousness also depends on the background against which a bird is observed (Hailman 1977, 1979, Burtt 1986, Endler 1990, Johnson 1991, Götmark 1994, Götmark and Unger 1994). The more a bird's colour contrasts with that of the background, the more conspicuous it is (Hailman 1977, 1979, Burtt 1986). So far, we have only dealt with what Götmark and Unger (1994) call "close quarter conspicuousness." In this case, conspicuousness is independent of background, since it is measured when an observer is close to a bird or has it in the hand. It was therefore necessary to consider "long-distance conspicuousness" or "detectability" (Guilford and Dawkins 1991, Götmark and Unger 1994), in association with the coloration of the background (Götmark 1994). We selected the colour Leaf Green (No. 146) (Smithe 1975) as being representative of a simplified background of vegetation (see the Appendix for the V and C indices of Leaf Green). For males of each species, the contrast of a bird with its background in terms of V index, B_V, is defined as

[7] $B_V = 3.63/V$

if V is less than 3.63, which is the value of the background. If V is more than 3.63, the ratio is inverted. In this case and the following two, we flipped the equations so that the numerator was always greater than the numerator because we were only interested in the importance of the ratio, not its direction. The same procedure was applied to sexual dichromatism indices of the plumage (see the next section). Similarly, the contrast of a bird with its background in terms of C index, B_C, is

[8] $B_C = 3.3/C$

where 3.3 is the C index of the background. The calculations are similar for the contrast of the bird with its background in terms of Munsell power, $B_{V \bullet C}$:

[9] $B_{V \bullet C} = 12.0/(V \bullet C)$

where 12.0 is the Munsell power of the background.

Sexual dichromatism indices

To quantify dichromatism as objectively as possible, we calculated the V, C, and $V \bullet C$ indices for females of our 10 species in the same way as for males. For each species, the sexual dichromatism index of the plumage in terms of the V index, D_V, is defined as

[10] $D_V = V_m/V_f$

where V_m is the V index of the male, and V_f, the V index of the female. The sexual dichromatism of the plumage in terms of the C index, D_C, is

[11] $D_C = C_m/C_f$.

Finally, the sexual dichromatism of the plumage in terms of Munsell Power, $D_{V \bullet C}$, is

$$[12] \quad D_{V \bullet C} = (V \bullet C)_m / (V \bullet C)_f.$$

Results

V, C, and V • C indices

Males whose breeding plumage contained a large amount of yellow and white, colours with a high V index, such as the Yellow Warbler, Dark-eyed Junco, and Song Sparrow, obtained the highest V scores (Table 1). Those with darker colours or with more black in their plumage, like the Indigo Bunting and Northern Oriole, obtained lower V scores, while the almost completely black male Red-winged Blackbird had the lowest V score. Males of species with highly saturated yellow, orange, red, and blue, like the Yellow Warbler, Northern Oriole, Scarlet Tanager, and Indigo Bunting, obtained the highest C scores (Table 1). On the other hand, black, grayish or brownish birds, such as male Red-winged Blackbirds, Dark-eyed Juncos, and Song Sparrows, had the lowest C scores. Finally, males with the highest V • C scores were those of species with colours with high V • C indices, yellow, red, orange and blue: Yellow Warbler, Scarlet Tanager, Northern Oriole, and Indigo Bunting (Table 1). Males in breeding plumage with the lowest V • C scores were those of the Red-winged Blackbird and Dark-eyed Junco.

There was considerable agreement between the rankings of males obtained by the different observers using the three indices. The rankings were significantly correlated in 65 out of 66 comparisons for V indices, (Table 2), and all rankings were significantly correlated for C and V • C indices (Tables 3 and 4). All the correlations between the rankings of museum specimens and rankings by observers using a field guide were significant. However, when the significance level was adjusted for multiple testing, only 25, 61, and 50 out of 66

Table 1. Value (V), chroma (C), and Munsell power (V · C) indices measured in males and females of 10 species by Y. de R. using Peterson (1994), and sexual dichromatism indices calculated from indices for males and females.

	Males			Females			Sexual dichromatism		
	V	C	V · C	V	C	V · C	D_v	D_c	$D_{v \cdot c}$
Yellow Warbler	7.50	9.28	71.10	6.21	8.87	59.80	1.21	1.05	1.19
Black-throated Blue Warbler	5.36	5.45	23.95	5.45	2.45	13.98	1.02	2.23	1.69
Hooded Warbler	5.09	5.80	40.76	6.23	8.34	56.34	1.22	1.39	1.33
Red-winged Blackbird	1.68	1.17	2.75	5.89	1.74	10.95	3.51	1.48	3.98
Northern Oriole	4.16	7.60	46.25	6.04	6.90	49.36	1.45	1.10	1.07
Scarlet Tanager	3.65	11.82	53.12	5.32	5.68	31.66	1.46	2.08	1.68
Lapland Longspur	5.46	1.51	7.09	6.53	1.86	9.83	1.20	1.11	1.39
Dark-eyed Junco	6.02	0.72	4.10	6.05	0.84	4.77	1.01	1.17	1.16
Indigo Bunting	4.83	9.00	43.66	4.89	3.12	14.77	1.01	2.88	2.96
Song Sparrow	5.47	2.59	11.30	5.47	2.59	11.30	1.00	1.00	1.00

Table 2. Spearman's rank correlation coefficients for comparisons of V indices obtained from males of 10 species by naive observers using Peterson (1994) and by Y. de R. using Peterson (1994) and museum specimens.

	Exp.	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Spec.	0.939*†	0.927*†	0.879*	0.721*	0.855*	0.830*	0.733*	0.661*	0.842*	0.879*	0.842*
Exp.		0.927*†	0.855*	0.806*	0.927*†	0.842*	0.830*	0.830*	0.952*†	0.830*	0.927*†
P1			0.915*†	0.733*	0.879*	0.867*	0.879*	0.758*	0.782*	0.964*†	0.891*†
P2				0.758*	0.903*†	0.915*†	0.867*	0.770*	0.612*	0.879*	0.879*
P3					0.891*†	0.927*†	0.891*†	0.818*	0.758*	0.721*	0.915*†
P4						0.903*†	0.927*†	0.903*†	0.746*	0.855*	0.988*†
P5							0.915*†	0.770*	0.721*	0.842*	0.915*†
P6								0.903*†	0.672*	0.867*	0.952*†
P7									0.552	0.806*	0.927*†
P8										0.685*	0.758*
P9											0.891*†

Note: "Spec." refers to museum specimens examined by Y. de R.; "exp." refers to Y. de R. using Peterson (1994); P1 to P10 are naive observers using Peterson (1994).

*P < 0.05.

†Significant after Bonferroni correction (P < 0.00076).

Table 3. Spearman's rank correlation coefficients for comparisons of C indices obtained from males of 10 species by naive observers using Peterson (1994) and by Y. de R. using Peterson (1994) and museum specimens.

	Exp.	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Spec.	1.000*†	0.976*†	1.000*†	0.964*†	0.988*†	0.988*†	0.976*†	0.927*†	0.927*†	0.976*†	0.988*†
Exp.		0.976*†	1.000*†	0.964*†	0.988*†	0.988*†	0.976*†	0.927*†	0.927*†	0.976*†	0.988*†
P1			0.976*†	0.939*†	0.964*†	0.964*†	0.939*†	0.939*†	0.842*	0.927*†	0.952*†
P2				0.964*†	0.988*†	0.988*†	0.976*†	0.927*†	0.927*†	0.976*†	0.988*†
P3					0.927*†	0.952*†	0.903*†	0.855*	0.903*†	0.976*†	0.988*†
P4						0.964*†	0.988*†	0.915*†	0.891*†	0.952*†	0.964*†
P5							0.952*†	0.952*†	0.939*†	0.964*†	0.976*†
P6								0.903*†	0.915*†	0.939*†	0.952*†
P7									0.842*	0.867*	0.879*
P8										0.952*†	0.939*
P9											0.988*

Note: For details see Table 2.

*P < 0.05.

†Significant after Bonferroni correction (P < 0.00076).

Table 4. Spearman's rank correlation coefficients for comparisons of V · C indices obtained from males of 10 species by naive observers using Peterson (1994) and by Y. de R. using Peterson (1994) and museum specimens.

	Exp.	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Spec.	0.988*†	1.000*†	0.976*†	0.939*†	0.927*†	0.952*†	0.988*†	0.867*	0.903*†	0.976*†	0.988*†
Exp.		0.988*†	0.964*†	0.952*†	0.879*	0.939*†	0.976*†	0.903*†	0.879*	0.951*†	1.000*†
P1			0.976*†	0.939*†	0.927*†	0.952*†	0.988*†	0.867*	0.903*†	0.976*†	0.988*†
P2				0.939*†	0.903*†	0.952*†	0.988*†	0.867*	0.915*†	0.976*†	0.964*†
P3					0.794*	0.988*†	0.927*†	0.879*	0.915*†	0.939*†	0.952*†
P4						0.842*	0.915*†	0.685*	0.794*	0.903*†	0.879*
P5							0.939*†	0.842*	0.939*†	0.964*†	0.939*†
P6								0.879*	0.927*†	0.988*†	0.976*†
P7									0.806*	0.855*	0.903*†
P8										0.964*†	0.879*
P9											0.952*†

Note: For details see Table 2.

*P < 0.05.

†Significant after Bonferroni correction (P < 0.00076).

pairs of rankings remained significantly correlated for V, C, and V • C respectively (Tables 2, 3, and 4).

Within-plumage contrast indices

The W_V, W_C, and $W_{V \bullet C}$ indices of male birds varied greatly among species (Table 5). Males of species with large dark patches surrounded by light colours (or vice versa), like the Northern Oriole, Hooded Warbler, and Scarlet Tanager, and those with dark upper parts and light underparts, such as the Dark-eyed Junco and Song Sparrow, obtained high W_V indices. More evenly coloured males, such as those of the Red-winged Blackbird, Yellow Warbler, and Indigo Bunting, had the lowest W_V indices. Males of species with large weakly saturated patches surrounded by saturated colours (or vice versa), like those of the Northern Oriole and Scarlet Tanager, had the highest W_C indices. Males with only saturated colours or only weakly saturated colours, such as those of the Yellow Warbler and Red-winged Blackbird, obtained the lowest W_C indices. Finally, males in breeding plumage with the highest $W_{V \bullet C}$ indices were those with patches of colours with low V • C indices surrounded by colours with high V • C indices, like the Northern Oriole and Hooded Warbler. Males that are more evenly coloured in terms of V • C index, such as the Yellow Warbler and Indigo Bunting, obtained the lowest $W_{V \bullet C}$ indices.

Contrast with the background

While male Red-winged Blackbirds contrast greatly in V index with the vegetation because they are very dark (Table 5), the male Yellow Warbler contrasts in a very similar way because of its brightness. The male Scarlet Tanager, whose plumage brightness is close to that of the vegetation, obtained the lowest B_V index. Birds with highly unsaturated colours, like male Dark-eyed Juncos and Red-winged Blackbirds, and birds with highly saturated colours, like male Scarlet Tanagers and Indigo Buntings, contrast most with moderately saturated vegetation in terms of C index (Table 5). Males of species closer in colour to the vegetation in saturation, like Song Sparrows and Black-throated Blue Warblers obtained the

Table 5. Indices of within-plumage contrast and contrast with the background* measured in males of 10 species by Y. de R. using Peterson (1994).

	Within-plumage contrast			Contrast with the background		
	W_v	W_c	$W_{v \cdot c}$	B_v	B_c	$B_{v \cdot c}$
Yellow Warbler	0.05	0.05	0.13	2.07	2.73	5.94
Black-throated Blue Warbler	0.78	4.64	4.93	1.48	1.65	2.00
Hooded Warbler	1.26	4.55	25.28	1.40	1.76	3.40
Red-winged Blackbird	0.00	0.00	0.00	2.16	2.82	4.35
Northern Oriole	2.10	12.14	52.69	1.15	2.30	3.86
Scarlet Tanager	0.90	7.99	24.01	1.01	3.58	4.43
Lapland Longspur	0.85	0.70	1.29	1.51	2.18	1.69
Dark-eyed Junco	0.62	0.48	0.36	1.66	4.61	2.92
Indigo Bunting	0.08	0.13	0.17	1.33	2.73	3.65
Song Sparrow	0.60	2.52	0.12	1.51	1.27	1.06

*The habitat is represented by the colour Leaf Green (No. 146) (Smithe 1975).

lowest B_C indices. Males in breeding plumage with high V • C indices, such as those of the Yellow Warbler and Scarlet Tanager, had the highest $B_{V \bullet C}$ indices relative to the vegetation, while those with colours of moderately low V • C indices, like those of the Lapland Longspur, obtained the lowest $B_{V \bullet C}$ indices (Table 5).

Sexual dichromatism indices

In 8 out of the 10 species examined, females obtained higher V indices than males (Table 1). In six of these, the males have a greater proportion of black in their plumage. However, C indices were higher in males in 5 of the 10 species. In five species, females had higher V • C indices than males. In four of these, males have a greater proportion of black in their plumage than females. Males obtained the highest V • C indices in four species. The D_V index is high in the Red-winged Blackbird, while it is closer to 1 in other species (Table 1). D_C indices are highest in the Indigo Bunting, Black-throated Blue Warbler, and Scarlet Tanager and lowest in the Song Sparrow, Lapland Longspur, and Yellow Warbler. Based on the $D_{V \bullet C}$ indices, the highest sexual dichromatism of the plumage was found, not unexpectedly, in the Red-winged Blackbird, followed by the Indigo Bunting and Black-throated Blue Warbler. The Song Sparrow, Northern Oriole, and Yellow Warbler had the lowest $D_{V \bullet C}$ indices.

Discussion

The conspicuousness of an animal is influenced by several physiological, physical, and ethological factors (Hailman 1977, Baker and Parker 1979, Burtt 1986, Endler 1990, Götmark 1994, Götmark and Unger 1994). The method described here takes physical factors into account by using several indices, each focussing on an aspect of conspicuousness. However, rankings of the ten species used in this study differ from one index to another. The V index gives high scores to birds adorned with bright overall coloration, such as the Yellow Warbler, and low scores to birds with dark plumage, like the Red-winged Blackbird. The C index is high in the case of birds with saturated colours (e.g., the Scarlet Tanager) and low in species with weakly saturated coloration (e.g., the Dark-eyed Junco). Species with a strong combination of V and C indices obtain the highest V • C indices, and thus have colours that attract more attention according to Judd and Wyszecki (1963). Among them are the Yellow Warbler, Northern Oriole, and Scarlet Tanager. In the case of the within-plumage contrast indices (W_V, W_C, and $W_{V \bullet C}$), birds with a blend of light and dark colours (e.g., the Hooded Warbler), saturated and weakly saturated colours (e.g., the Northern Oriole), or colours with low and high V • C indices (e.g., Scarlet Tanager) obtain the highest scores. More evenly coloured birds, such as the Yellow Warbler, obtain lower scores and are thus more conspicuous according to these indices. Finally, species with dark and weakly saturated plumages like the Red-winged Blackbird, birds with bright colours like the Yellow Warbler, and birds with highly saturated colours like the Scarlet Tanager have the highest scores for contrast with a green background (B_V, B_C, and $B_{V \bullet C}$).

Another interesting result is the strong correlation between the rankings of the observers using field guides and those obtained with museum specimens. This shows that even if colours were not exactly the same in field guides and on specimens, they were ranked in the same manner. Consequently, field guides may be used in assessing bird conspicuousness. One could object that the results might depend upon the field guide used and that, if another field guide had been used, the rankings would not have been significantly correlated with those obtained with museum specimens. However, rankings obtained by observers using the National Geographic Society (1987) guide were correlated with those obtained by observers using Peterson's (1989, 1994) field guides and those obtained with museum specimens (Y. de Repentigny, H. Ouellet, and R. McNeil, unpublished data).

Our conspicuousness indices cannot be used individually because each omits some aspects of conspicuousness. For instance, the V, C and V • C indices give low scores to the Red-winged Blackbird (e.g., a V index of 1.68), and do not account for the fact that this bird contrasts well with the vegetation, hence high indices of contrast with the background (e.g., a B_V index of 2.16). A bird with weakly saturated colours like the Song Sparrow obtains low C (2.59) and V • C (11.30) indices, but this effect is offset by its low within-plumage contrast scores (e.g., a $W_{V \bullet C}$ index of 0.12). Within-plumage contrast indices are high for the Northern Oriole (e.g., a $W_{V \bullet C}$ index of 52.69), consequently its conspicuousness is weak according to these indices, which do not take into account its high C (7.60) and V • C (46.25) indices. Therefore, the different indices in our method should be applied in combination, using multivariate analysis software packages available to researchers (SAS, SPSS, etc.). The indices proposed in our study can be incorporated into a principal component analysis, which allows one to summarize in a few dimensions most of the variability contained in the dispersion matrix of a great number of descriptors (Legendre and Legendre 1984). A canonical correlation analysis (Legendre and Legendre 1984) can also be used. In doing so, it is possible to detect which aspects of conspicuousness affect the other set of variables.

The method we propose allows one to quantify the sexual dichromatism of the plumage according to three aspects: lightness (V), chroma (C), and Munsell power (V • C). In our examples, some species are more dimorphic in terms of V (e.g., Red-winged Blackbird) and others in terms of C (e.g., Indigo Bunting). Species with a strong D_V or D_C index also have a high $D_{V \bullet C}$ index; it is thus possible to use only the latter in quantifying sexual dichromatism. Dichromatism indices could also be used in combination with conspicuousness. Workers are sometimes interested in both male conspicuousness and sexual dichromatism of the plumage when studying sexual selection in birds (e.g., Weatherhead et al. 1991).

Some of our results may appear unusual, but are nonetheless explainable. For instance, females had higher V and V • C indices than males in several species (e.g., Red-winged Blackbird and Hooded Warbler). However, it should be remembered that males of some species obtained lower V and V • C indices because their plumage is darker or less saturated. This might help these males to appear more conspicuous against a more saturated or brighter habitat than their females. Burtt (1986) found that in wood warblers, colours are darker among males than among females and that males have heightened contrast. Nevertheless, it is possible that females can be as conspicuous as males under certain circumstances. Götmark and Hohlfält (1995) observed that females of the Pied Flycatcher *(Ficedula hypoleuca)* and Chaffinch *(Fringilla coelebs)* were as detectable as their male counterparts in certain habitats. Other surprising results are the high crypsis scores obtained from birds like the Northern Oriole according to the within-plumage contrast indices (W_V, W_C, and $W_{V \bullet C}$ indices of 2.10, 12.14, and 52.69, respectively). In interpreting these indices, we decided to stress the importance of within-plumage contrast for disruptive coloration (Cott 1957, Hailman 1977, Götmark and Hohlfält 1995). However, it should be kept in mind that colour contrasts may also emphasize signals and shape or silhouette in certain cases (Hailman 1977) and may accordingly produce not disruption, but rather the opposite effect (Portmann 1959). In addition, little is known about where an observing bird during a display and thus what he or she sees. For instance, a male Red-winged Blackbird observing another male's display from the top of a cattail sees the red epaulet against the black body. A female watching the same display from the mud below the cattails sees a black silhouette against a bright sky. Therefore, our within-plumage contrast indices should be used with some caution. Finally, some may find it surprising to see a bird like the Song Sparrow yield a high conspicuousness score (the V index). It should be remembered that the V index for this bird is high because it has a lot of white in its plumage, and white is a "colour" with a high V index.

The strong correlations among the scores obtained by different observers show the general repeatability of our method. Each observer was given a text explaining as clearly as possible how to ascribe colours to the birds' different body regions, but it is possible that a few observers misinterpreted some of the directives. Although 7 out of 10 of our observers came from an ornithological club, this does not imply that they were homogeneous in terms of general ornithological knowledge, scientific skills, or time spent matching colours. Some of them probably took more time and were more careful in ascribing colours to the different body regions than others. Moreover, the perception of colours may differ somewhat from one observer to another (Tovée 1995a). These factors may account for the differences in the observers' rankings. In addition, less comparisons remained significant after application of the Bonferroni correction, especially in the case of V indices. This implies that human observers experience more difficulties in assessing the value of a colour than its chroma. Not all indices were tested, but since the contrast indices are based on the same colours ascribed to the birds as in the V, C, and V • C indices, we believe that the correlations would have been significant in these cases also. Because females' scores are based on the same method, these results also should have been consistent among the observers.

Because the method is based on the Munsell colour system (Smithe 1975), it does not necessarily correspond to what birds see. Spectrophotometric equipment is conceived to match the sensitivity of the human eye (Endler 1990). Colour vision in birds is at least tetrachromatic, and UV sensitivity seems to be widespread in birds, while human vision is trichromatic and blind to UV light (see reviews by Varela et al. 1993, Bennett and Cuthill 1994). In addition, birds' eyes have oil droplets that filter the light entering the cones (Varela et al. 1993, Bennett and Cuthill 1994). This implies that birds can see more hues, including some unknown to humans (Burkhardt 1989, Bennett et al. 1994, Finger and Burkhardt 1994). Moreover, UV light may contribute to the perception of hue (Bennett et al. 1996). Many colours reflect in the UV range and most likely look different to birds and humans (Burkhardt 1989, Finger and Burkhardt 1994). For instance, two reds that look similar to humans may look different to birds because they reflect different amounts of UV light. However, we did not use hue in our method of quantifying plumage conspicuousness, only value (brightness) and chroma (saturation). Bennett et al. (1994) mentioned that colour variables for which different photoreceptor types add a component (e.g., achromatic brightness), rather than creating an extra dimension, may be less susceptible to differences in perception between human and birds. Brightness is a function of the summed contributions from all cone types, so the full wavelenght range to which the animals studied are sensitive should be taken into account when measuring radiance (Bennett et al. 1994). Some feathers reflect strongly in the UV spectrum (Burkhardt 1989, Finger and Burkhardt 1994) and because of this may look brighter to birds than to humans. However, Radwan (1993) found that UV light does not increase the brightness of most feathers that appear dull in the "visible" range, though it may add to the conspicuousness of plumages already bright by human standards. Some colours, like most browns and blacks, appear to reflect almost no UV light (Burkhardt 1989, Finger and Burkhardt 1994). As for chroma perception, the convergence in visual systems is extensive (see Endler 1990). Endler (1990) found chroma and brightness calculated from radiospectrometric measurements to be generally correlated to Munsell chroma and Munsell value respectively. Furthermore, the results of psychophysical experiments showed that within the "visible" spectrum, the photopic spectral sensitivities of diurnal vertebrates, including birds, are similar (Burtt 1986). Therefore, it is not incorrect to quantify plumage chroma and value according to the Munsell colour system, even if this system is dependent upon human vision.

The function of UV sensitivity is still unclear (Varela et al. 1993, Bennett and Cuthill 1994). UV vision may be useful for orientation, foraging, or signalling (Parrish et al. 1984, Maier 1992, Bennett and Cuthill 1994, Tovée 1995b). There is meagre evidence that birds communicate in the UV spectrum (Bennett and Cuthill 1994). Bennett et al. (1996) found that the UV component of male ornamental traits is important in female choice in Zebra Finches *(Taeniopygia guttata)*, but removal of the UV component may have made the birds look abnormal, not necessarily less conspicuous. Because the keratin of unpigmented feathers backscatters some UV light, UV reflectance from pigmented feathers can often be explained as a "passive" component of colours of longer wavelengths (Andersson 1996), and this could be true for iridescent colours as well. Thus, strong UV reflectance by gorgets of sunangel hummingbirds *(Heliangelus* spp.*)* does not necessarily mean that these birds communicate with the aid of UV light, contrary to what Bleiweiss (1994) suggested. According to Finger and Burkhardt (1994), the signal value of an iridescent colour is perhaps based not so much on a certain excitation ratio between different colour channels, but rather on the phenomenon of iridescence itself.

There is relatively little UV radiation in natural daylight compared with the "visible" spectrum (Maier 1992). Furthermore, UV light is easily scattered by air particles, and this would lead to distant objects appearing blurred and indistinct when UV light is used (Tovée 1995b). Therefore, using UV coloration may not be the best way of signalling to conspecifics. Moreover, as Parrish et al. (1984) pointed out: "it is doubtful that birds make use of these patterns for mate recognition, because the males of most species readily advertize their sex by visible-reflectance patterns or colours, songs, courtships, or other behavioral mechanisms." Taking this into consideration, it is not so surprising to learn that surveys have failed to detect cryptic UV-based sexual dichromatism across a wide range of avian groups (Parrish et al. 1984, Bleiweiss 1994). E.H. Burtt, Jr. (personal communication) photographed warblers of the genera *Vermivora, Oporornis,* and *Dendroica* of eastern North America with UV-sensitive film, but could find no difference between their appearance with and without UV reflection. Similarly, Erick Greene (personal communication) found that male Lazuli Buntings *(Passerina amoena)* reflect only extremely weakly in the near-UV range (mainly on the lower mandible), and do not reflect at all in the regular UV range. Females do not reflect UV light either, except very weakly on the bill. Erick Greene had originally thought that these birds might be very bright in the UV range, since their colour has an iridescent sheen. Finally, the Magpie *(Pica pica)* and Jay *(Garrulus glandarius)* reflect little UV light (Götmark 1997). This again shows that it may not be incorrect to quantify the chroma and value of bird plumage according to the Munsell colour system, which is based on the part of the spectrum visible to humans.

Endler (1990) suggested the use of reflectance spectroradiometers to more objectively quantify colour. The "segment classification" method used by Endler (1990) to quantify value, chroma, and hue from spectroradiometric measurements depends only upon the physical properties of light, and attempts to capture some properties common to most vertebrate and invertebrate visual systems. However, this method is only adequate for trichromatic animals whose visual sensitivities are known (Endler 1990, Bennett et al. 1994). Other problems arising from the use of spectroradiometry are the correspondence between reflectance scores and a human concept such as "conspicuousness" and between the sensory abilities of the animals and those of the spectroradiometer (Zuk and Decruyenaere 1994). Thus, it has not been demonstrated satisfactorily that such a method is better than the Munsell system for quantifying plumage conspicuousness.

The method presented here is not flawless, as it overlooks some aspects of coloration, such as countershading or enhancement of shape (Hailman 1977), and the fact that habitats are not homogeneous in their coloration (Hailman 1977, Götmark and Hohlfält 1995). We used a very simplified background which overlooked the fact that birds might sometimes be seen against a blue sky or a brownish background, or against a background composed of several colours intermingled in an irregular pattern. Detailed studies about the part of the displaying bird that an observer sees and the background against which this observer watches the display are needed. Ambient light, which differs among habitats and also affects the conspicuousness of signals that depend on reflected light (Burtt 1986, Endler 1990, Götmark and Unger 1994), should also be taken into account. Hue, which is likely to be involved in conspicuousness (Hailman 1977), was not considered for conceptual reasons. For intraspecific comparisons, instead of using field guides, which do not illustrate subspecific or individual colour variation, one should use museum specimens. However, field guides can be used in cases of interspecific comparisons (e.g., Hamilton and Zuk 1982). Another problem is that the entire bird is evaluated, while sometimes only parts of it are visible to the observer. For example, a flying hawk cannot see the under-tail coverts of a ground-dwelling junco. A solution in such cases would be to quantify conspicuousness by using only the parts of the body that are relevant to the study. However, in studies dealing with evolutionary factors controlling plumage conspicuousness, the entire body should be used. Finally, since we used mean indices for the entire body, we did not take into account the coloration patterns of the plumage, except in the case of within-plumage contrast. These patterns are often ethologically or ecologically relevant (Hailman 1977). For example, a streaked breast that helps to camouflage a bird and a breast with a big spot that is used in signalling to conspecifics could yield the same score. Nonetheless, compared with methods used previously to quantify conspicuousness (Baker and Parker 1979, Hamilton and Zuk 1982, Read 1987, Read and Harvey 1989, Johnson 1991, Weatherhead et al. 1991, Götmark 1994, Martin and Badyaev 1996), our indices have the advantage of being based on measurable and repeatable data, which are more independent of the judgment of one or several observers. Here, each observer has to match plumage colours with reference colours. Furthermore, this method takes into account "long-distance conspicuousness" (Guilford and Dawkins 1991, Götmark and Unger 1994), while most previous methods do not (Götmark 1994). We also believe that our sexual dichromatism indices are an extension of other methods (Shutler and Weatherhead 1990), as they take into account the degree of differentiation between male and female plumage.

We feel that our method, because it is practical and yields repeatable results, can be of use to researchers working on many aspects of the evolution of coloration in birds. It could also be used to assess the conspicuousness of fleshy parts, as one only needs to match the colours of these parts to the colours shown in Smithe (1975). For example, Bortolotti et al. (1996) could have used our indices to quantify the conspicuousness of the ceres, lores, and tarsi of American Kestrels *(Falco sparverius).*

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Appendix. Colours and their indices from Smithe (1975).

No.	Name of colour	V	C
13	Geranium Pink	4.99	13.8
14	Scarlet	4.54	16.4
17	Spectrum Orange	6.51	15.5
18	Orange Yellow	7.80	13.5
29	Brownish Olive	3.98	2.0
32	Chestnut	3.31	5.0
43	Grayish Olive	4.67	2.8
46	Olive-Green	4.00	3.8
50	Yellowish Olive-Green	4.60	6.2
52	Olive Yellow	7.00	7.0
55	Spectrum Yellow	8.34	12.4
56	Straw Yellow	7.94	6.2
57	Sulphur Yellow	7.86	6.2
61	Apple Green	7.08	8.0
66	Sky Blue	6.79	6.8
67	Cerulean Blue	4.84	9.3
79	Glaucous	4.98	1.0
85	Light Neutral Gray	6.01	0.5*
87	Medium Plumbeous	4.67	0.8
88	Pratt's Payne's Gray	6.57	3.3
89	Jet Black	1.46	0.6
108	Crimson	3.06	10.4

Appendix. Continued.

No.	Name of colour	V	C
108b	Spinel Red	5.04	13.4
119	Sepia	2.20	0.5
119c	Light Drab	5.83	2.5
121	Vandyke Brown	3.01	1.4
121a	Prout's Brown	3.40	3.3
121b	Brussels Brown	4.15	4.2
123	Raw Umber	4.45	4.4
124	Buff	7.77	5.5
132b	Mahogany Red	4.03	7.2
146	Leaf Green	3.63	3.3
168	Cobalt Blue	4.11	12.3
168a	True Blue	4.93	10.6
168d	Light Sky Blue	8.23	2.8
170a	Ultramarine Blue	4.30	8.6
170b	Dull Violaceous Blue	5.17	9.4
219	Sepia	2.72	1.4
340	Robin Rufous	4.44	6.1
	Average White	9.50*	0.5*

*Estimated by Henri Ouellet.

Chapitre 2

Song versus plumage in some North American Oscines: testing the tradeoff hypothesis

Par

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(Article soumis sous une forme légèrement différente à American Naturalist)

Abstract: Sexual selection is thought to have favoured the development of both song and plumage, but other selective pressures may impose constraints. Darwin suggested that there is a negative correlation between song and plumage complexity, but this hypothesis, which we dubbed the tradeoff hypothesis, has not been tested. We have examined the tradeoff hypothesis on 123 species of North American Oscines. Canonical correlation analyses were used to assess the relationship between a set of variables measuring plumage conspicuousness and another measuring song complexity. Data were corrected to take phylogenetic autocorrelation into account. A weak positive correlation was found between plumage conspicuousness and song complexity. The positive correlation can be explained by the evolution of the traits that may help a male to mate rapidly in regions where the breeding season is short. Factors such as the influence of habitat structure on the evolution of songs and plumages, predation rates, differences in mating systems and in targets of sexual selection, and experimental errors can explain the weakness of this correlation.

Introduction

The diversity of songs and plumages and the probable causes of their evolution have attracted much study (for an overview, see Kroodsma and Miller 1982, Burtt 1986, Searcy and Andersson 1986, Butcher and Rohwer 1989, Kroodsma and Miller 1996). One hypothesis for the occurrence and elaboration of conspicuous plumages, sexual dichromatism, and complex songs states that these secondary sexual characters give greater fitness to their bearers (Darwin 1871). This can be achieved either by male-male competition or by female choice of a mate (Searcy and Yasukawa 1983). Both forms of selection occur in birds and operate on the plumages and songs of males (Catchpole 1979, Searcy and Andersson 1986, Butcher and Rohwer 1989). According to different theories of signal selection, these traits may be reliable indicators of phenotypic or genotypic quality (Zahavi 1991), or enclose false information that would help males gain fitness by deceiving either potential mates or competitors (for example, the "Beau Geste hypothesis", Krebs 1977). In both cases, however, more elaborate signals lead to a greater fitness for their senders.

Sexual selection favours the evolution of increasingly complex songs and increasingly conspicuous plumages, as well as sexual dichromatism. In some species, for example the Song Sparrow (*Melospiza melodia,* Hiebert et al. 1989), Western Meadowlark (*Sturnella neglecta,* Horn et al. 1993), Pied Flycatcher (*Ficedula hypoleuca,* Saetre et al. 1994, Lampe and Saetre 1995), Yellowhammer (*Emberiza citrinella,* Sundberg 1995, Sundberg and Dixon 1996), European Starling (*Sturnus vulgaris,* Mountjoy and Lemon 1996), and European warblers of the genus *Acrocephalus* (Catchpole 1980, 1987), more mates are attracted by individuals with more elaborate songs or more elaborate plumages. Do males of a species need both an elaborate song and a conspicuous plumage to attract females or repel territorial competitors? In other words, is there a negative correlation between plumage conspicuousness and song complexity in birds? Darwin (1871) thought so. He wrote that "It is... remarkable that birds which sing well are rarely decorated with brilliant colours or other ornaments. (...) Hence bright colours and the power of song seem to replace each other. We can perceive that if the plumage did not vary in brightness, or if bright colours were dangerous to the species, other means would be employed to charm the female; and melody of voice offers one such means". Similarly, Pettingill (1985) wrote "The "best" songsters—i.e., those giving loud, extended song with a strong musical quality—are among songbirds in which the males are usually dull in colour and closely resemble the females. Such males, it is believed, depend more on sounds than they do on appearance for the identification of their species and stimulation of mates". However, neither Darwin nor Pettingill tested this hypothesis (hereafter referred to as the tradeoff hypothesis), which is nonetheless favoured in the literature (e.g., Stein 1958, Armstrong 1973, Kroodsma 1977, Catchpole 1980; see also references in Read and Weary 1992). A related version of the tradeoff hypothesis is Gilliard's (1956, 1969) transferral effect hypothesis, according to which bowerbirds (*Amblyornis* sp.) which build highly elaborate bowers have less conspicuous plumages than bowerbirds who build less complicated bowers.

Other relationships between plumage and song are possible. Hamilton and Barth (1962) found an association between increased sexual dichromatism and relatively short periods for the establishment and maintenance of pair-bonds. Pronounced sexual dichromatism can help birds of temperate latitudes pair rapidly compared with their tropical counterparts. If plumage conspicuousness and song complexity serve a similar function, one could predict that contrary to what Darwin thought, a male, especially in temperate regions, is more fitted if he has a complex song and a conspicuous plumage very different from that of the female. That is, there is simultaneous sexual selection on all traits. Another possibility is that because of the interaction between factors favouring their elaborateness and others constraining it, these traits are uncorrelated across species.

Only Shutler and Weatherhead (1990) and Read and Weary (1992) have considered the relationship between song and plumage evolution. In a study of North American warblers, Shutler and Weatherhead (1990) found that males of the more dichromatic species deliver shorter songs more often than males of less dimorphic species, but that these songs are not more complex. However, when excluding monochromatic species that generally nest on the ground and thus have developed a less conspicuous plumage because of predation pressures, they noted an increase in song complexity with an increase in the degree of sexual dichromatism. This is contrary to the tradeoff hypothesis. In a comparative study on the evolution of song in birds, Read and Weary (1992), using species from five different taxa (Tyrannoidea, Corvoidea, Fringilloidea, Sylvioidea, Turdoidea), found no relationship between song complexity and plumage conspicuousness.

Unfortunately, Shutler and Weatherhead's (1990) results are restricted to the Parulidae. Moreover, the only aspect of plumage coloration considered was sexual dichromatism. Read and Weary (1992) quantified plumage conspicuousness based on assessments by human panelists: birds were ranked on a scale of one to six. The degree of sexual dichromatism of species was not considered.

The present study tests the tradeoff hypothesis stating that song and plumage elaborateness are inversely correlated in songbirds. We used canonical correlation analyses to assess the correlation between a set of variables measuring plumage elaborateness (including sexual dichromatism) and a set of variables measuring song complexity. The meaning of the term "song" varies from author to author (Spector 1994) and the evidence for its functions is often indirect (Kroodsma and Byers 1991). Here, "song" refers to a sound delivered exclusively or mainly by males, exclusively or mainly during the breeding season, used for long-range communication and advertisement, territorial defense, mate attraction, and maintenance of pair bonds. This definition applies mainly to passerines (and some non-passerines, see Spector 1994) in temperate regions. In many tropical species, both males and females often sing, and song is mainly used to defend the territory year-round, including during the breeding and nonbreeding periods. In this case, female and male roles converge (Morton 1996). Furthermore, sexual plumage dichromatism may be more important for pair formation in species of temperate regions where the breeding season is shorter than in tropical regions and where species are often monomorphic (Hamilton and Barth 1962). Extra-pair fertilization, which may be an important component of sexual selection (Møller and Birkhead 1994), is infrequent in tropical passerines (Morton 1996). On this basis, we assume that sexual selection is stronger in species of temperate regions. For these reasons, and as a first step to clarifying the relationships between song complexity and plumage conspicuousness in songbirds, we chose to study only the North American representatives of five families with a wide range of songs and colours: the Emberizidae (15 genera), Parulidae (14 genera), Icteridae (8 genera), Cardinalidae (5 genera), and Thraupidae (1 genus) (American Ornithologists' Union 1997). This sample comprises nearly all members of these families that commonly breed north of the Mexican border for which song recordings were available.

Materials and methods

Song complexity

There is no consensus for a definition of song complexity. A number of characteristics have been used, among which are: song duration (Kroodsma 1977, Shutler and Weatherhead 1990, Read and Weary 1992), repetition rate per unit of time (Shutler and Weatherhead 1990, Read and Weary 1992), the actual time spent singing during a given period of time, expressed as a percentage or a ratio (Kroodsma 1977, Shutler and Weatherhead 1990), song or syllable repertoire (Kroodsma 1977, Catchpole 1980, Catchpole and McGregor 1985, Shutler and Weatherhead 1990, Read and Weary 1992, Mountjoy and Lemon 1996), maximal frequency, minimal frequency, and frequency range (Shutler and Weatherhead 1990). An additional measure of song complexity is versatility (Hartshorne 1973): if a bird repeats the same song indefinitely, it is said to be "non-versatile", but if it possesses a repertoire of songs which alternate during periods of vocal activity, it is said to be "versatile". Versatile singers can produce songs either with "eventual variety" (i.e., repeat the same song type many times before switching to the next) or with "immediate variety" (i.e., alternate rapidly the different song types).

On this basis, Kroodsma and Verner (1978) defined a "total versatility index". This index, used in the case of song types, results from the product of the number of song types uttered in a ten-song bout ("song type versatility") multiplied by the number of transitions ("transition versatility") from one type to another in the same bout, including the transition between the tenth song and the eleventh. This index has been modified by Conner et al. (1986) so that one can use it with syllable types and measure within-song complexity. This index, called syllable-type versatility, is formulated as follows:

[1] Syllable-type versatility index = $(S \times T)/N$

where S is the number of syllable types per song, T is the number of transitions from one type to another per song, and N is the total number of syllables per song.

If a song characteristic appears complex to individuals of a species, it is not necessarily the case for those of another species (Kroodsma 1982, Read and Weary 1992). A "comparability problem" (Kroodsma 1982, Read and Weary 1992) is therefore present, where various species may have adopted different solutions when faced with selective pressures driving them to increase the complexity of their songs. Moreover, there are energetic and physiological constraints on both the temporal organization and the sound frequencies of songs (Lambrechts 1996). It seemed best to use several variables in measuring song complexity. Read and Weary (1992) made the distinction between "between-song complexity", which includes the notion of song and syllable repertoires, and "within-song complexity", which refers to the number of syllable types in a song and song-type versatility. As field data for between-song complexity were not available for all species, we deal here only with within-song complexity. To estimate the size of song and syllable repertoires, it would have been necessary to intensively record many individuals in each species, as did Horn et al. (1993) and Ewert and Kroodsma (1994). Although our method does not take between-song complexity into account, it has the advantage of putting the emphasis on the immediate complexity of song, that is, the complexity enclosed in the song structure and independent of the individual's song or syllable repertoires. Furthermore, it seems that in certain species song repertoire cannot be used by females and male competitors to assess the quality of a male (Byers 1995).

From recordings made by ornithologists and/or generally available commercially (see Appendix 1), we computerized the song of individuals from 123 North American Emberizidae, Parulidae, Icteridae, Cardinalidae, and Thraupidae. The common and scientific names of these species are found in Appendix 2. Males in some species use different songs in different contexts and the complexity of these songs can vary (Staicer 1996). Although the date and the location of the recordings were known in some cases, details concerning the time and the context in which the songs were recorded were not always available. Spectrograms of the songs were traced using the Canary 1.1 software (Charif et al. 1993). The sampling rate during the transfer of the songs onto disk was 23 kHz and spectrograms were traced with a 352.94 Hz filter bandwidth, which resulted in a moderate temporal resolution and a moderate frequency resolution. We tried as much as possible to use only one song per individual, so that the data remained independent when we calculated mean values for song complexity. In some species of warblers, we found the same individuals on two recordings coming from different sources. The procedure was then to exclude one of the two recordings from the analysis. For each individual of each species, we measured the following variables:

(1) Song duration (DUR).

(2) Number of syllable types in the song (SYLL). The term syllable refers to the 2Ms unit (2 meaning a second-order unit, and Ms meaning that sequencing was the morphological principle used to generate the unit) described by Thompson et al. (1994). This use of the term syllable is similar to that made by Staicer (1989).

(3) Number of transitions (TRANS) from one syllable type to another in the song (see Conner et al. 1986). Sometimes, the transition was gradual, that is, the syllable shape changed in graded way from one type to another (see Staicer 1996). In such cases, we counted only one transition.

(4) Total number of syllables, different or not, in the song (TOT).

(5) Syllable-type versatility index (INDEX) as adapted by Conner et al. (1986; see equation 1).

(6) Maximum frequency (FMAX) found in the song, in kHz.

(7) Miminum frequency (FMIN) reached by the bird in its song, in kHz.

(8) Frequency range (RANGE), the difference between (6) and (7), in kHz.

Variables (1), (6), (7), and (8) were measured directly on the computer screen using cursors.

The sample size ranges from one to thirty-five songs per species. When more than one song was used for a given species, we calculated the mean for each of the song complexity variables as described above. The song complexity data are available from the authors upon request.

Plumage conspicuousness and sexual dichromatism

When Darwin (1871) and Pettingill (1985) wrote about plumage elaborateness, they were interested not only in the conspicuousness of the plumages but also in their sexual dichromatism. Our method (de Repentigny et al. 1997; Chapter 1) used the Munsell colour system (Smithe 1975) to measure plumage conspicuousness and plumage sexual dichromatism in a repeatable way, as independently as possible of human judgments. The Munsell colour system defines a colour by three characteristics: hue (the dominant wavelength of light), value (degree of brightness) and chroma (degree of saturation). Since value and chroma are quantified on a scale and are easily represented by numbers, we used them as conspicuousness indices. The hue scale is circular and does not have lower and upper limits, and it is not clear what hues are complementary or contrast most with each other (Hailman 1977). Consequently, hue was not used in the present study.

Following Burtt (1986), we divided the plumages of the 123 selected species into nineteen regions, each region occupying a certain percentage of the plumage. Because the value and chroma of colours are found in Smithe (1975), the numerical values of colours matching best those depicted on the plates of the Peterson field guides (1990, 1994) were ascribed to each body region of males in breeding plumage. Colour matching took place in the laboratory under fluorescent light but next to a window to provide indirect sunlight. Field guides may be used in assessing bird conspicuousness because the scores obtained using these guides do not differ significantly from those recorded on museum specimens (de Repentigny et al. 1997; Chapter 1). For the species not illustrated in Peterson guides, the National Geographic Society field guide (1987) was used. If a body region consisted of more than one colour, the fraction of the region occupied by each colour was estimated and the average value (V) and chroma (C) and the resulting average product $V \bullet C$ for that region were calculated. In the next procedure, the V, C, and $V \bullet C$ scores of each body region were multiplied by the percentage of the plumage covered by that region, and the results of each region were summed. This generated the following indices:

(1) Total plumage value (V). The value is a measure of brightness.

(2) Total plumage chroma (C). The chroma is a measure of saturation.

(3) Total plumage Munsell power ($V \bullet C$), which correlates with the power of the bird's colours to attract attention in humans.

To take into account the fact that adjacent colours in a plumage can contrast, we determined the colour with the highest V and that with the lowest. Then we divided the latter by the former and multiplied the result by the percentage of the plumage covered by the least abundant of the two colours, which gave a V within-plumage contrast. We did the same thing for C and $V \bullet C$. That way, a high within-plumage contrast score indicates a high degree of crypsis in V, C, or $V \bullet C$, while a low within-plumage contrast score indicates a high degree of detectability, recognition or conspicuousness. Therefore, to make the variables more intuitively comprehensible, we multiplied these scores by constant of -1, so that low (more negative) scores mark crypsis and high (less negative) ones denote conspicuousness. Three within-plumage contrast indices were thus obtained:

(4) Within-plumage contrast in value (W_V).

(5) Within-plumage contrast in chroma (W_C).

(6) Within-plumage contrast in Munsell power ($W_{V \bullet C}$).

A uniformly coloured bird such as the common grackle *(Quiscalus quiscula)* would obtain high (less negative) within-contrast indices, while a multi-coloured bird like the hooded warbler *(Wilsonia citrina)* would have low (more negative) within-contrast indices.

To quantify "long-distance conspicuousness" or "detectability" (see Götmark 1994), which is influenced by the coloration of the background, we selected in Smithe (1975) the colour Leaf Green (No. 146) as representative of a simplified background of vegetation. We then divided the V, C, and V • C of the colours representing the habitat by the V, C, and V • C of the males (or the reverse if the latter were higher). The results were used as indices for measuring the contrast between birds and their habitat:

(7) Contrast of a bird with its background in value (B_V).

(8) Contrast of a bird with its background in chroma (B_C).

(9) Contrast of a bird with its background in Munsell Power ($B_{V \bullet C}$).

Finally, we calculated V, C, and V • C indices for the females of the selected species in the same way as for males. Male V, C and V • C scores were then divided by their respective female V, C, and V • C scores, or the reverse if a female score was greater. The ratios thus obtained were used as sexual dichromatism indices:

(10) Sexual dichromatism in value (D_V).

(11) Sexual dichromatism in chroma (D_C).

(12) Sexual dichromatism in Munsell power ($D_{V \bullet C}$).

These twelve indices were used as variables describing plumage elaborateness and results for each species are also available from the authors upon request.

Correction for the phylogenetic autocorrelation

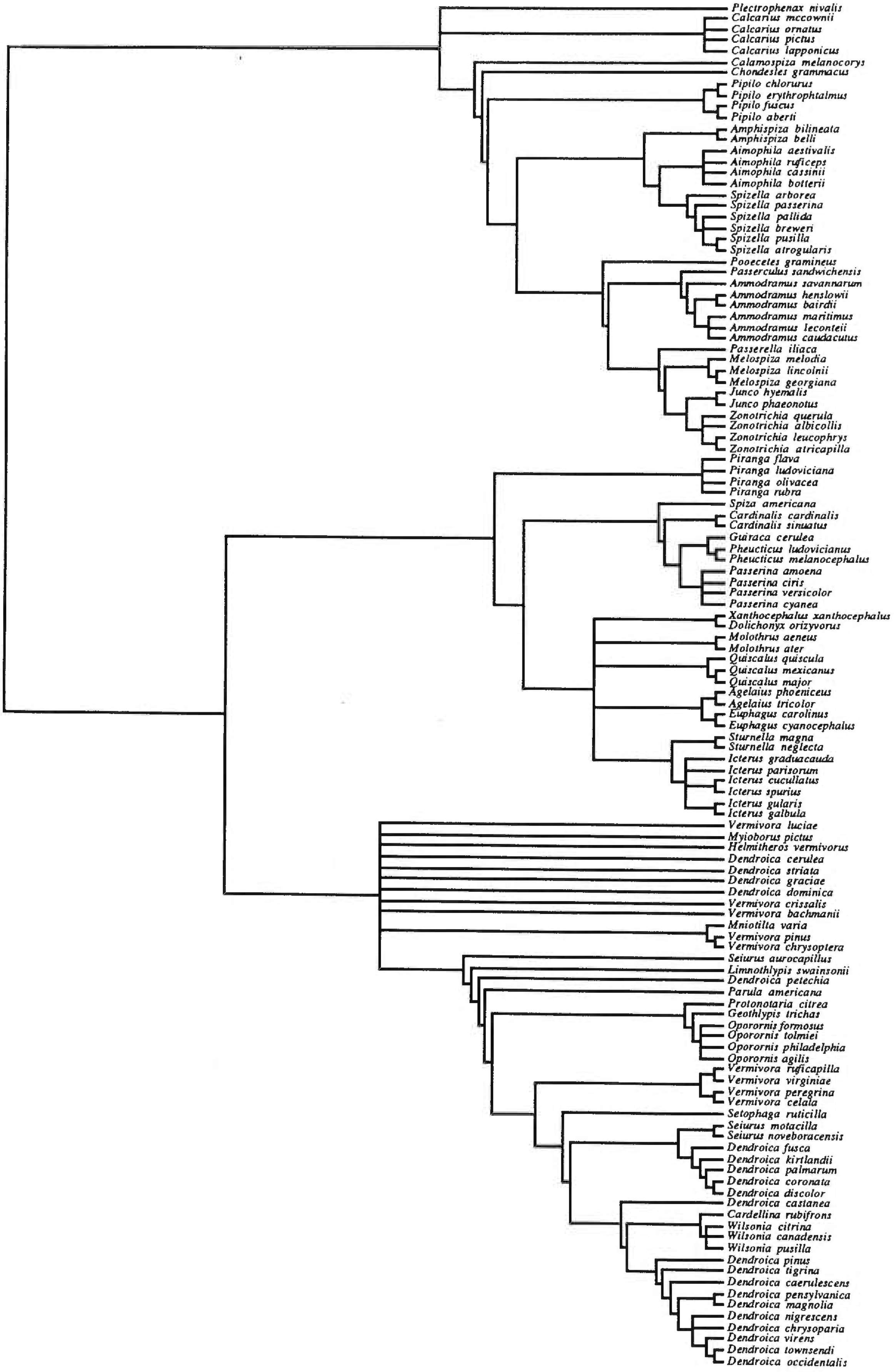
Species are descended from common ancestors in a hierarchical way and hence cannot be considered as points drawn independently from the same distribution (Felsenstein 1985, Martins and Garland 1991, Garland et al. 1993, Martin and Clobert 1996). For instance, two species could have similar songs mainly because they are closely related. To take phylogenetic autocorrelation into account when comparing the species to verify if there exists a relationship between the evolution of plumage and that of song, we used Felsenstein's (1985) independent contrasts method (see also Garland et al. 1992). This method, based on a brownian evolution model (where successive changes are considered independent), calculates differences, or contrasts, between trait values of all pair of species, current and ancestral. These contrasts are then standardized by dividing them by their standard deviation, which is the square root of their branch lengths. This gives n - 1 contrasts from n original tip species that can be considered as drawn independently from a bivariate normal distribution with means zero and variances unity.

We first constructed a phylogenetic hypothesis using the information available in recent studies and mostly based on molecular data (Sibley and Ahlquist 1990, Zink and Avise 1990, Lanyon 1994, Dodge et al. 1995, Freeman and Zink 1995, Martin and Clobert 1996, Zink and Blackwell 1996). When differences existed among the various sources as for the topology of the tree, we applied the strict consensus method (Sokal and Rohlf 1981), except in cases where information from a source allowed to specify the relationships in a previously unresolved polytomy (e.g., sparrows of the genus *Spizella*, Dodge et al. 1995). Species for which there is no information were placed at the same level as their congeners located on the lowest branches of the tree. Finally, as branch lengths were not comparable because of the use of different methods, we set all branches equal to 1, which amounts to a speciational model (Garland et al. 1993). Our phylogenetic hypothesis is shown in Fig. 1. We could then calculate standardized independent contrasts for each variable according to this tree with the PDTREE program included in the PDAP package (Garland et al. 1993).

Statistical analysis

We used a canonical correlation analysis (Hotteling 1936) to see if there is a correlation between our two sets of variables. This method proceeds by finding the highest correlation between linear combinations (canonical variables) of two groups of variables. There can be more than one combination. We can see the canonical correlation as a double principal

Figure 1. Phylogenetic hypothesis used in this study. See Appendix 2 for common names.


Plectrophenax nivalis
Calcarius mccownii
Calcarius ornatus
Calcarius pictus
Calcarius lapponicus
Calamospiza melanocorys
Chondesles grammacus
Pipilo chlorurus
Pipilo erythrophtalmus
Pipilo fuscus
Pipilo aberti
Amphispiza bilineata
Amphispiza belli
Aimophila aestivalis
Aimophila ruficeps
Aimophila cassinii
Aimophila botterii
Spizella arborea
Spizella passerina
Spizella pallida
Spizella breweri
Spizella pusilla
Spizella atrogularis
Pooecetes gramineus
Passerculus sandwichensis
Ammodramus savannarum
Ammodramus henslowii
Ammodramus bairdii
Ammodramus maritimus
Ammodramus leconteii
Ammodramus caudacutus
Passerella iliaca
Melospiza melodia
Melospiza lincolnii
Melospiza georgiana
Junco hyemalis
Junco phaeonotus
Zonotrichia querula
Zonotrichia albicollis
Zonotrichia leucophrys
Zonotrichia atricapilla
Piranga flava
Piranga ludoviciana
Piranga olivacea
Piranga rubra
Spiza americana
Cardinalis cardinalis
Cardinalis sinuatus
Guiraca cerulea
Pheucticus ludovicianus
Pheucticus melanocephalus
Passerina amoena
Passerina ciris
Passerina versicolor
Passerina cyanea
Xanthocephalus xanthocephalus
Dolichonyx orizyvorus
Molothrus aeneus
Molothrus ater
Quiscalus quiscula
Quiscalus mexicanus
Quiscalus major
Agelaius phoeniceus
Agelaius tricolor
Euphagus carolinus
Euphagus cyanocephalus
Sturnella magna
Sturnella neglecta
Icterus graduacauda
Icterus parisorum
Icterus cucullatus
Icterus spurius
Icterus gularis
Icterus galbula
Vermivora luciae
Myioborus pictus
Helmitheros vermivorus
Dendroica cerulea
Dendroica striata
Dendroica graciae
Dendroica dominica
Vermivora crissalis
Vermivora bachmanii
Mniotilta varia
Vermivora pinus
Vermivora chrysoptera
Seiurus aurocapillus
Limnothlypis swainsonii
Dendroica petechia
Parula americana
Protonotaria citrea
Geothlypis trichas
Oporornis formosus
Oporornis tolmiei
Oporornis philadelphia
Oporornis agilis
Vermivora ruficapilla
Vermivora virginiae
Vermivora peregrina
Vermivora celata
Setophaga ruticilla
Seiurus motacilla
Seiurus noveboracensis
Dendroica fusca
Dendroica kirtlandii
Dendroica palmarum
Dendroica coronata
Dendroica discolor
Dendroica castanea
Cardellina rubifrons
Wilsonia citrina
Wilsonia canadensis
Wilsonia pusilla
Dendroica pinus
Dendroica tigrina
Dendroica caerulescens
Dendroica pensylvanica
Dendroica magnolia
Dendroica nigrescens
Dendroica chrysoparia
Dendroica virens
Dendroica townsendi
Dendroica occidentalis

components analysis. In both cases, the same procedure is applied. It consists in reducing the dimensionality to a few linear functions which express as much variation as possible from the original variables, the restriction being that the functions have to be orthogonal. The canonical model chooses the linear functions of the two sets that express a maximum of covariance, the restriction again being that these functions have to be orthogonal. It is as if we carried out a principal component analysis in both groups and then rotated the canonical axes so that they are superimposed. We performed canonical correlation analyses, first on the plumage conspicuousness variables and those of song complexity, and then on their independent contrasts, using version 6 of the SAS/STAT™ package (SAS Institute Inc. 1987) for the 123 selected species of Oscines. A redundancy analysis (Gittins 1985) was also carried out with the help of the SAS/STAT™ package to calculate the amount of variance in one set of variables that was explained by the other set. A redundancy coefficient is equal to the square of the canonical correlation coefficient between two canonical variables multiplied by the proportion of variance in a domain explained by the canonical variables of the other domain (Gittins 1985). This measure is more conservative and takes into account the fact that the canonical variables sometimes explain a weak proportion of the variance of their domain.

Results

Uncorrected data

The canonical correlation analysis showed relationships between song complexity and plumage elaborateness across the species studied. The first (0.650, $F = 1.80$, $P < 0.001$) and second (0.571, $F = 1.37$, $P < 0.05$) canonical correlations were statistically significant. Therefore, there was two independent linear relationships between the song complexity variable set and the plumage elaborateness variable set. In other words, the linear relationship between these two sets seems bidimensional. The first canonical correlation shows that 42.3% of the variance of the first canonical variable of plumage (i.e., the first linear combination of plumage variables, hereafter called COLOUR1) is explained by the first canonical variable of song (hereafter called SONG1) and vice versa. Similarly, the amount of variance in COLOUR2 explained by SONG2 and vice versa reached 32.6%. We will see later that these measures are somewhat liberal and that there is a better way of calculating the variance of a domain that is explained by the canonical variable of the other domain.

As a rule of thumb, canonical correlations smaller than 0.30 are considered trivial (Cooley and Lohnes 1985). We chose to apply the same reasoning to the correlations between the original variables and their canonical variables. For plumage variables, if correlations with a coefficient below 0.30 are excluded, we see that the variables W_V, $B_{V \bullet C}$, and D_V all contribute to the canonical variable COLOUR1 in the same direction, while V contributes in the opposite direction (Table 1). Therefore, COLOUR1 expresses characteristics common to the first three variables as for their behaviour towards the linear function SONG1, while it expresses opposite characteristics for V. As for COLOUR2, it indicates a common behaviour of variables W_V, W_C, $W_{V \bullet C}$, and B_V towards the linear function SONG2, but an opposite behaviour for C and V • C.

In the song variable set, TRANS, TOT, and FMIN are all positively correlated to SONG1 (Table 1). Therefore, SONG1 represents essentially the expression of these variables. SONG2, on the other hand, points to a common behaviour of TOT, FMAX, and RANGE, and to an opposite behaviour of INDEX towards canonical variable COLOUR2.

The correlations between the original variables and the canonical variable of the opposite set are weaker (Table 1). This is normal, since these correlations are the product of the correlation of the original variables with their canonical variable multiplied by the canonical correlation between the two canonical variables. There is a positive correlation between SONG1 and V, and a negative correlation between the same canonical variable and $B_{V \bullet C}$. As SONG1 is mainly the positive expression of TRANS, TOT, and FMIN, there is an indication of a positive correlation between these aspects of song complexity and total

Table 1. Correlations between original variables and canonical variables in the selected species of Oscines.

Variables	Correlation with COLOUR1	Correlation with COLOUR2	Correlation with SONG1	Correlation with SONG2
Colour variables				
V	0.705	-0.033	0.459	-0.019
C	-0.163	0.452	-0.106	0.259
$V \cdot C$	-0.105	0.486	-0.069	0.277
W_V	-0.368	-0.733	-0.240	-0.419
W_C	0.052	-0.641	0.034	-0.366
$W_{V \cdot C}$	0.069	-0.814	0.045	-0.465
B_V	-0.237	-0.462	-0.154	-0.264
B_C	-0.124	-0.103	-0.081	-0.059
$B_{V \cdot C}$	-0.571	-0.124	-0.371	-0.071
D_V	-0.433	-0.212	-0.281	-0.121
D_C	0.023	-0.042	0.015	-0.024
$D_{V \cdot C}$	-0.240	-0.2729	-0.156	-0.156
Song variables				
SYLL	0.181	0.130	0.278	0.228
TRANS	0.211	0.088	0.324	0.155
TOT	0.260	-0.298	0.400	-0.521
INDEX	0.128	-0.210	0.196	0.367
DUR	0.177	0.028	0.272	0.050
FMAX	0.180	-0.436	0.276	-0.763
FMIN	0.441	-0.024	0.679	-0.041
RANGE	-0.147	-0.426	-0.227	-0.746

plumage value, but also of a negative correlation between them and contrast with the background in Munsell power. Plumage variables W_V, W_C, and $W_{V \bullet C}$ are all negatively correlated to SONG2, which expresses INDEX positively, and TOT, FMAX, and RANGE negatively. Thus, within-plumage contrast varies directly as syllable-type versatility, but inversely as the total number of syllables of the song, maximum frequency, and frequency range.

The correlation between COLOUR1 and FMIN is positive (Table 1). Since COLOUR1 expresses variables W_V, $B_{V \bullet C}$, and D_V negatively and V positively, this indicates a positive correlation between total plumage value and minimum frequency, but a negative relationship between the latter on one hand, and within-plumage contrast in value, contrast with the background in Munsell power, and sexual dichromatism in value on the other. There is also a negative correlation between COLOUR2 and variables FMAX and RANGE. COLOUR2 being the negative expression of W_V, W_C, $W_{V \bullet C}$, and B_V and the positive expression of C and $V \bullet C$., there is an indication of a positive correlation between maximum frequency and frequency range in the first instance, and within-plumage contrast in the second. However, the same song complexity variables are also negatively correlated with total plumage chroma and total plumage Munsell power.

According to the redundancy analysis, canonical variables COLOUR1 and COLOUR2 explain only 11.0% and 20.1% of the total variance of plumage variables respectively. The proportions of multivariate variance in the plumage domain explained by SONG1 and SONG2, or redundancy, are even lower, at 4.7 and 11.2%. This contrasts sharply with the proportions of variance of the canonical variables COLOUR1 and COLOUR2 explained by SONG1 and SONG2, which are about 42 and 33%. Redundancy coefficients take into account not only the correlation between corresponding canonical variables, but also the variance of variables explained by the canonical variables of their respective domains. SONG1 and SONG2 also explain only 13.0 and 20.3% of the variance of the song variables. Consequently, COLOUR1 and COLOUR2 explains only 5.5 and 12.2% of the variance of the song variables respectively.

In summary, the first two canonical relations shows relationships between plumage conspicuousness and song complexity, though the pattern of variation is complex and the correlations are sometimes negative, sometimes positive. However, because of the phylogenetic nonindependence of the species, the results of this analysis are untrustworthy and have been presented here for the sake of comparison with those of the next section.

Independent contrasts

With independent contrasts, the canonical correlation analysis again showed a correlation between song complexity and plumage elaborateness across the species studied. However, in this case, only the first canonical correlation (0.595, F = 1.46, $P < 0.005$) was statistically significant. Therefore, there was only one independent linear relationship between the song complexity variable set and the plumage elaborateness variable set. The first canonical correlation shows that 35.4% of the variance of the canonical variable COLOUR1 is explained by the canonical variable SONG1 and vice versa.

For plumage variables, a after the exclusion correlations with a coefficient below 0.30 are excluded, we see that the variables W_C, $W_{V \bullet C}$, B_V, B_C, $B_{V \bullet C}$, D_V, D_C, and $D_{V \bullet C}$ (the variables measuring within-plumage contrast, the contrast with the background and those measuring plumage dichromatism) all contribute to the canonical variable COLOUR1 in the same direction (Table 2). Therefore, COLOUR1 expresses characteristics common to the first six variables as for their behaviour towards the linear function SONG1.

As for song variables, we see that FMAX, DUR, RANGE, TOT, and, to a lesser extent, SYLL, are all positively correlated to SONG1 (Table 2). We can consider the canonical variable SONG1 as essentially the expression of these variables, and that it indicates a common behaviour of these variables towards the linear function COLOUR1.

There are positive correlations between SONG1 and W_C, $W_{V \bullet C}$, B_C, D_V, D_C and $D_{V \bullet C}$ (Table 2). As SONG1 is mainly an expression of FMAX, DUR, RANGE, TOT and SYLL, there is an indication of a positive correlation between maximum frequency, song duration, frequency range, and the total number of syllables in the song on one hand and plumage

Table 2. Correlations between independent contrasts of original variables and canonical variables in the selected species of Oscines.

Variables	Correlation with COLOUR1	Correlation with SONG1
Colour variables		
V	-0.026	-0.015
C	-0.194	-0.115
V · C	-0.269	-0.160
W_V	0.255	0.152
W_C	0.532	0.316
$W_{V \cdot C}$	0.595	0.354
B_V	0.354	0.210
B_C	0.473	0.281
$B_{V \cdot C}$	0.377	0.224
D_V	0.587	0.349
D_C	0.450	0.268
$D_{V \cdot C}$	0.495	0.294
Song variables		
SYLL	0.194	0.327
TRANS	0.164	0.276
TOT	0.292	0.491
INDEX	0.113	0.191
DUR	0.317	0.533
FMAX	0.333	0.560
FMIN	0.035	0.059
RANGE	0.327	0.550

uniformity, contrast with the background, and sexual dichromatism, on the other. In other words, contrary to what the tradeoff hypothesis predicts, the more a plumage is elaborate, the more complex the song is.

Correlations between COLOUR1 and TOT, DUR, FMAX, and RANGE are positive (Table 2). Since COLOUR1 expresses variables W_C, $W_{V \bullet C}$, B_V, B_C, $B_{V \bullet C}$, D_V, D_C, and $D_{V \bullet C}$ positively, this indicates a positive correlation between the within-plumage contrast, sexual dichromatism, and contrast with the background variables in the first instance, and the song complexity variables mentioned above in the second. Again, this indicates a positive relationship between plumage elaborateness and song complexity.

According to redundancy analysis, the canonical variable COLOUR1 explains only 17.5% of the total variance of plumage variables, while SONG1 explains only 17.1% of the variance of the song variables. Consequently, the proportion of multivariate variance in the plumage domain explained by SONG1 is 6.2%, while COLOUR1 explains only 6.0% of the variance of the song variables.

In summary, the first canonical relation shows that there is a weak positive correlation between W_C, $W_{V \bullet C}$, B_V, B_C, $B_{V \bullet C}$, D_V, D_C, and $D_{V \bullet C}$, and FMAX, DUR, RANGE, TOT, and SYLL to a lesser extent. Since the W, B and D variables are indices of the bird's within-plumage contrast, contrast with its background and of sexual dichromatism, we note that the more the male of a species is conspicuous and different from the female, the more it has a complex song in terms of maximum frequency, song duration, frequency range, total number of syllables in the song, and number of different syllable types in the song. Therefore, plumage elaborateness increases with song complexity, though the link between these traits is rather loose.

Discussion

The results obtained in this study from analyses taking phylogenetic autocorrelation into account do not support the tradeoff hypothesis in the Oscines studied. Instead, we found a weak but significant positive correlation between song complexity and plumage elaborateness. Taking the results of the canonical correlation analysis as a model, contrast with the background in value, chroma and Munsell power, sexual dichromatism in value, chroma and Munsell power, and within-plumage contrast in chroma and Munsell power are plumage elaborateness features that are most influenced by the evolution of song complexity. Indices measuring conspicuousness irrespective of the background (total plumage value, total plumage chroma, total plumage Munsell power) do not contribute to the model. Therefore, it is important to take into account the background against which the bird is seen when measuring conspicuousness. Pioneering steps in this direction have been made by workers like Endler and Théry (1996), but more studies are needed. Again based on canonical correlations, the total number of syllables, different or not, in the song, the number of different syllable types in the song, song duration, frequency range, and maximum frequency are the song complexity variables that are most influenced by the evolution of plumage elaborateness. While the first four variables intuitively make sense in terms of complexity, one may wonder why the maximum frequency contributes to the model. There are two explanations. Firstly, according to Morton's (1982) "motivational-structural rules" model, higher frequencies would convey an "appeasing" quality while lower frequencies would be perceived as "aggressive" by birds. A song with an emphasis on higher frequencies would thus appeal more to a prospective mate. Secondly, higher frequencies are predicted to attenuate more in all habitats (Wiley 1991). A bird singing at higher frequencies would probably spend more time and more energy before being noticed. This is consistent with Zahavi's (1991) signal selection theory, which implies that a reliable signal must have a cost, so that only individuals of high quality can afford to produce it. This would justify the waste found in some signals (Zahavi 1991). Thus, only birds of high quality could afford to sing at frequencies that propagate less well, and for this reason, maximum frequency could be viewed as a measure of song complexity.

Results from conventional statistical tests differed strongly from those obtained with the independent contrasts method. Some correlations between song complexity and plumage conspicuousness variables were reversed and the variables of a set explained more variance of the variables of other set when the nonindependence of the species was not taken into account. This may be due to closely related species in this study being more similar or dissimilar than distantly related ones and exemplifies the need to correct for phylogenetic autocorrelation when making interspecific comparisons (Garland et al. 1993).

Why would there be a positive correlation between song complexity and plumage conspicuousness in North American Oscines? The selected species breed in temperate regions, where the period for the establishment of pair bonds is short, contrary to stable environments of tropical latitudes (Hamilton and Barth 1962). Hamilton and Barth (1962) found an association between increased sexual plumage dichromatism and relatively short periods for the establishment and maintenance of pair bonds. It is conceivable that males, in temperate regions where the breeding season is short, would need not only a sexually dichromatic plumage, but would also take advantage of being conspicuous and having a complex song to establish a territory and find a mate rapidly. In other words, sexual selection would simultaneously operate on song and plumage, so that species experiencing more intense selection would have both conspicuous song and plumage. However, the evidence that sexual dichromatism reduces the time needed to acquire a territory or a mate in temperate zone birds is, to our knowledge, limited to that provided by Hamilton and Barth (1962), and to this day, the reasons for the association of sexual dichromatism with habitat are still unclear (Price 1996). This is an area that needs field research. It would also be interesting to know whether or not there is a relationship between song or plumage elaborateness and the duration of the breeding period in the species studied.

However, the positive correlation between song complexity and plumage conspicuousness is weak. Each set explains only about 6% of the variance of the other, and consequently, it is difficult, almost impossible, to find species that completely fit the model. Therefore, the possibility that song and plumage are uncorrelated across species cannot be ruled out. The factors that can influence both song complexity, plumage conspicuousness, and the relationship between them, and hence explain the remaining 94% of variation are discussed below.

Environmental factors

The environment in which birds live influences the structure of their vocalizations (Wiley and Richards 1982, Brenowitz 1986, Wiley 1991). In forested habitats, the reverberation of sound due to surrounding vegetation entails a fast degradation of signals with rapid and repetitive frequency modulations (trills, buzzes) and favours the evolution of signals made of non-repetitive and slowly modulated whistles (Wiley and Richards 1982, Brenowitz 1986, Wiley 1991). In open habitats, the amplitude fluctuations caused by atmospheric turbulences favour the development of signals with high rates of repetition, such as trills, because portions of information of non-repeated whistles would be lost otherwise (Wiley and Richards 1982, Brenowitz 1986). Songs appear simpler in open habitats because of this high repetition rate. This will be verified in a forthcoming paper (de Repentigny et al. in prep.).

Another ecological factor that can affect the evolution of bird songs is the diversity of avian communities. Acoustic competition between species sharing a common habitat may lead to evolutive divergence of vocalizations (Catchpole 1979). Among North American wrens, the three species that sing with immediate variety are those found in communities with the lowest avifaunal diversity (Kroodsma 1977).

The environment presumably influences the evolution of plumage as well. For instance, birds are more visible to each other in open areas because of the absence of tall plants (Catchpole 1979, Lazarus and Symonds 1992). Consequently, plumage coloration may be less important in these habitats.

Predation also influences the evolution of plumage coloration (Butcher and Rohwer 1989). Conspicuous coloration in males may be favoured by predation in some species and selected against in others (Götmark 1993). Species in which males signal that they are unprofitable or unpalatable preys fall in the former category (Baker and Parker 1979, Götmark 1993, 1994), while those in which predation favours a cryptic male plumage belong to the latter (Götmark 1993). Thus, predation pressures would not have the same effect on the evolution of plumage coloration and hence on that of song complexity in all species. However, predation on adult songbirds is rarely quantified (Götmark and Post 1996). It is therefore difficult to compare species on the basis of the influence of predation on the evolution of plumage coloration. On the other hand, nest predation has been quantified in some species and Martin and Badyaev (1996) found that plumage brightness is negatively correlated with nest predation in females, but not in males, at least in taxa where only females incubate eggs and brood young. Their results suggest that nest predation may sometimes cause variation in female coloration and hence variation in sexual dichromatism independently of sexual selection on males.

The need for durable plumage selects for melanic colours in the tail and wings (Burtt 1986). These are dark colours. Therefore, signals require light colours to contrast with the background and the surrounding plumage. Light colours are less durable than melanic ones and must be in protected parts of the tails and wings. Tail spots are on the medial vane of the outermost tail feathers and away from the tip, whereas wing bars are in the area of the wing that receives laminar airflow (Burtt and Gatz 1982). The end result is that colors and patterns can be very similar among a large set of birds (Burtt and Gatz 1982).

Morphological and behavioural factors

Sexual selection acts more strongly on polygynous than on monogamous species and this strong sexual selection leads to increased sexual dichromatism in the former (Searcy and Yasukawa 1983). Even though some of the selected species are polygynous (Searcy and Yasukawa 1983, Björklund 1991, Webster 1992), we did not take mating systems into account when we looked for a correlation between plumage conspicuousness and song complexity. Besides plumage conspicuousness, sexual dichromatism and song complexity, sexual selection can also lead to sexual size dimorphism (Webster 1992), males being generally larger than females in higher vertebrates (Wheeler and Greenwood 1983). Larger males have an advantage over smaller ones in aggressive interactions (Searcy and Yasukawa 1983). Furthermore, larger birds are also easier to see (Hailman 1977), which may give them an advantage in female choice as well. Some of the selected species show sexual size dimorphism (Searcy and Yasukawa 1983, Björklund 1991, Webster 1992), but we did not include it in our measures of conspicuousness. On the other hand, the frequencies in bird songs are strongly related to body size, smaller birds being more efficient at producing high frequencies than larger ones (Wiley 1991 and references therein). However, we did not use body size in our analysis. Finally, processes like social competition or mate choice by males can favour bright female plumage and thus reduce sexual dichromatism in some species (Irwin 1994).

Experimental factors

Wiley (1991) noted that measurements of extreme frequencies are rather problematic because they depend on detecting the limits of traces on spectrograms. In addition, it is sometimes difficult to tell complex syllables made of several notes (which are individual traces on a spectrogram [Thompson et al. 1994]) from series of simple syllables made of only one note, and trills of the same syllable repeated many times from a buzzy syllable. Finally, males in some species use different songs in different contexts and the complexity of these songs can vary (Staicer 1996). We have no information as to the context in which the songs were recorded.

The conspicuousness of a colour depends on its background (Hailman 1977, Burtt 1986), and the same bird appears more or less conspicuous depending on the background against which it is seen (Götmark and Hohlfält 1995). However, in this study, we used a single simplified background (de Repentigny et al. 1997; Chapter 1), overlooking the fact that birds might sometimes be seen against a blue sky or a brownish background, or against a background composed of several colours intermingled in an irregular pattern. Another factor that we did not take into account is ambient light, which differs among habitats and also affects the conspicuousness of signals that depend on reflected light (Burtt 1986, Endler 1990, Götmark and Unger 1994). Unfortunately, its effect is virtually unstudied except for a few exceptions (e.g., Endler and Théry 1996).

The concepts of song complexity and plumage conspicuousness remain poorly defined and difficult to translate into quantifiable entities. For example, we did not take into account the "between-song complexity" (Read and Weary 1992), or song or syllable repertoires, when measuring song complexity. However, repertoire size seems to be strongly influenced by sexual selection in several species (e.g., Catchpole 1980, 1987, Horn et al. 1993, Lampe and Saetre 1995, Mountjoy and Lemon 1996). On the other hand, it seems that in certain species the song repertoire cannot be used by females and male competitors to assess the quality of a male (Byers 1995). As for our plumage conspicuousness indices, they are based on the human visual system, which differs from that of birds, but this issue has been discussed in detail elsewhere (de Repentigny et al. 1997; Chapter 1).

Our results concern only North American representatives of five families of passerines. More extensive analyses will have to be carried out with other species before the tradeoff hypothesis can be confirmed or invalidated in a decisive manner and before our conclusions can be extended to all songbirds. Part of the effort should be directed towards species living in tropical areas. In these areas, year-round territorality is common, male and female roles converge, and extra-pair fertilization is infrequent (Morton 1996). Therefore, sexual selection is likely to be weaker in species inhabiting tropical regions and this may influence the relationship between song complexity and plumage conspicuousness. Nonetheless, the present study shows that the tradeoff hypothesis cannot apply universally.

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Appendix 1. Recordings of bird songs used in this study.

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Appendix 2. Common and scientific names of the bird species used in the present study.

Common name	Scientific name	Common name	Scientific name
Lucy's Warbler	*Vermivora luciae*	Townsend's Warbler	*D. townsendi*
Blue-winged Warbler	*V. pinus*	Hermit Warbler	*D. occidentalis*
Golden-winged Warbler	*V. chrysoptera*	Black-throated Green Warbler	*D. virens*
Tennessee Warbler	*V. peregrina*	Golden-cheeked Warbler	*D. chrysoparia*
Orange-crowned Warbler	*V. celata*	Blackburnian Warbler	*D. fusca*
Nashville Warbler	*V. ruficapilla*	Yellow-throated Warbler	*D. dominica*
Virginia's Warbler	*V. virginiae*	Grace's Warbler	*D. graciae*
Bachman's Warbler	*V. bachmanii*	Pine Warbler	*D. pinus*
Colima Warbler	*V. crissalis*	Kirtland's Warbler	*D. kirtlandii*
Northern Parula	*Parula americana*	Prairie Warbler	*D. discolor*
Yellow Warbler	*Dendroica petechia*	Palm Warbler	*D. palmarum*
Chestnut-sided Warbler	*D. pensylvanica*	Bay-breasted Warbler	*D. castanea*
Magnolia Warbler	*D. magnolia*	Blackpoll Warbler	*D. striata*
Cape May Warbler	*D. tigrina*	Cerulean Warbler	*D. cerulea*
Black-throated Blue Warbler	*D. caerulescens*	Black-and-white Warbler	*Mniotilta varia*
Yellow-rumped Warbler	*D. coronata*	American Redstart	*Setophaga ruticilla*
Black-throated Gray Warbler	*D. nigrescens*	Prothonotary Warbler	*Protonotaria citrea*

Appendix 2. Continued.

Common name	Scientific name	Common name	Scientific name
Worm-eating Warbler	*Helmitheros vermivorus*	Smith's Longspur	*C. pictus*
Swainson's Warbler	*Limnothlypis swainsonii*	Chestnut-collared Longspur	*C. ornatus*
Louisiana Waterthrush	*Seiurus motacilla*	Snow Bunting	*Plectrophenax nivalis*
Northern Waterthrush	*S. noveboracensis*	Lark Bunting	*Calamospiza melanocorys*
Ovenbird	*S. aurocapillus*	Fox Sparrow	*Passerella iliaca*
Kentucky Warbler	*Oporornis formosus*	Song Sparrow	*Melospiza melodia*
Connecticut Warbler	*O. agilis*	Lincoln's Sparrow	*M. lincolnii*
Mourning Warbler	*O. philadelphia*	Swamp Sparrow	*M. georgiana*
MacGillivray's Warbler	*O. tolmiei*	White-throated Sparrow	*Zonotrichia albicollis*
Common Yellowthroat	*Geothlypis trichas*	Harris' Sparrow	*Z. querula*
Hooded Warbler	*Wilsonia citrina*	White-crowned Sparrow	*Z. leucophrys*
Wilson's Warbler	*W. pusilla*	Golden-crowned Sparrow	*Z. atricapilla*
Canada Warbler	*W. canadensis*	Dark-eyed Junco	*Junco hyemalis*
Red-faced Warbler	*Cardellina rubifrons*	Yellow-eyed Junco	*J. phaeonotus*
Painted Redstart	*Myioborus pictus*	Savannah Sparrow	*Passerculus sandwichensis*
McCown's Longspur	*Calcarius mccownii*	Seaside Sparrow	*Ammodramus maritimus*
Lapland Longspur	*C. lapponicus*	Sharp-tailed Sparrow	*A. caudacutus*

Appendix 2. Continued.

Common name	Scientific name	Common name	Scientific name
Le Conte's Sparrow	*Ammodramus lecontii*	Rufous-crowned Sparrow	*A. ruficeps*
Henslow's Sparrow	*A. henslowii*	Green-tailed Towhee	*Pipilo chlorurus*
Baird's Sparrow	*A. bairdii*	Rufous-sided Towhee	*P. erythrophtalmus*
Grasshopper Sparrow	*A. savannarum*	Brown Towhee	*P. fuscus*
American Tree Sparrow	*Spizella arborea*	Abert's Towhee	*P. aberti*
Chipping Sparrow	*S. passerina*	Hepatic Tanager	*Piranga flava*
Clay-colored Sparrow	*S. pallida*	Summer Tanager	*P. rubra*
Brewer's Sparrow	*S. breweri*	Scarlet Tanager	*P. olivacea*
Field Sparrow	*S. pusilla*	Western Tanager	*P. ludoviciana*
Black-chinned Sparrow	*S. atrogularis*	Dickcissel	*Spiza americana*
Vesper Sparrow	*Pooecetes gramineus*	Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Lark Sparrow	*Chondestes grammacus*	Black-headed Grosbeak	*P. melanocephalus*
Black-throated Sparrow	*Amphispiza bilineata*	Northern Cardinal	*Cardinalis cardinalis*
Sage Sparrow	*A. belli*	Pyrrhuloxia	*C. sinuatus*
Bachman's Sparrow	*Aimophila aestivalis*	Blue Grosbeak	*Guiraca cerulea*
Botteri's Sparrow	*A. botterii*	Lazuli Bunting	*Passerina amoena*
Cassin's Sparrow	*A. cassinii*	Indigo Bunting	*P. cyanea*

Appendix 2. Continued.

Common name	Scientific name	Common name	Scientific name
Varied Bunting	*Passerina versicolor*	Brewer's Blackbird	*E. cyanocephalus*
Painted Bunting	*P. ciris*	Bronzed Cowbird	*Molothrus aeneus*
Altamira Oriole	*Icterus gularis*	Brown-headed Cowbird	*M. ater*
Hooded Oriole	*I. cucullatus*	Bobolink	*Dolichonyx orizyvorus*
Northern Oriole	*I. galbula*		
Orchard Oriole	*I. spurius*		
Audubon's Oriole	*I. graduacauda*		
Scott's Oriole	*I. parisorum*		
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*		
Red-winged Blackbird	*Agelaius phoeniceus*		
California Blackbird	*A. tricolor*		
Eastern Meadowlark	*Sturnella magna*		
Western Meadowlark	*S. neglecta*		
Common Grackle	*Quiscalus quiscula*		
Boat-tailed Grackle	*Q. major*		
Great-tailed Grackle	*Q. mexicanus*		
Rusty Blackbird	*Euphagus carolinus*		

Chapitre 3

Song complexity and plumage conspicuousness are not constrained by habitat structure in selected North American Oscines

Par

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Abstract: We investigated the influence of habitat structure on song complexity and plumage conspicuousness in 123 species of North American Oscines. These species were grouped into four categories according to their general habitat: deciduous forest, coniferous forest, semi-open (e.g., bushes, clearings, forest edges), and open. Three-group and two-group classifications were also used. From the current knowledge of patterns in frequency-dependent attenuation and degradation of acoustic signals in different environments, we predicted that species of more open habitats should have songs with higher maximum frequencies and a wider frequency range than forest-dwelling species but similar minimum frequencies. The number of syllable types per song, the number of transitions from one syllable type to another, and the syllable-type versatility index were predicted to be lower in more open habitats than in forests, and the total number of syllables and duration to be higher and longer. For plumage coloration variables, based on known patterns of opacity noise (i.e., barriers to propagation of visual signals) in different environments, we predicted close-quarter conspicuousness, within-plumage contrast, long-distance conspicuousness, and plumage sexual dichromatism indices to be higher in forests than in more open habitats, and higher again in deciduous forests than in coniferous ones. ANOVA tests, used in conjunction with null distributions of F statistics taking the nonindependence of the species into account, revealed no differences in mean values for all variables among habitats and thus provided no evidence that the song complexity, plumage conspicuousness and sexual dichromatism parameters used in this study are constrained by habitat structure.

Introduction

Darwin (1871) wrote that "It is... remarkable that birds which sing well are rarely decorated with brilliant colours or other ornaments. (...) Hence bright colours and the power of song seem to replace each other". Most observers have uncritically accepted Darwin's hypothesis (see references in Read and Weary 1992), and only Shutler and Weatherhead (1990) and Read and Weary (1992) have tested the hypothesis. Shutler and Weatherhead (1990) restricted their research to the Parulidae and the only aspect of plumage coloration they considered was sexual dichromatism. Read and Weary (1992) used a method of quantifying plumage conspicuousness based on scores given by observers on a scale from 1 to 6 according to whether they found the birds conspicuous or not, without taking into account the degree of sexual dichromatism.

In a recent study, de Repentigny et al. (submitted; see also Chapter 2) looked for possible relationships between song complexity and plumage conspicuousness in 123 North American species from the families Emberizidae, Parulidae, Cardinalidae, Icteridae, and Thraupidae (American Ornithologists' Union 1997). Using a different method of quantifying conspicuousness based on measurable and repeatable data (de Repentigny et al. 1997), as well as several measures of song complexity, they found, contrary to Darwin's assertion, that song and plumage elaborateness were positively correlated. To explain such results, environmental, morphological, behavioural, and experimental factors were suggested (de Repentigny et al. submitted).

Among the environmental factors, the influence of habitat structure on avian vocalizations is considered important (Wiley and Richards 1982, Brenowitz 1986, Wiley 1991). Indeed, acoustic signals travelling through a habitat, from a singer to a listener, are subject to overall attenuation by spherical spreading and, in addition, to frequency-dependent attenuation, reverberation, and irregular amplitude fluctuation (Wiley and Richards 1978, 1982). Birds use their songs mainly for communication at long range (Wiley and Richards 1982). Selection should favour signals that are minimally attenuated and degraded during propagation in order to avoid ambiguity and increase the efficiency of acoustic communication (Wiley and Richards 1982).

At all emission heights, except within a metre or so from the ground, and in all habitats, the lower the frequency, the better the sound carries (Marten and Marler 1977, Marten et al. 1977, Wiley and Richards 1982). Since increased scattering of higher frequencies in forest vegetation is thought to be partly counterbalanced by a scattering from atmospheric turbulence in the open, frequency-dependent attenuation should be approximately the same in both types of habitats (Wiley and Richards 1978). However, differences in the range of acceptable frequencies may still be present. For example, diurnal birds tend to sing earlier in the morning when conditions are calmer (Wiley and Richards 1982). Under such conditions, frequencies above 3-4 kHz attenuate less in open habitats than in forests (Wiley and Richards 1982). In addition, there may be more insect-generated high frequency ambient noise in forests (Ryan and Brenowitz 1985). Finally, reverberation also increases with frequency (Wiley and Richards 1982) and there is more reverberation in forests because of scattering in the foliage (Wiley and Richards 1982, Wiley 1991). Forest birds tend to have songs with a lower maximum frequency and therefore narrower frequency ranges than birds of open habitats (Tubaro and Segura 1995 and references therein). There may also be differences between different types of forested habitats. For instance, Marten and Marler (1977) found that frequency-dependent attenuations caused by scattering from vegetation were lower in coniferous forests than in deciduous forests with leaves, because conifer needles scatter little sound at frequencies below 10 kHz when compared with the broad leaves of deciduous trees (Wiley and Richards 1982).

In forested habitats, the reverberation of sound by surrounding vegetation entails a fast degradation of signals with rapid and repetitive frequency modulations (trill, buzzes) and favours the evolution of signals made of non-repetitive and slowly modulated whistles (Wiley and Richards 1982, Brenowitz 1986, Wiley 1991). In open habitats, the irregular amplitude fluctuations caused by atmospheric turbulences are the main source of acoustic degradation. This favours the development of signals with high rates of repetition, such as trills, because portions of information in non-repeated whistles would be lost otherwise (Wiley and Richards 1982, Brenowitz 1986). These predictions have been supported by extensive observational studies involving a large number of species (Morton 1975, Wiley 1991), studies of single species inhabiting a wide range of habitats (e.g., Handford 1988, Tubaro et al. 1993), and by a computer simulation study (Brown and Handford 1996).

Habitat structure presumably influences the evolution of plumage coloration as well. The main source of opacity noise (physical obstacles) affecting the transmission of optical signals in terrestrial habitats is vegetation (Hailman 1977). Birds are thought to be more visible in open areas because of the absence of a tall plant cover (Hailman 1977, Catchpole 1979, Lazarus and Symonds 1992). This has been confirmed by Dale and Slagsvold (1996) in field experiments with Pied Flycatchers *(Ficedula hypoleuca)*. These authors observed that unmated territorial males responded more rapidly (courtship or aggression) to caged conspecifics in open than in closed habitats, even when controlling the effect of plumage coloration.

There can also be differences in opacity noise among forest habitats. For example, Hailman (1977) noted that viewing in a horizontal direction can be done over longer distances in a coniferous than in a deciduous forest, because the branches of conifers tend to radiate horizontally from a single trunk, creating a nearly layered optical environment. In broad-leaved trees, branches tend to grow upward and obliquely and then divide into smaller branches with irregular orientations.

We have examined the influence of habitat structure on song complexity and plumage conspicuousness in 123 North American species of songbirds in a wide range of habitats. We grouped the birds into four categories according to their general habitat: deciduous forest, coniferous forest, semi-open (e.g., bushes, clearings, forest edges), and open. The following parameters were used (de Repentigny et al. submitted) to quantify song complexity: song duration, number of syllable types in the song, number of transitions from one syllable type to another in the song, total number of syllables in the song, different or not, a syllable-type versatility index (Conner et al. 1986), maximum and minimum frequencies, and frequency range. From the patterns of frequency-dependent attenuation outlined above, we predicted that, on average, species of more open habitats should have songs with higher maximum frequencies and a wider frequency range than forest-inhabiting species, but similar minimum frequencies. In addition, since highly repetitive signals are favoured in open habitats, we expected the number of syllable types in the song, the number of transitions from one syllable type to another, and the syllable-type versatility index to be lower in more open habitats than in forests, while the total number of syllables should be higher. Finally, song duration should be longer in more open habitats, because it would increase the probability of a listener to recover at least a part of a signal truncated by a drop in amplitude caused by atmospheric turbulences. Redundancy of signal structure would then help the listener to reconstruct the incompletely received signal (Römer and Lewald 1992).

To quantify plumage conspicuousness, de Repentigny et al. (submitted) used the following indices: value (V), chroma (C), and Munsell Power ($V \bullet C$), which measure conspicuousness independently of background; W_V, W_C, and $W_{V \bullet C}$ measure the contrast between colours within the plumage; B_V, B_C, and $B_{V \bullet C}$ measure the contrast between the bird and its background; and D_V, D_C, and $D_{V \bullet C}$ are sexual dichromatism indices. Sexual selection (Darwin 1871) is one of the most popular explanations for the occurrence of conspicuous plumages and sexual dichromatism. According to Darwin (1871), secondary sexual characters give greater fitness to their bearers. This can be achieved via male-male competition or female choice of a mate (Searcy and Yasukawa 1983). Both forms of selection occur in birds and operate on the plumages of males (Butcher and Rohwer 1989). Because birds are visible from greater distances in open than in closed habitats regardless of plumage coloration, we predicted that plumage conspicuousness may be less important for birds living in the former than for those found in the latter. Therefore, we expected all the conspicuousness and sexual dichromatism indices to be lower in open habitats than in forests. In addition, since viewing in the horizontal direction can be done over higher distances in coniferous than deciduous forests (Hailman 1977), we predicted that all conspicuousness and sexual dichromatism indices should be lower in the former.

It appeared that the number of habitat categories could affect the outcome of such a study (for instance, see Wiley 1991). Therefore, we performed additional analyses with two- and three-group classifications, lumping habitat categories together, to verify the consistency of the results.

Materials and methods

Song complexity

The songs of 123 North American species of Emberizidae, Parulidae, Cardinalidae, Icteridae, and Thraupidae were computerized and spectrograms were traced (for details, see de Repentigny et al. submitted; Chapter 2). We used only one song per individual to keep the data independent when calculating mean values for song complexity. For each individual of each species, we measured the following variables:

(1) Song duration (DUR), in seconds.

(2) Number of syllable types in the song (SYLL).

(3) Number of transitions from one syllable type to another in the song (TRANS).

(4) Total number of syllables, different or not, in the song (TOT).

(5) Syllable-type versatility index (INDEX). This index is formulated as follows:

[1] Syllable-type versatility index = (SYLL X TRANS)/TOT.

(6) Maximum frequency (FMAX) found in the song, in kHz.

(7) Minimum frequency (FMIN) reached by the bird in its song, in kHz.

(8) Frequency range (RANGE), the difference between (6) and (7), in kHz.

More details about these variables and their measurements can be found in de Repentigny et al. (submitted; see also Chapter 2). The sample size ranges from 1 to 35 songs per species. When more than one song were used for a given species, we calculated the mean for each of the song complexity variables as described above. The song complexity data are available from the authors upon request.

Plumage conspicuousness

To quantify plumage conspicuousness and sexual dichromatism, we used a method, described in details elsewhere (de Repentigny et al. 1997; Chapter 1), which is based on the Munsell colour system (Smithe 1975). This system defines a colour by three characteristics: hue (the dominant wavelength of light), value (degree of brightness) and chroma (degree of saturation). Since value and chroma are quantified on a scale and are easily represented by numbers, we used them as conspicuousness indices. The hue scale is circular and does not have lower and upper limits, and it is not clear what hues are complementary or contrast most with each other (Hailman 1977). Consequently, hue was not used in the present study.

Following Burtt (1986), we divided the plumages of the 123 selected species into nineteen regions, each region occupying a certain percentage of the plumage. Because the value and chroma of colours are found in Smithe (1975), the numerical values of colours matching best those depicted on the plates of the Peterson field guides (1990, 1994) were ascribed to each region of males in breeding plumage. Colour matching took place in the laboratory under fluorescent light but next to a window to provide indirect sunlight. Field guides may be used in assessing bird conspicuousness because the scores obtained using these guides do not differ significantly from those recorded on museum specimens (de Repentigny et al. 1997; Chapter 1). For the species not illustrated in the Peterson guides, the National Geographic Society field guide (1987) was used. If a region consisted of more than one colour, the fraction of the region occupied by each colour was estimated and the average value (V) and chroma (C) and the resulting average product $V \bullet C$ for that region were calculated. In the next procedure, the V, C, and $V \bullet C$ scores of each region were multiplied by the percentage of the plumage covered by that region, and the results of each region were summed. This generated the following indices:

(1) Total plumage value (V). The value is a measure of brightness.

(2) Total plumage chroma (C). The chroma is a measure of saturation.

(3) Total plumage Munsell power ($V \bullet C$), which correlates with the power of the bird's colours to attract attention. Indices (1), (2) and (3) quantify "close-quarter conspicuousness" (Götmark and Unger 1994).

To take into account the fact that adjacent colours in a plumage can contrast, we determined the colour with the highest V and that with the lowest. Then we divided the latter by the former and multiplied the result by the percentage of the plumage covered by the least abundant of the two colours, which gave a V within-plumage contrast. We used the same procedure for C and $V \bullet C$. That way, a high within-plumage contrast score indicates a high degree of crypsis in V, C, or $V \bullet C$, while a low within-plumage contrast score indicates a high degree of detectability, recognition or conspicuousness. Therefore, to make the variables more intuitively comprehensible, we multiplied these scores by constant of -1, so that low (more negative) scores mark crypsis and high (less negative) ones denote conspicuousness. Three within-plumage contrast indices were thus obtained:

(4) Within-plumage contrast in value (W_V).

(5) Within-plumage contrast in chroma (W_C).

(6) Within-plumage contrast in Munsell power ($W_{V \bullet C}$).

To quantify "long-distance conspicuousness" or "detectability" (see Götmark 1994), which is influenced by the coloration of the background, we selected in Smithe (1975) the colour Leaf Green (no. 146) as representative of a simplified background of vegetation. We then divided the V, C, and $V \bullet C$ of the colours representing the habitat by the V, C, and $V \bullet C$ of the males (or the reverse if the latter were higher). The results were used as indices for measuring the contrast between birds and their habitat:

(7) Contrast of a bird with its background in value (B_V).

(8) Contrast of a bird with its background in chroma (B_C).

(9) Contrast of a bird with its background in Munsell Power ($B_{V \bullet C}$).

Finally, we calculated V, C, and $V \bullet C$ indices for the females of the selected species in the same way as for males. Male V, C and $V \bullet C$ scores were then divided by their respective female V, C, and V • C scores, or the reverse if a female score was greater. The ratios thus obtained were used as sexual dichromatism indices:

(10) Sexual dichromatism in value (D_V).

(11) Sexual dichromatism in chroma (D_C).

(12) Sexual dichromatism in Munsell power ($D_{V \bullet C}$).

These twelve indices were used as variables describing plumage conspicuousness and results for each species are available from the authors upon request.

Grouping of birds according to their habitat

We grouped the selected species into four categories according to their predominant habitat: (1) deciduous forest, (2) coniferous forest, (3) semi-open (e.g., bushes, brushes, thickets, forest edges, and clearings), and (4) open. We chose to distinguish between deciduous forest and coniferous forest because of the above-mentioned differences in frequency-dependent attenuation due to scattering from vegetation and in opacity noise observed among forested habitats. The three-group classification was obtained by lumping (1) and (2) together, and the two-group classification by merging (1) with (2), and (3) with (4). The common and scientific names of the species as well as the habitat category to which they were assigned appear in the Appendix. To ascertain that this grouping is as accurate as possible, we referred to several sources where habitats are described (e.g., Bent 1953, 1958, 1968, Godfrey 1986, Peterson 1990, 1994, the relevant issues of the *Birds of North America* series).

Statistical analysis

We performed ANOVA tests to find significant differences among the habitat categories of the two-group, three-group, and four-group classifications for each song complexity, plumage conspicuousness, and sexual dichromatism variable. These analyses were conducted using Statview SE+Graphics™ (Abacus Concepts Inc., Berkeley, CA). However, species cannot be considered as points drawn independently from the same distribution because they are descended from common ancestors (Felsenstein 1985, Garland et al. 1993). For instance, two species could have similar songs mainly because they are closely related, or conversely, could have developed very different songs to avoid acoustic competition if they live in the same habitat. These hierarchical relationships may lead to bias (eitheir overestimation or underestimation) in the degrees of freedom used in conventional statistical tests and hence to untrustworthy significance levels (Garland et al. 1993 and references therein).

To obtain null distributions of F statistics for hypothesis testing that take the nonindependence of the species into account, we used the method proposed by Garland et al. (1993). With the help of the PDSIMUL software included in the PDAP package (Garland et al. 1993), we performed 1000 empirically scaled computer simulations of evolution along the tree specified in our phylogenetic hypothesis (see Fig. 1 in Chapter 2; de Repentigny et al submitted) for each of the song complexity, plumage conspicuousness, and sexual dichromatism parameters. As branch lengths were not comparable because the information came from various sources using different methods (see Chapter 2, and references therein; de Repentigny et al. submitted), we set all branches equal to 1, and the model of evolutionary change chosen is known as speciational Brownian motion (Garland et al. 1993). In this model, all successive changes are associated with speciation events, are uncorrelated to each other and to the character's starting value, and are equally likely to be negative or positive (Garland et al. 1993). For each parameter, we set the starting value equal to its mean for the 123 selected species, and the means and variances of the simulated data sets equal to those of the real one. We used the highest and lowest values found among the species as limits to the range of possible states for each variable, and the bounded simulations were performed with the "Hard Bounce" algorithm. That is, if the next move of a trait located, say, 5 units from the lower limit was 12 units towards that limit, it stepped 5 units towards the limit, bounced, and stepped the remaining 7 units away from it, ending up 2 units further away from the boundary than when it started. Also, since the simulations were performed for two variables at the same time, we fixed the correlation between the two variables in the simulated data sets as equal to that in the real data set. Finally, we used the software PDANOVA, also included in the PDAP package (Garland et al. 1993), to compute the F ratios of the 1000 simulated data sets for each song complexity variable, as in conventional ANOVA tests. We then used Statistix version 4.1 (Analytical Software Co.) to read in the ASCII files of F ratios output by PDANOVA and calculate the 95th percentile of these distributions. If, for a given variable, the F ratio for the real data set exceeded the upper 95th percentile of the null distribution, we could conclude that there was a significant difference in the mean value of this variable among habitat categories. In such a case, we then performed pairwise ANOVA tests to find which pairs of categories were responsible for the difference, using the same procedure as that described above.

Frequencies in bird songs are strongly related to body size, smaller birds being more efficient at producing high frequencies than larger ones (Ryan and Brenowitz 1985, Wiley 1991). Therefore, we performed ANCOVA tests to examine differences in FMAX and FMIN among habitat categories, using the cube root of body mass as a covariate. This variable was chosen as the covariate because the resonant frequency of a sound source generally varies inversely characteristic linear dimensions of the resonator (Kinsler and Frey 1962). We obtained the mean body mass of adult males for each species from Dunning (1993). However, there were no data available for Bachman's Warbler *(Vermivora bachmanii)*, which was therefore excluded from the analysis. We also corrected the critical F ratios of these ANCOVA tests for phylogenetic nonindependence, again using the method proposed by Garland et al. (1993).

Results

According to the results of conventional ANOVA tests, there were significant differences among in mean values of some song and plumage variables among habitats (Tables 1 and 2). However, after correction for phylogenetic nonindependence, statistical analyses provided no evidence of an influence of habitat structure on the vocalizations and plumage coloration

Table 1. ANOVA table of the effects of habitat structure on song complexity variables.

	Four-group classification			Three-group classification			Two-group classification		
Variables	$F_{(3,119)}$	P value	Corrected P value	$F_{(2,120)}$	P value	Corrected P value	$F_{(1,121)}$	P value	Corrected P value
DUR	0.862	0.463	0.916	0.628	0.536	0.900	0.536	0.466	0.849
SYLL	3.285	0.023	0.517	4.571	0.012	0.437	3.531	0.063	0.580
TRANS	1.607	0.191	0.733	1.970	0.144	0.659	0.688	0.408	0.816
TOT	0.723	0.540	0.925	1.041	0.356	0.835	0.781	0.379	0.808
INDEX	2.475	0.065	0.630	3.142	0.047	0.565	1.778	0.185	0.670
FMAX	1.338	0.266	0.850	1.797	0.170	0.755	0.641	0.425	0.831
FMIN	5.414	0.001	0.396	6.474	0.002	0.409	11.315	0.001	0.331
RANGE	6.701	0.000	0.305	9.908	0.000	0.248	11.464	0.001	0.318

Table 2. ANOVA table of the effects of habitat structure on plumage conspicuousness variables.

	Four-group classification			Three-group classification			Two-group classification		
Variables	$F_{(3,119)}$	P value	Corrected P value	$F_{(2,120)}$	P value	Corrected P value	$F_{(1,121)}$	P value	Corrected P value
V	2.898	0.038	0.674	3.926	0.022	0.598	5.418	0.022	0.571
C	8.178	0.000	0.176	11.617	0.000	0.158	1.729	0.191	0.696
$V \cdot C$	9.121	0.000	0.153	13.322	0.000	0.130	2.472	0.119	0.658
W_v	2.171	0.095	0.691	2.864	0.061	0.606	5.764	0.018	0.452
W_c	2.760	0.045	0.576	3.726	0.027	0.504	1.185	0.279	0.744
$W_{v \cdot c}$	2.808	0.043	0.540	3.734	0.027	0.443	3.127	0.080	0.535
B_v	3.693	0.014	0.565	5.061	0.008	0.495	1.167	0.282	0.787
B_c	2.021	0.115	0.713	2.990	0.054	0.598	0.947	0.333	0.779
$B_{v \cdot c}$	2.013	0.116	0.685	2.978	0.055	0.544	2.848	0.094	0.571
D_v	2.391	0.072	0.616	3.511	0.033	0.467	2.125	0.148	0.593
D_c	0.453	0.716	0.939	0.163	0.850	0.967	0.000	0.995	0.997
$D_{v \cdot c}$	2.273	0.083	0.301	0.360	0.038	0.450	1.634	0.204	0.613

of the 123 selected species. With the four-group classification, ANOVA tests revealed no statistically significant differences in mean values for the song complexity, plumage conspicuousness, and sexual dichromatism variables among the categories of birds differing in general habitat (Tables 1 and 2). The P values ranged between 0.31 for RANGE and 0.93 for TOT among song parameters, and between 0.15 for V • C and 0.94 for D_C among plumage coloration variables. Therefore, no variation among habitats came even close to significance for any of the song complexity, plumage conspicuousness and sexual dichromatism parameters used in this study. The results obtained with the three-group and two-group classifications were similar (Tables 1 and 2), and differences in minimal and maximal frequencies among habitat categories remained nonsignificant even after they had been adjusted for body size (not shown).

Discussion

We predicted that if selection favours vocalizations that are minimally attenuated and degraded to maximize the range of communication, species of more open habitats should have songs with higher maximum frequencies and a wider frequency range than forest-dwelling species, but similar minimum frequencies. Moreover, we expected the number of syllable types per song, the number of transitions from one syllable type to another per song, and the syllable-type versatility index to be lower in more open habitats than in forests, while the total number of syllables per song should be higher and the song duration longer. Except for the similarity of minimum frequencies, the results from statistical analyses do not support these predictions. Consequently, we conclude that habitat structure places no constraint on the song complexity parameters considered in this study.

These findings contrast with those of other observational studies (Morton 1975, Wiley 1991) which revealed an association between physical properties of habitats and song structure. This discrepancy is not that surprising even when considering that many of the species used in the present study and that of Wiley (1991) are the same. There are several differences between the two studies. We were interested in examining the effect of habitat structure on the song complexity features used by de Repentigny et al. (submitted; see also Chapter 2) in their study of relationships between song and plumage among species from five different families and occurring throughout North America. We therefore restricted our analyses to these species, whereas Wiley's (1991) sample included nearly all territorial oscines breeding in the eastern part of the continent. Furthermore, not all song parameters considered in the two studies are the same. Wiley (1991) concentrated on the influence of the environment on frequencies and patterns of amplitude modulation, such as presence or absence of sidebands and buzzes and minimal period of repeated elements. On the other hand, as mentioned above, some of the song complexity parameters we measured (e.g., TRANS) can be affected by habitat structure. However, this effect depends on the temporal properties of the song, which we have not measured. For instance, trill rate may predict more accurately the efficiency of a signal propagating through a habitat than the presence or absence of a trill. Songs of Rufous-collared Sparrows *(Zonotrichia capensis)* inhabiting both open and forested habitats include trills, but trills are slower in the latter habitat (Tubaro et al. 1993), which suggests that this might be the case. Besides, we face the same difficulties that led Wiley (1991) to warn against a narrow interpretation of the results: only a few songs per species were used and details concerning the time, context, and habitat in which the songs were recorded were not always available. Environments were classified into general categories, and each species was assigned to a single habitat type. Wiley (1991) classified habitats into six groups (broad-leaved or mixed forest, coniferous forest, parkland or forest edge, shrubland, grassland, and marshes), which he lumped into two (forest and parkland, and open habitats) in some analyses. We grouped birds into two, three or four categories, but the outcome was similar in all cases. Therefore, we do not think that the discrepancies between our results and those of Wiley (1991) are due to different classifications being used in the two studies. An additional difference between the two studies lies in the method for taking phylogenetic relationships into account. We used the computer simulation method

(Garland et al. 1993), whereas Wiley (1991) employed phylogenetic regressions (Grafen 1989). Finally, another possibility is that the habitat in which some species are found has been altered while the features of their songs still reflect adaptations to the original vegetation (Handford 1988). However, it is unlikely that all the species used in the present study have experienced major changes in the structure of their habitat, and studies dealing with large numbers of species are generally able to reveal the general trends in signal structure across different habitat types (Brown and Handford 1996).

Although the song complexity parameters used in our study are not constrained by habitat structure, this does not mean that bird vocalizations are not influenced by it. In many species, song may have evolved for communication with biologically significant receivers at some optimal distance related to the usual spacing of individuals rather than for communication at maximal distances (Wiley and Richards 1978, 1982, Lemon et al. 1981). Nevertheless, songs of these species could incorporate features that are subject to frequency-dependent attenuation and degradation, which would serve as cues indicating the distance of a singing conspecific to a recipient (Wiley and Richards 1978, 1982, Morton 1982, 1986). Several studies have shown that songbirds can use the degradation of conspecific song during transmission through the environment to judge the distance of a singer (Richards 1981, McGregor et al. 1983, McGregor and Falls 1984, McGregor and Krebs 1984, Shy and Morton, 1986, Naguib 1995, 1996, Wiley and Godard 1996). This may explain why many forest-inhabiting species include rapid repetitions and sidebands in their songs (Richards and Wiley 1980, Wiley 1991).

Because birds are visible from greater distances in open than in closed habitats regardless of plumage coloration, we predicted that plumage conspicuousness may be less important for birds living in the former than for those found in the latter. Consequently, we expected, long-distance conspicuousness, close-quarter conspicuousness, within-plumage contrast and plumage sexual dichromatism indices to be higher in forested habitats than in more open habitats, and higher in deciduous than in coniferous forests. Again, our results do not support these predictions. Close-quarter conspicuousness of plumages may be similar among habitats because vegetation is less likely to prevent birds from seeing each others at short range in forests. Therefore, at close quarters, forest-dwelling birds may be as detectable, irrespective of plumage coloration, as those living in more open areas. The selected species breed in temperate regions and Hamilton and Barth (1962) found an association between increased sexual plumage dichromatism and relatively short periods for the establishment of pair-bonds in temperate latitudes. Strong plumage sexual dichromatism would facilitate sexual recognition and thus help birds to mate rapidly. This would benefit males of all species used in this study, irrespective of their habitat. It is less clear why within-contrast indices should be similar in all habitats. A strong contrast between adjacent colour patches often leads to the disruption of an animal's outline (Cott 1957, Hailman 1977). Vegetation can hinder an animal's view of an approaching predator (Lazarus and Symonds 1992 and references therein). Consequently, if predation rates are similar among habitats, it could be as important for forests birds to decrease their detectability to predators by breaking their silhouette as it is for birds of open habitats. Long-distance conspicuousness indices may be similar among groups of birds living in different environments for similar reasons. However, predation on adult songbirds is rarely quantified (Götmark and Post 1996).

The conspicuousness of a colour depends on its background (Hailman 1977, Burtt 1986), and the same bird appears more or less conspicuous depending on the background against which it is seen (Götmark and Hohlfält 1995). However, in this study, we used a single simplified background (de Repentigny et al. 1997; Chapter 1), overlooking the fact that birds might sometimes be seen against a blue sky or a brownish background, or against a background composed of several colours intermingled in an irregular pattern. Another factor that we did not take into account is ambient light, which differs among habitats and also affects the conspicuousness of signals that depend on reflected light (Burtt 1986; Endler 1990; Götmark and Unger 1994). Unfortunately, its effect is virtually unstudied except for a few exceptions (e.g., Marchetti 1993, Endler and Théry 1996). The conspicuousness of a bird is also inflenced by its movements. For example, male individuals of some *Phylloscopus* species make themselves temporarily more conspicuous by flashing their bright colour patches in display (Marchetti 1993). Finally, the method we used in this study overlooks other aspects of coloration that might affect conspicuousness, such as countershading or enhancement of shape (Hailman 1977).

Results from conventional tests differed markedly from those obtained with the computer simulation method. The significant differences in mean values of plumage conspicuousness and song complexity variables observed among habitat categories when phylogenetic relationships were not taken into account may be due to species in each habitat category being closely related and therefore sharing more song and plumage features because of their relatedness. This illustrates the importance of correcting for the nonindependence of species when making interspecific comparisons (Garland et al. 1993).

We have demonstrated that habitat structure places no contraint on the song complexity, plumage conspicuousness, and sexual dichromatism parameters used by us (de Repentigny et al. submitted; Chapter 2). Therefore, differences in acoustics and in opacity noise among habitats cannot account for the weakness of the positive correlation found between song complexity and plumage conspicuousness among 123 species of North American passerines. However, this conclusion should be used with caution. As we mentioned above, the method used in this study to quantify conspicuousness and sexual dichromatism is not flawless. In addition, the avian visual system is different from that of humans, as per our earlier discussion (de Repentigny et al. 1997; Chapter 1). The habitat occupied by birds of a given species may vary among individuals of a population and among different populations (Wiley 1991). Consequently, the assignation of each species to a single habitat type may affect not only the results of analyses performed on song parameters, but also those involving plumage coloration features. Finally, when making predictions, we disregarded the fact that other selection pressures may impose severe constraints on colour and pattern variation.. For instance, the need for durable plumage selects for melanic colours in the tail and wings (Burtt 1986). Since these colours are dark, signals require light colours to contrast with the background and the surrounding plumage. Light colours are less durable than melanic ones and must be in protected parts of the tails and wings. Tail spots are on the medial vane of the outermost tail feathers and away from the tip, whereas wing bars are in the area of the wing that receives laminar airflow (Burtt and Gatz 1982). Consequently, colors and patterns can be very similar among a large set of birds (Burtt and Gatz 1982). Visibility is not the only, and perhaps not the most important, selective pression operating on plumage colour. Therefore, an influence of the environment on the evolution of plumage conspicuousness cannot be completely ruled out.

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Appendix. Bird species used in the present study, and general habitat to which they were assigned

Common and scientific names	Habitat*	Common and scientific names	Habitat
Lucy's Warbler *(Vermivora luciae)*	S	Yellow-rumped Warbler *(D. coronata)*	C
Blue-winged Warbler *(V. pinus)*	S	Black-throated Gray Warbler *(D. nigrescens)*	C
Golden-winged Warbler *(V. chrysoptera)*	S	Townsend's Warbler *(D. townsendi)*	C
Tennessee Warbler *(V. peregrina)*	C	Hermit Warbler *(D. occidentalis)*	C
Orange-crowned Warbler *(V. celata)*	S	Black-throated Green Warbler *(D. virens)*	C
Nashville Warbler *(V. ruficapilla)*	S	Golden-cheeked Warbler *(D. chrysoparia)*	C
Virginia's Warbler *(V. virginiae)*	S	Blackburnian Warbler *(D. fusca)*	C
Bachman's Warbler *(V. bachmanii)*	D	Yellow-throated Warbler *(D. dominica)*	D
Colima Warbler *(V. crissalis)*	S	Grace's Warbler *(D. graciae)*	C
Northern Parula *(Parula americana)*	C	Pine Warbler *(D. pinus)*	C
Yellow Warbler *(Dendroica petechia)*	S	Kirtland's Warbler *(D. kirtlandii)*	C
Chestnut-sided Warbler *(D. pensylvanica)*	S	Prairie Warbler *(D. discolor)*	S
Magnolia Warbler *(D. magnolia)*	C	Palm Warbler *(D. palmarum)*	S
Cape May Warbler *(D. tigrina)*	C	Bay-breasted Warbler *(D. castanea)*	C
Black-throated Blue Warbler *(D. caerulescens)*	D	Blackpoll Warbler *(D. striata)*	C

*D = deciduous forest; C = coniferous forest; S = semi-open; O = open.

Appendix. Continued

Common and scientific names	Habitat	Common and scientific names	Habitat
Cerulean Warbler *(Dendroica cerulea)*	D	Canada Warbler *(W. canadensis)*	D
Black-and-white Warbler *(Mniotilta varia)*	D	Red-faced Warbler *(Cardellina rubifrons)*	C
American Redstart *(Setophaga ruticilla)*	D	Painted Redstart *(Myioborus pictus)*	D
Prothonotary Warbler *(Protonotaria citrea)*	D	McCown's Longspur *(Calcarius mccownii)*	O
Worm-eating Warbler *(Helmitheros vermivorus)*	D	Lapland Longspur *(C. lapponicus)*	O
Swainson's Warbler *(Limnothlypis swainsonii)*	D	Smith's Longspur *(C. pictus)*	O
Louisiana Waterthrush *(Seiurus motacilla)*	D	Chestnut-collared Longspur *(C. ornatus)*	O
Northern Waterthrush *(S. noveboracensis)*	D	Snow Bunting *(Plectrophenax nivalis)*	O
Ovenbird *(S. aurocapillus)*	D	Lark Bunting *(Calamospiza melanocorys)*	O
Kentucky Warbler *(Oporornis formosus)*	D	Fox Sparrow *(Passerella iliaca)*	C
Connecticut Warbler *(O. agilis)*	S	Song Sparrow *(Melospiza melodia)*	S
Mourning Warbler *(O. philadelphia)*	S	Lincoln's Sparrow *(M. lincolnii)*	S
MacGillivray's Warbler *(O. tolmiei)*	S	Swamp Sparrow *(M. georgiana)*	S
Common Yellowthroat *(Geothlypis trichas)*	S	White-throated Sparrow *(Zonotrichia albicollis)*	S
Hooded Warbler *(Wilsonia citrina)*	D	Harris' Sparrow *(Z. querula)*	S
Wilson's Warbler *(W. pusilla)*	S	White-crowned Sparrow *(Z. leucophrys)*	S

Appendix. Continued

Common and scientific names	Habitat	Common and scientific names	Habitat
Golden-crowned Sparrow *(Zonotrichia atricapilla)*	S	Vesper Sparrow *(Pooecetes gramineus)*	O
Dark-eyed Junco *(Junco hyemalis)*	C	Lark Sparrow *(Chondestes grammacus)*	O
Yellow-eyed Junco *(J. phaeonotus)*	C	Black-throated Sparrow *(Amphispiza bilineata)*	O
Savannah Sparrow *(Passerculus sandwichensis)*	O	Sage Sparrow *(A. belli)*	O
Seaside Sparrow *(Ammodramus maritimus)*	O	Bachman's Sparrow *(Aimophila aestivalis)*	S
Sharp-tailed Sparrow *(A. caudacutus)*	O	Botteri's Sparrow *(A. botterii)*	O
Le Conte's Sparrow *(A. leconteii)*	O	Cassin's Sparrow *(A. cassinii)*	O
Henslow's Sparrow *(A. henslowii)*	O	Rufous-crowned Sparrow *(A. ruficeps)*	O
Baird's Sparrow *(A. bairdii)*	O	Green-tailed Towhee *(Pipilo chlorurus)*	S
Grasshopper Sparrow *(A. savannarum)*	O	Rufous-sided Towhee *(P. erythrophtalmus)*	S
American Tree Sparrow *(Spizella arborea)*	S	Brown Towhee *(P. fuscus)*	S
Chipping Sparrow *(S. passerina)*	S	Abert's Towhee *(P. aberti)*	S
Clay-colored Sparrow *(S. pallida)*	S	Hepatic Tanager*(Piranga flava)*	C
Brewer's Sparrow *(S. breweri)*	O	Summer Tanager *(P. rubra)*	C
Field Sparrow *(S. pusilla)*	O	Scarlet Tanager *(P. olivacea)*	D
Black-chinned Sparrow *(S. atrogularis)*	O	Western Tanager *(P. ludoviciana)*	C

Appendix. Continued

Common and scientific names	Habitat	Common and scientific names	Habitat
Dickcissel *(Spiza americana)*	O	Scott's Oriole *(I. parisorum)*	S
Rose-breasted Grosbeak *(Pheucticus ludovicianus)*	D	Yellow-headed Blackbird *(Xanthocephalus xanthocephalus)*	O
Black-headed Grosbeak *(P. melanocephalus)*	D	Red-winged Blackbird *(Agelaius phoeniceus)*	O
Northern Cardinal *(Cardinalis cardinalis)*	S	California Blackbird *(A. tricolor)*	O
Pyrrhuloxia *(C. sinuatus)*	S	Eastern Meadowlark *(Sturnella magna)*	O
Blue Grosbeak *(Guiraca cerulea)*	S	Western Meadowlark *(S. neglecta)*	O
Lazuli Bunting *(Passerina amoena)*	S	Common Grackle *(Quiscalus quiscula)*	O
Indigo Bunting *(P. cyanea)*	S	Boat-tailed Grackle *(Q. major)*	O
Varied Bunting *(P. versicolor)*	S	Great-tailed Grackle *(Q. mexicanus)*	O
Painted Bunting *(P. ciris)*	S	Rusty Blackbird *(Euphagus carolinus)*	C
Altamira Oriole *(Icterus gularis)*	S	Brewer's Blackbird *(E. cyanocephalus)*	O
Hooded Oriole *(I. cucullatus)*	S	Bronzed Cowbird *(Molothrus aeneus)*	O
Northern Oriole *(I. galbula)*	S	Brown-headed Cowbird *(M. ater)*	S
Orchard Oriole *(I. spurius)*	S	Bobolink *(Dolichonyx orizyvorus)*	O
Audubon's Oriole *(I. graduacauda)*	S		

Conclusion

Les résultats obtenus dans cette étude à partir de l'ensemble formé par les représentants nord-américains des Emberizidae, Parulidae, Cardinalidae, Icteridae et Thraupidae ne corroborent pas l'hypothèse de Darwin (1871), selon laquelle il y a une corrélation négative entre la complexité du chant et la visibilité du plumage. Les caractéristiques temporelles, spectrales et syntaxiques du chant que nous avons retenues, ainsi que la méthode de mesure quantitative de la visibilité du plumage décrite dans le deuxième chapitre de cet ouvrage, nous ont permis de détecter une faible corrélation positive entre ces deux groupes de variables. D'après le modèle qui ressort de l'analyse des corrélations canoniques, le contraste avec l'arrière-plan en termes de brillance, de saturation et de puissance de Munsell, le dimorphisme sexuel du plumage en termes de brillance, de saturation et de puissance de Munsell, et le contraste intra-plumage en termes de saturation et de puissance de Munsell sont les caractéristiques du plumage qui contribuent le plus à sa visibilité. Les indices de mesure de la visibilité "à courte portée" du plumage ne sont pas impliqués dans le modèle, ce qui démontre bien l'importance de ne pas négliger l'influence de l'arrière-plan lorsqu'on évalue cette visibilité. Selon les résultats de la même analyse, le nombre total de syllabes, différentes ou non, dans le chant, le nombre de syllabes différentes dans le chant, la durée, l'intervalle de fréquences et la fréquence la plus élevée représentent les variables définissant le mieux la complexité du chant.

On peut se demander pourquoi la complexité du chant et la visibilité du plumage auraient évolué de concert au sein du groupe d'espèces étudié. Un explication possible réside dans le fait que ces espèces se reproduisent en milieu tempéré, où les oiseaux disposent de peu de temps pour s'apparier (Hamilton et Barth 1962). Hamilton et Barth (1962) ont constaté une association entre un dimorphisme sexuel du plumage accru et des périodes relativement courtes pour la formation des couples. On peut présumer qu'il serait avantageux pour les mâles d'espèces vivant dans des régions au climat tempéré de posséder un plumage non seulement très différent de celui des femelles, mais également très voyant, en plus d'avoir un chant complexe. En effet, cela leur permettrait d'établir un territoire et de se trouver une partenaire rapidement. Cependant, la corrélation positive observée entre la complexité du chant et la visibilité du plumage est faible. Chaque ensemble de variables n'explique qu'une faible pourcentage de la variation observée dans l'autre ensemble. Il faut donc chercher ailleurs l'explication de la plus grande partie de cette variation.

Les résultats présentés dans le troisième chapitre de cet ouvrage indiquent que la structure de l'habitat ne semble pas affecter l'évolution de plumages plus ou moins visibles, et que si cette structure peut influencer l'évolution des vocalisations des oiseaux, elle ne semble pas limiter l'expression de la complexité de leur chant. D'autres facteurs peuvent toutefois jouer un rôle dans l'évolution du plumage et du chant. Ainsi, la pression de prédation peut favoriser l'évolution d'un plumage marqué chez les espèces où les mâles indiquent par ce moyen qu'ils constituent des proies peu intéressantes ou d'un goût désagréable (Baker et Parker 1979, Götmark 1993, 1994), ou la restreindre chez d'autres espèces où il est plus avantageux pour les mâles de se camoufler (Götmark 1993). Malheureusement, il n'existe que peu d'information quant aux taux de prédation sur les oiseaux chanteurs adultes (Götmark et Post 1996). En revanche, le taux de prédation sur les nids a été mesuré chez certaines espèces, et il existerait une corrélation négative entre l'intensité de la prédation sur les nids et la visibilité du plumage chez les femelles, mais non chez les mâles, du moins au sein des taxons où seules les femelles couvent les oeufs et les jeunes (Martin et Badyaev 1996). Ces résultats suggèrent que dans certains cas, la prédation sur les nids peut causer une variation dans la coloration du plumage des femelles et de là dans le dimorphisme sexuel du plumage sans que des changements chez les mâles ne soient impliqués.

La nécessité de posséder un plumage durable favorise la sélection de formes mélaniques d'ailes et de queues (Burtt 1986). La coloration des signaux doit donc être plus pâle afin que ceux-ci tranchent bien sur l'arrière-plan et le plumage qui les entoure. Les couleurs pâles ne possèdent pas le degré de résistance des pigments mélaniques et doivent être utilisées dans les parties des ailes et de la queue les mieux protégées des dégâts que peuvent provoquer les mouvements aériens lors du vol (Burtt et Gatz 1982). Par conséquent, les couleurs et motifs peuvent se ressembler énormément chez un grand nombre d'espèces (Burtt et Gatz 1982).

Certaines des espèces comprises dans cette étude sont polygynes (Searcy et Yasukawa 1983, Björklund 1991, Webster 1992). Or, il appert que le processus de sélection sexuelle agit de façon plus intense et entraîne donc une augmentation du dimorphisme sexuel chez les espèces polygynes par rapport à celles qui sont monogames (Searcy et Yasukawa 1983). En outre, la sélection sexuelle peut mener non seulement à l'apparition de chants complexes, de plumages voyants et du dimorphisme sexuel du plumage, mais également à l'évolution du dimorphisme sexuel de taille (Wesbster 1992). Un tel dimorphisme de taille s'observe chez quelques-unes des espèces à l'étude (Searcy et Yasukawa 1983, Björklund 1991, Webster 1992). Les fréquences qu'on retrouve dans le chant des oiseaux sont intimement liées à la taille corporelle de ces derniers, les petits oiseaux produisant des fréquences élevées plus efficacement que ne le font les gros (Wiley 1991 et les références qui s'y trouvent). Enfin, des phénomènes tels que la compétition sociale ou le choix d'une partenaire par les mâles peuvent favoriser l'évolution d'un plumage femelle voyant et ainsi contribuer à la réduction du dimorphisme sexuel du plumage chez certaines espèces (Irwin 1994).

Le choix des variables et la façon dont elles ont été mesurées peuvent également avoir affecté les résultats obtenus au cours de cette étude. Ainsi, il est difficile de déterminer exactement quelles sont les fréquences les plus basses et les plus élevées des chants car ces mesures dépendent de la détection des limites des traces sur les spectrogrammes (Wiley 1991). De plus, on peut parfois confondre une syllabe composée de plusieurs notes avec une série de syllabes composées d'une seule note, et les trilles formés d'une seule syllabe répétée plusieurs fois très rapidement avec une syllabe au son semblable à un bourdonnement. Les mâles de certaines espèces utilisent différents chants selon le contexte et la complexité de ces chants peut varier (Staicer 1996). Or, l'information quant au contexte dans lequel les chants utilisés durant cette étude ont été enregistrés n'était pas disponible.

La visibilité d'une couleur dépend de son arrière-plan (Hailman 1977, Burtt 1986), et le même oiseau peut paraître plus ou moins voyant selon l'arrière-plan contre lequel il est vu

(Götmark et Hohlfält 1995). Dans le cadre de cette étude, cependant, le même arrière-plan simplifié a été utilisé pour mesurer la visibilité du plumage de tous les oiseaux. En outre, nous n'avons pas pris en considération que la couleur de la lumière ambiante diffère d'un milieu à l'autre et que cette variation influence la visibilité des signaux dont l'effet dépend de la lumière réfléchie (Burtt 1986, Endler 1990, Götmark et Unger 1994).

Les concepts de complexité du chant et de visibilité du plumage demeurent problématiques. Par exemple, nous n'avons pas tenu compte de la complexité inter-chant ("between-song complexity", Read et Weary 1992), c'est-à-dire des répertoires de chants et de syllabes, dans la mesure de la complexité du chant. La sélection sexuelle semble influencer fortement la taille du répertoire chez certaines espèces (voir Catchpole 1980, 1987, Horn et al. 1993, Lampe et Saetre 1995, Mountjoy et Lemon 1996 pour des exemples). Chez d'autres espèces, il paraît impossible que le répertoire de chants puisse être utilisé par des femelles ou des compétiteurs mâles pour juger de la qualité d'un mâle (Byers 1995). La méthode de mesure quantitative de la visibilité du plumage utilisée dans le cadre de cette étude repose sur le système des couleurs de Munsell, et l'appareillage spectrophotométrique sur lequel se fonde ce système épouse la sensibilité de l'oeil humain (Endler 1990), laquelle diffère de celle de l'oeil des oiseaux (Bennett et al. 1994). Malgré tout, il existe également des points communs entre ces deux systèmes visuels (Endler 1990, Burtt 1986), et tel que nous l'avons mentionné dans le premier chapitre de cet ouvrage, il n'est pas incorrect de mesurer la brillance et la saturation du plumage selon le système des couleurs de Munsell.

Les différences observées dans les deuxième et troisième chapitre de cette thèse entre les résultats des épreuves d'hypothèses traditionnelles et ceux obtenus à partir de méthodes tenant compte de l'autocorrélation phylogénétique illustrent bient la nécessité de prendre ce facteur en considération lorsqu'on effectue des comparaisons interspécifiques. En effet, les corrélations ou différences de moyennes entre groupes d'espèces notées lors de telles études peuvent parfois n'être dues qu'à l'effet de la parenté évolutive entre les espèces (Felsenstein 1985, Garland et al. 1993).

Les résultats obtenus dans le cadre de cette étude ne touchent que les représentants nord-américains de cinq familles de Passeriformes. Des analyses plus approfondies devront être effectuées avant que l'on ne puisse confirmer ou rejeter les idées de Darwin de façon décisive et avant que les conclusions présentées dans cet ouvrage ne puissent être appliquées à tous les oiseaux chanteurs. Une attention particulière devrait être accordée aux espèces vivant en milieu tropical, où les territoires sont souvent défendus toute l'année, les rôles du mâle et de la femelle convergent, et la fertilisation de femelles par des mâles autres que leur partenaire au sein du couple ne s'observe que rarement (Morton 1996). On s'attend donc à ce que la sélection sexuelle soit plus faible chez ces espèces, ce qui pourrait influencer la relation entre la complexité du chant et la visibilité du plumage. Néanmoins, la présente étude montre bien que l'affirmation de Darwin quant à une corrélation négative entre la complexité du chant et la visibilité du plumage ne s'applique pas de façon universelle.

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