National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

Male song and sexual selection in the European Starling

Donald James Mountjoy

Department of Biology

McGill University

Montreal, Canada.

February 1994

A thesis submitted to the Faculty of

Graduate Studies and Research

in partial fulfilment of the requirements of the degree of

Doctor of Philosophy

National Library of Canada
Bibliothèque nationale du Canada

Acquisitions and Bibliographic Services Branch
Direction des acquisitions et des services bibliographiques

395 Wellington Street
Ottawa, Ontario
K1A 0N4

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-94690-3

Canada

ABSTRACT

The function of the complex song of the European Starling (*Sturnus vulgaris*) was examined. Song playback experiments showed that both male and female starlings were attracted by song, and complex song inhibited males from entering nestboxes. Wild starlings (at least two years old when first recorded) showed extensive changes in the composition of their song phrase repertoires and most also increased the size of their repertoires, which will result in a correlation between age and repertoire size in this species. Females prefer males that have more complex song, and this preference remained significant when preferences for certain nest sites were controlled. Males with larger repertoires did not spend more time incubating or make more feeding visits to nestlings than did males with smaller repertoires. The evolution of complex song in the European starling is consistent with an age-indicator model of sexual selection, in which aspects of male quality correlated with age are advertised by the complexity of male song.

RESUME

La fonction du chant complexe chez l'étourneau sansonnet (*Sturnus vulgaris*) a été étudiée. Des expériences basées sur des retransmissions de chants enregistrés ont démontrés que les mâles et les femelles étourneaux sont attirés par le chant et que la retransmission de chants complexes inhibe l'entrée des mâles dans les nichoirs. Les étourneaux sauvages (âgés d'au moins deux ans au moment du premier enregistrement) ont démontrés des changements considérables dans la composition du répertoire de phrases de leur chant, la plupart des oiseaux accroîssant aussi la taille de leur répertoire et ceci résultant en une corrélation entre l'âge et la taille du répertoire chez cette espèce. Les femelles préféraient les mâles ayant des chants plus complexes, cette préférence se maintenant de façon significative lorsque les préférences pour certains sites de nidification étaient contrôlées. Les mâles ayant un grand répertoire ne passaient pas plus de temps à incuber ou à faire des visites pour nourrir les oisillons que les mâles ayant un répertoire plus limité. L'évolution du chant complexe chez l'étourneau sansonnet est compatible avec un modèle de sélection sexuelle d'un indice de l'âge, où les caractéristiques reliées à la qualité du mâle qui sont elle-même reliés à l'âge sont affichées par la complexité du chant du mâle.

TABLE OF CONTENTS

CHAPTER 3: Female choice for complex song in the European starling:
a field experiment.

CHAPTER 4: Male song complexity and parental care in the European
Starling.

LIST OF TABLES

CHAPTER 1:

CHAPTER 2:

CHAPTER 3:

LIST OF FIGURE CAPTIONS

CHAPTER 2:

CHAPTER 3:

CHAPTER 4:

PREFACE

The faculty of Graduate Studies and Research requires the following statement to be reprinted.

"Candidates have the option, subject to the approval of their Department, of including, as part of their thesis, copies of the text of a paper(s) submitted for publication, or the clearly-duplicated text of a published paper(s), provide that these copies are bound as an integral part of the thesis .

- If this option is chosen, connecting texts, providing logical bridges between the different papers, are mandatory.
- The thesis must still conform to all other requirements of the "Guidelines Concerning Thesis Preparation" and should be in a literary form that is more than a mere collection of manuscripts published or to be published. The thesis must include, as separate chapters or sections: (1) a Table of Contents, (2) a general abstract in English and French, (3) an introduction which clearly states the rationale and objectives of the study, (4) a comprehensive general review of the background literature to the subject of the thesis, when this review is appropriate, and (5) a final overall conclusion and/or summary.
- Additional material (procedural and design data, as well as descriptions of equipment used) must be provided where appropriate and in sufficient detail (eg. in appendices) to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.

- In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis of who contributed to such work and to what extent; supervisors must attest to the accuracy of such claims at the Ph. D. Oral Defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of the different authors of co-authored papers."

In accordance with the above I offer the following. All four chapters of this thesis are in the format of manuscripts, and my supervisor, R. E. Lemon, will be the second author of each paper. I am responsible for originating, executing, and writing up all of the research reported in these chapters (with technical and other assistance as noted in the acknowledgements); Dr. Lemon has provided financial support, suggestions during the planning of the research, and editorial comments on the writing of the manuscripts within the normal bounds of graduate supervision. Chapter 1 has been published in the journal Behavioral Ecology and Sociobiology (Mountjoy and Lemon 1991. 28: 97-100); I have taken the opportunity to correct a few typographical errors which appeared in the original paper. Chapter 2 has been accepted for publication by the journal Animal Behaviour, and Chapter 3 has been submitted to Behavioral Ecology and Sociobiology. Chapter 4 will also be submitted to an appropriate journal. I have retained the use of the first person plural in all of these chapters, and there is some redundancy between the introductory material in the various chapters as a result of their having been prepared as independent publications. The format for literature citations and some other editorial details also corresponds to the requirements of the respective journals and is thus not completely consistent between chapters.

CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

1. Chapter 1 is only the second study to provide direct evidence that passerine song attracts females, which has long been assumed to be one of the two main functions of bird song. It also is the first study to document male attraction by song into a 'defended' area, contrary to the assumption that song normally serves as a deterrent to male intrusion.

2. Chapter 1 is the third study to provide direct experimental evidence that song complexity increases the effectiveness of song as a deterrent to intruding males. It is the first of these studies to demonstrate this effect in a species which is a 'continuous' singer, with long songs that are not highly stereotyped.

3. Chapter 2 is one of the few studies to document extended song learning which leads to an increase in repertoire size after an individual's first breeding season; furthermore, it is only the second study to provide evidence that this increase in repertoire size continues beyond the individual's second breeding season.

4. Chapter 3 is the second field study to provide evidence for a female preference for mates with more complex song which is not confounded by possible associations with territory quality. It is the first study to demonstrate this preference in a species in which repertoire size is known to be associated with an aspect of male quality, specifically the age of the male.

5. Chapter 4 is the first study to directly examine the potential relationship between the repertoire size of individual males and their contribution to parental care. It does not find any support for the idea that males with larger repertoires provide more parental care, although this possibility has been suggested in the literature on a number of occasions.

ACKNOWLEDGEMENTS

My first thanks go to my supervisor, Bob Lemon, for taking me into his lab, providing generous support in various forms, making useful suggestions at all stages, and for having enough confidence in me to let me basically go off at my own tangent. Thanks also to the members of my supervisory committee, Don Kramer and Graham Bell, for their comments, criticisms, and suggestions along the way. Our meetings were not always the most relaxing points during these years, but I survived and may even be better for it. Able assistance in the field was provided by Lucie Robidoux, Catherine Tessier, and Dorothy Howard. Amy Valachovic and Jennifer Hunter were willing to risk lung cancer or worse while printing out sonagrams in the lab. Mr. W. Joyce at MacDonald Farm, Mr. E.R. Thompson at the Morgan Arboretum, and especially Dr. Roger Bider at the Ecomuseum (who even came to campus late at night to clear my name) allowed me to attract unloved birds to their home turf. Many thanks to the lab mates, Todd Winquist, Danny Weary, Stephane Perreault, and George, who commented on manuscripts and discussed many other aspects of science, birds, and life. Miscellaneous but not necessarily minor thanks also to Mike Clarke, Dave Kernaghan, Bob Montgomerie, all at the Image Centre, Beth Kwavnick, Dr. M. Beecher, Dr. M. West, and an anonymous reviewer, for their varied contributions. Stimulating discussions with the Behavioral Ecology group and the Bell Evolution group helped to enliven life here. B. Bird shared a few of his many insights into starling behaviour. Many other people from the 6th floor, Concordia, Thomson House and elsewhere contributed greatly to the quality of student life, and if I have made any glaring omissions because my mind is frazzling just a bit at this stage, please consider yourself thanked at this point.

Finally, and especially, many thanks to Jennifer Templeton who assisted in the field at 5 A.M., got hauled in to security with me at night, tolerated my erratic hours, helped at the computer, with the editorial pencil, and at just about every other stage along the way; and we've still managed to stay married - amazing.

GENERAL INTRODUCTION

In certain species of birds evolution has resulted in songs which are long and extremely complex, or in individuals possessing a large repertoire of simpler songs. Many other species though seem to accomplish the same basic functions of mate attraction and territorial defence through the use of a single short, simple song. Such a difference raises the question of why complex songs might be favoured in some species. Darwin (1871) suggested that the evolution of song structure might be influenced by a female preference for more beautiful songs. This suggestion received little attention until it was revived and expanded upon by Nottebohm (1972), who speculated that a male's vocal performance might not only affect how soon he acquired a mate but might also aid in obtaining a larger territory or accelerating the female's reproductive cycle. Since that time the study of the function of song repertoires has become a primary focus of song research (Kroodsma and Byers 1991).

The first field investigation of the function of song complexity was Howard's (1974) study of the Northern Mockingbird (*Mimus polyglottos*), and it revealed that correlations existed between repertoire size and both pairing date (a measure of female preference) and territory quality, and indicated that it could be difficult to determine whether females were choosing mates based on their repertoire size or on the basis of territory quality. Much subsequent work has been aimed at attempting to separate the effects of these two potential functions of complex song.

The intra-sexual function of song repertoires has been well supported, for certain species at least, by direct experimental evidence. Krebs et al. (1978) demonstrated that vacant Great Tit (*Parus major*) territories remained unoccupied longer when large repertoires were broadcast than when a single song type was used, and Yasukawa (1981) similarly showed that a repertoire was more effective in reducing trespass rates in Red-winged Blackbirds (*Agelaius phoeniceus*). Males of both of these species possess a small or medium sized repertoire of relatively short and simple songs. Correlations have also been reported between repertoire size and territory size or quality in Great Reed Warblers (*Acrocephalus arundinaceus*, Catchpole 1986) and

Western Meadowlarks (*Sturnella neglecta*, Horn et al. 1993), suggesting that an effect of repertoires on territorial competition may be widespread.

The underlying reason why repertoire size should influence competition between males is not clear, although a number of hypotheses have been suggested. Searcy and Andersson (1986) reviewed four possible explanations. Switching between song types may signal aggressive intentions, as has been suggested for Western Meadowlarks (Falls and D'Agincourt 1982) and Song Sparrows (*Melospiza melodia*, Kramer and Lemon 1983). This hypothesis seems to be most applicable to species with short discrete songs and is unlikely to apply to species with long complex song ('continuous' singers) such as Winter Wrens (*Troglodytes troglodytes*) or European Starlings (*Sturnus vulgaris*), in which much of the song diversity is represented by the large number of different syllable or phrase types within each song. A second possible explanation is that song repertoires simulate a high density of territorial males and may deter prospecting males that wish to avoid densely settled areas (the "Beau Geste hypothesis", Krebs 1977). Again, this hypothesis would seem more applicable to species with short discrete songs. Yasukawa and Searcy (1985) tested this hypothesis with Red-winged Blackbirds and found that, instead of declining, intrusion rates tended to increase with higher densities of territorial males. Slater (1978) has also pointed out that under this hypothesis it is difficult to explain the tendency, noted in many species, to repeat songs several times before switching to the next song type. Searcy and Andersson (1986) conclude that the Beau Geste hypothesis has not been adequately supported for any species. A third explanation is that repertoires serve as an indication of a male's resource holding power. This hypothesis could be applicable to species with either short discrete songs or with long complex songs, but requires that there be some mechanism for ensuring the reliability of a correlation between repertoire size and the ability of a male to defend resources. One possibility is that in species where repertoire size increases with age (e.g. Red-winged Blackbird) song may be an indicator of a male's experience, and experience may enhance a male's resource holding power (Yasukawa 1981). Finally, a fourth possible explanation is that repertoires reduce habituation in listeners for no adaptive reason (Yasukawa and Searcy 1985).

Demonstrating that females prefer to mate with males with larger repertoires or more complex song has been somewhat more difficult than showing that song repertoires affect competition for territories. Although a few studies have found a correlation between repertoire size and pairing success (e.g. Yasukawa et al. 1980, Catchpole 1986, Eens et al. 1991), this association has usually been confounded by an association between repertoire size and territory quality. The only clear evidence from a natural setting for female choice of males with large repertoires is Catchpole's (1980) study of Sedge Warblers (*Acrocephalus schoenobaenus*). Pairing date showed a strong negative correlation with repertoire size, and this remained significant after controlling for the order of territory settlement (a measure of preferences for particular territories).

The other major source of evidence for females preferences for large repertoires has been laboratory studies which have used the techniques developed by Searcy and Marler (1981) to test female response to song. By implanting females with oestradiol it was found that copulation solicitation displays could be evoked by song stimuli, and the number and strength of these displays serves as an index of the strength of female response. This method has been utilized in tests of female response to repertoire size for seven species in which males possess song or syllable repertoires (reviewed by Searcy 1992) and it has been consistently found that females display more for larger repertoire sizes. However, the interpretation of these results is complicated by the fact that in two of these species detailed field studies have failed to find any evidence for a mating advantage for males with large repertoires (McGregor et al. 1981, Searcy 1984). As well, female Common Grackles (*Quiscalus quiscula*) displayed more for repertoires than single song types, although male Common Grackles do not have repertoires (Searcy 1992). Thus it is not clear how well these laboratory results reflect what is actually occurring in the field.

As is the case for the intra-sexual function of song repertoires, it is not fully understood why females should prefer to mate with males that have complex song, although several hypotheses have been suggested. One possibility is that song repertoires have evolved through an evolutionary feedback process based on the genetic covariance between a male trait and the female preference for it, or 'Fisherian sexual selection' (Fisher 1958). This process requires that variation in repertoire size has some genetic basis, and there is evidence to suggest this. Differences in repertoire size among species (DeVoogd et al. 1993), populations (Canady et al. 1984) and, perhaps, among individuals (Nottebohm et al. 1981, but see Kirn et al. 1989) are associated with differences in the volume of certain brain nuclei that are involved in song production. Differences in brain nuclei volume between two populations of Marsh Wrens (*Cistothorus palustris*) appear to be genetically based (Canady et al. 1984). However, in species where repertoire size increases with age, the correlation between the expression of the trait and the genetic variation is likely to be weak, and this will weaken the genetic covariance between male trait and female preference. A second explanation for female response to song repertoires is that repertoire size may be an indicator of genetic quality. This might be true if older males were of higher than average genetic quality, having survived various selective forces that removed other less fit individuals (Trivers 1972), and if repertoire size increases with age. Hypotheses of sexual selection based on viability differences have been controversial because it is likely that genetic variance for overall fitness will be low, but there may be sufficient variation for such a mechanism to be possible (Charlesworth 1987). Much of the intense debate over models of sexual selection has centred over the Fisherian and 'good genes' models outlined above (Andersson and Bradbury 1987), but a third possibility is also relevant to the evolution of song repertoires. That is the possibility that song repertoires serve as indicators of material benefits that may be gained by the female. These benefits might include a high quality territory, food supplied to the female or her young, or any other benefit provided by the male (Searcy and Andersson 1986). The males of most passerine bird species do provide some material benefits, in some cases extensive, so this factor may be of considerable importance. Catchpole (1982) suggested that the association between monogamy and large repertoires among European *Acrocephalus* warblers might be due to monogamous females selecting males that would be better at supplying food. This idea is supported by a broader comparative study by Read and Weary (1992) that found relationships between song repertoire size and male contribution to nest building and to male provisioning of the young. The mechanism by which the reliability of an association between repertoire size and male care would be maintained is not clear, but again an association between male age and repertoire size could be relevant, if older males are more experienced breeders and provide better care or other resources.

In this thesis, I attempt to address some of these questions relating to the functions of song complexity and explanations for why birds should respond to such a signal. At the beginning of my research I selected the European Starling (*Sturnus vulgaris*) as the most appropriate study animal. I wished to study a species that had a highly complex song, reasoning that such a species in which song complexity had been strongly exaggerated would be the most suitable for answering questions about the functions of song complexity. Although little had been published about the song of starlings at this time, it was obvious that this species has a very complex song which includes a great diversity of sounds, including frequent mimicry of other species (Hindmarsh 1984). The fact that starlings readily nest in artificial nestboxes was another important factor, as this habit not only facilitates study of the species in general but also made possible the sort of experiments described in Chapters 1 and 3. The abundance of starlings in the Montreal area was another practical consideration in this choice. Finally, many aspects of the species' basic biology have been well studied (Feare 1984), enabling me to make certain research plans in an informed manner.

My initial investigations of starling song involved the use of playback experiments to investigate the response of both male and female starlings to the presence or absence of song, and to variation in the complexity of this song. These experiments, described in Chapter 1, indicated that song does function to attract female starlings. They also indicated that song in itself is not effective as a territorial deterrent in this species, as males were actually attracted by song as well, but more complex song did inhibit males from actually entering a nestbox. Females did not show the same avoidance of complex song as did males, but too few responded to determine in this experiment whether they actually preferred complex song.

In order to understand why males and females may respond to differences in song repertoire it is important to understand what factors are responsible for the variation among individuals in the size of their repertoires. One possibility that is relevant to several of the hypotheses discussed above is that repertoire size may increase with age. I examine this possibility in Chapter 2, and find that yearling male starlings have smaller repertoires of song phrases than older birds. Individual adults (at least two years old) continue to increase their repertoire size over time, as well as extensively modifying the composition of their repertoires.

In Chapter 3 I describe a field experiment which further examined the possibility that females prefer to mate with males that have large repertoires. Males with large repertoires did acquire mates more rapidly than males with smaller repertoires and, although there were significant preferences for particular nest sites, the correlation between repertoire size and pairing success remained significant when nest site preferences were statistically controlled.

One potential explanation for the female preference for males with large repertoires is that these older males provide more parental care. In Chapter 4 I test this hypothesis but do not find any support for the idea. Male starlings with larger repertoires did not spend more time incubating, nor did they make more feeding visits to nestlings. I argue that Fisherian sexual selection is unlikely to be able to explain the female preference for large repertoires, as the development of the trait is largely non-genetic and females are likely to experience some costs in mate choice. The evolution of song complexity in the European Starling is most consistent with an age-indicator model of sexual selection, in which females gain genetic benefits from mating with older males.

LITERATURE CITED

Andersson, M. B., and J. W. Bradbury. 1987. Introduction. Pp. 1-8 in J. W. Bradbury and M. B. Andersson, eds. Sexual selection: testing the alternatives. John Wiley and Sons, Chichester.

Canady, R. A., D. E. Kroodsma, and F. Nottebohm. 1984. Population differences in complexity of a learned skill are correlated with the brain space involved. Proc. Nat. Acad. Sci. 81: 6232-6234.

Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour 74: 149-166.

Catchpole, C. K. 1982. The evolution of bird sounds in relation to mating and spacing behavior. Pp. 297-319 in D. E. Kroodsma and E. H. Miller, eds. Acoustic communication in birds. Vol. 1. Academic Press, New York.

Catchpole, C. K. 1986. Song repertoires and reproductive success in the Great Reed Warbler, *Acrocephalus arundinaceus*. Behav. Ecol. Sociobiol. 19: 439-445.

Charlesworth, B. 1987. The heritability of fitness. Pp. 21- 40 in J. W. Bradbury and M. B. Andersson, eds. Sexual selection: testing the alternatives. John Wiley and Sons, Chichester.

Darwin, C. 1871. The descent of man and selection in relation to sex. John Murray, London.

DeVoogd, T. J., J. R. Krebs, S. D. Healy, and A. Purvis. 1993. Relations between song repertoire size and the volume of brain nuclei related to song: comparative evolutionary analyses amongst oscine birds. Proc. R. Soc. Lond. B 254: 75-82.

Eens, M., R. Pinxten, and R. F. Verheyen. 1991. Male song as a cue for mate choice in the European starling. Behaviour 116: 210-238.

Falls, J. B., and D'Agincourt, L. G. 1982. Why do meadowlarks switch song types? Can. J. Zool. 60: 3400-3408.

Feare, C. J. 1984. The starling. Oxford University Press, Oxford.

Fisher, R. A. 1958. The genetical theory of natural selection. Dover Publications, New York.

Hindmarsh, A. M. 1984. Vocal mimicry in starlings. Behaviour 90: 302-324.

Horn, A. G., T. E. Dickinson, and J. B. Falls. 1993. Male quality and song repertoires in western meadowlarks (*Sturnella neglecta*). Can. J. Zool. 71: 1059-1061.

Howard, R. D. 1974. The influence of sexual selection and interspecific competition on mockingbird song (*Mimus polyglottos*). Evolution 28: 850-871.

Kirn, J. R., R. P. Klower, D. E. Kroodsma, and T. J. DeVoogd. 1989. Song-related brain regions in the red-winged blackbird are affected by sex and season but not repertoire size. J. Neurobiol. 20: 139-163.

Kramer, H., and R. E. Lemon. 1983. Dynamics of territorial singing between neighbouring song sparrows (*Melospiza melodia*). Behaviour 85: 198-223.

Krebs, J. R. 1977. The significance of song repertoires: The Beau Geste hypothesis. Anim. Behav. 25: 475-478.

Krebs, J. R., R. Ashcroft, and M. I. Weber. 1978. Song repertoires and territory defence in the great tit. Nature 271: 539-542.

Kroodsma, D. E., and B. E. Byers. 1991. The function(s) of bird song. Amer. Zool. 31: 318-328.

McGregor, P. K., J. R. Krebs, and C. M. Perrins. 1981. Song repertoires and lifetime reproductive success in the great tit (*Parus major*). Am. Nat. 118: 149-159.

Nottebohm, F. 1972. The origins of vocal learning. Am. Nat. 106: 116-140.

Nottebohm, F., Kasparian, S., and Pandazis, C. 1981. Brain space for a learned task. Brain Res. 213: 99-109.

Read, A. F., and D. M. Weary. 1992. The evolution of bird song: comparative analyses. Phil. Trans. R. Soc. Lond. B 338: 165-187.

Searcy, W. A. 1984. Song repertoire size and female preferences in song sparrows. Behav. Ecol. Sociobiol. 14: 281-286.

Searcy, W. A. 1992. Song repertoires and mate choice in birds. Amer. Zool. 32: 71-80.

Searcy, W. A., and M. B. Andersson. 1986. Sexual selection and the evolution of song. Ann. Rev. Ecol. Syst. 17: 507-533.

Searcy, W. A., and P. Marler. 1981. A test for responsiveness to song structure and programming in female sparrows. Science 213: 926-928.

Slater, P. J. B. 1978. Beau Geste has problems. Anim. Behav. 26: 304.

Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136-179 in B. Campbell, ed. Sexual selection and the descent of man, 1871-1971. Aldine Press, Chicago.

Yasukawa, K. 1981. Song repertoires in the red-winged blackbird (*Agelaius phoeniceus*): A test of the Beau Geste hypothesis. Anim. Behav. 29: 114-125.

Yasukawa, K., J. L. Blank, and C. B. Patterson. 1980. Song repertoires and sexual selection in the red-winged blackbird. Behav. Ecol. Sociobiol. 7: 233-238.

Yasukawa, K., and W. A. Searcy. 1985. Song repertoires and density assessment in red-winged blackbirds: Further tests of the Beau Geste hypothesis. Behav. Ecol. Sociobiol. 16: 171-175.

CHAPTER 1

Song as an attractant for male and female European starlings, and the influence of song complexity on their response.

Summary. We tested the hypothesis that song acts as an attractant to females and a repellent to males in the European starling. We broadcast recorded song from speakers attached to nest-boxes, while paired boxes with silent speakers served as controls. As predicted, females were attracted to the 'song' boxes. Contrary to prediction, males were also attracted to the 'song' boxes. Singing by male starlings may be costly because it attracts competitors for limited nesting sites, but the cost cannot be avoided due to the need to attract a mate.

In a second experiment 'simple' song (composed of 20 different phrase types) and 'complex' song (40 phrase types) were played simultaneously. More males were captured at boxes where 'simple' song was played. Song complexity may function as an indicator of male quality and be used by male starlings to assess potential competitors.

INTRODUCTION

Bird song is usually considered to have two primary functions, territorial defence and mate attraction. Although both of these functions may be quite important, much more study has been devoted to the territorial aspect of song, perhaps because of the greater ease of studying this type of behavior. Territory defense often continues throughout the breeding season, and male passerines respond readily to playback of song within their territory with dramatic aggressive behavior. Evidence for the effectiveness of song as a deterrent to intrusion by conspecific males has come from a number of experimental studies (Peek 1972; Goransson et al. 1974; Krebs 1977; Smith 1979; Falls 1988).

In contrast, the importance of song for mate attraction has received much less attention. This function may be important for only a short portion of the breeding season and the behavior of the responding female is more subdued than that of a territorial male. The first experimental evidence that song attracts females was provided by Eriksson and Wallin (1986), who used play-back of pied and collared flycatcher (*Ficedula hypoleuca* and *F. albicollis*) songs. They found that 9 of 10 females were captured in nest-box traps where song was played.

In the case of the European starling (*Sturnus vulgaris*), there are several reasons for believing that mate attraction may be the more important of these two functions. Singing activity decreases markedly after pairing, but increases again after removal of the mate (Cuthill and Hindmarsh 1985). Starlings sing long, complex songs, the type of song that has been predicted to function primarily in mate attraction (Catchpole 1980), and Adret-Hausberger and Jenkins (1988) stated that song does not accompany interactions between males. If song does function primarily in female attraction in this species, then it is possible that complex song has been selected for through female choice (Darwin 1871, Nottebohm 1972). On the other hand, it has been suggested that starling song may function in territorial defense, and that individuals with more complex songs may be older individuals who should be superior competitors for nest sites (Feare 1984).

We conducted 2 experiments to investigate the response of starlings to song play-back. The first experiment tested the hypotheses that females are attracted by the song of males and that males are deterred by it. In this experiment a recording of natural song was played from a speaker attached to a nest-box, while the other box in each pair had only a silent speaker. In the second experiment we used edited recordings which differed in the number of different phrases they contained to test whether females preferred the more complex song and whether males might be more effectively deterred by complex song.

METHODS

The play-back experiments were carried out on the property of Macdonald College of McGill University at Ste. Anne de Bellevue, Quebec. The specific sites used were 1) Macdonald College Farm; 2) Macdonald Beef Barn, about 1.3 km north of the main farm; 3) Lods Research Station, about 0.7 km north-west of site 2. Only site 2 was used in 1988. The tapes were usually broadcast from 05:00 or 06:00 until 11:00 or 12:00, between 4 May and 6 June 1988 and between 6 April and 31 May 1989.

Recordings of starlings were obtained in the field during mid-March at Dorval (13 km from the experimental sites) and at Ste. Anne de Bellevue (0.8 km from the nearest experimental site). The 'natural song' tape consisted of a 162 sec segment of vigorous singing by one male from Ste. Anne de Bellevue, recorded on a 3 min endless loop cassette tape. This segment included 3 long songs and dozens of phrase groups. The 'complex' tape was composed of 40 different phrase types ('song types'in the terminology of Eens et al. 1989) extracted from field recordings of several males and re-recorded on a 3 min endless loop tape. Each phrase type was repeated 1-3 times within a unit, and a full unit of 40 phrase types lasted 1 min and 24 sec and was repeated twice on the tape. The 'simple A' and 'simple B' tapes comprised phrase types 1-20 and types 21-40, respectively, from the 'complex' tape. Each unit of 20 phrase types was repeated 4 times on an endless loop tape. The two 'simple' tapes were designed so that they were balanced with respect to the total length of the segments, the number of repeated phrases, and the relative complexity of the phrase types, such that 2 repetitions of either of the 'simple' units would have the same 'singing rate' and the same proportion of complex and repeated phrases as 1 repetition of the 'complex' unit. The actual lengths of 1 unit of 'simple A' and 'simple B' were 44 and 40.5 sec. The number of phrase types used on the tapes corresponds well to the natural variation in phrase repertoires of starlings (Adret-Hausberger and Jenkins 1988).

The tapes were played on Sony WM-D6C cassette recorders (1988) or Realistic SCP-31 tape players (1989) through Realistic MPA-40 or MPA-25 amplifiers to speakers attached directly underneath the nest-boxes. Peak intensity of the signal was standardised to 110 db at 10 cm. The nest-boxes were placed in pairs on the sides of barns or on metal posts in an open field. In 1988 4 pairs of boxes were used at site 2 and in 1989 2 pairs were placed at each of the 3 sites. The boxes in a pair were separated by 10 m. In Experiment 1 the 'natural song' tape was played at one speaker in a pair, while the other speaker was silent. A given box received song on every second experimental day. In Experiment 2 the 'complex' tape was played simultaneously with one of the 'simple' tapes, with 'simple A' and 'simple B' being used on alternate experimental days. The box which received 'complex' song was also alternated.

Starlings observed near the boxes were considered to have been attracted to that box if any of the following behaviors were noted: landing on top of the nest-box, fluttering directly in front of the nest-box, landing at the entrance hole of the nest-box, sticking the head inside the entrance hole, or entering the nest-box. Starlings defend an area of only about 1 m radius around their nest hole (Feare 1984), therefore only approaches within 1 m radius of the box were counted. To avoid statistical problems caused by the lack of independence of multiple values from the same individual, birds that visited an equal number of boxes of both types were excluded, but if a bird visited more boxes of a particular type it was considered to have been attracted to that box-type. Starlings that entered the nest-box were usually trapped using a simple trap modified from Stutchbury and Robertson (1986) and were sexed, aged, and colour-banded. Starlings that did not enter the boxes could often be sexed after close observation through a 20-45X Bushnell spotting scope.

RESULTS

In Experiment 1, females showed a strong attraction to the song boxes as predicted (Table 1). More surprisingly, males also showed a strong attraction to the 'natural song' boxes (Table 1). When all birds are considered, including the unsexed individuals, 90% of the birds were attracted to the 'natural song' boxes (Table 1). In addition, many birds landed near boxes and appeared interested in them but did not approach closely enough to conclude that they were attracted to a particular box.

In Experiment 2 we were interested in whether starlings would assess the complexity of the song and whether this would affect their subsequent behavior toward the hypothetical singer. Many of the birds approached the boxes before they could have had an opportunity to assess the complexity of the song, though, (in some instances flying directly in from a considerable distance away and landing on the boxes) and thus most of the measures used to indicate simple attraction to the song could not be used as evidence of a preference for one of the two song types. We therefore considered only those birds that actually entered a nest-box to have made a choice between the two song types. Too few females entered boxes to determine whether they showed a preference for either song type, although as predicted the only females captured were in complex song boxes (Table 2). Males, however, were significantly more likely to enter boxes where simple song was played (Table 2).

DISCUSSION

Experiment 1 demonstrated that females were attracted to play-back of male song. Although mate attraction has long been postulated to be an important function of the song of passerine birds (Howard 1920), this appears to be only the second experiment to provide support for this, following Eriksson and Wallin (1986). Gibson (1989) has

Table 1. Numbers of starlings that were attracted to nest-boxes with either play-back of natural starling song or no sound. Probabilities are based on binomial tests (one-tailed for females, two-tailed for other tests)

	Natural Song	No Sound	*P*
Females	12	0	0.0002
Males	17	3	0.0013
All birds	54	6	<0.001

Table 2. Numbers of starlings that entered nest-boxes with play-back of either 'complex' or 'simple' starling song. Probabilities are based on one-tailed binomial tests.

	Complex	Simple	*P*
Females	3	0	0.125
Males	1	9	0.01

also presented evidence that females in a non-passerine species (the sage grouse, *Centrocercus urophasianus*) are attracted to playback of male vocal display. The fact that similar results have been obtained in 3 families in 2 different avian orders, and representing 3 different spacing systems, suggests that female attraction to male vocalizations may indeed be a general phenomenon, as has long been suspected.

Experiment 1 provides the first experimental evidence that passerine song attracts intruding males into a 'defended' area. It is routine for males to be attracted to song when playback experiments are conducted within their territories, but they will not leave their own territory to approach the speaker.

Although the function of bird song as a deterrent to conspecific males has been generally accepted, it has been suggested that on a larger scale bird song may be used as a cue by other males to locate areas of suitable habitat (Svardson 1949, Hilden 1965, Persson 1971). Alatalo et al. (1982) attempted to test this hypothesis by comparing 4 experimental areas where pied flycatcher song was broadcast with 4 control areas where no song was played. They found that 3 pairs became established in the experimental area and none in the control areas, and concluded that song probably attracts other males. However, because the difference was not significant at the 0.05 level, and there was no evidence presented that the males preceded the females into the area, it seems best to interpret this result with caution. Alatalo et al. (1982) also suggested that song may repel males on a fine scale (up to 50m), as well as attracting males on a larger scale, based on the distribution of inhabited nest-boxes. Other factors beside song that may influence spacing cannot be ruled out though.

Although our finding that song attracts male starlings seems contrary to the accepted function of song as a territorial defense mechanism, intruding on an established male may be a successful option for the intruders. Suitable nest-sites are normally a limiting resource for cavity-nesting birds, and male starlings may be attracted by song because it indicates a nest site that they may be able to usurp. Wintering or early-arriving male starlings normally attempt to defend several cavities early in the season, but often lose possession of one or more of these potential nest sites to later arriving birds (Verheyen 1980). The attraction of competing males by song would be detrimental to the fitness of the territorial male if there is a possibility of losing possession of the nest cavity or a cost to deterring intruders, but this probably cannot be avoided due to the need to attract females to the same site. In order to fully understand the factors influencing the production of song this cost must be considered along with the other possible costs of song, such as the energetic costs of producing the sound, the increased conspicuousness of the singer to predators, and perhaps the announcement of the nest site to nest predators or brood parasites. We might expect, for example, that a low-quality male might sing less than a high quality male in order to minimize the risk of attracting competing males.

Assuming that males must sing to attract a female, there seems to be an advantage to singing a complex song. The fact that fewer males were captured in boxes with playback of complex song suggests that intruders are less likely to challenge a male that sings a complex song. Playback experiments with great tits (*Parus major*, Krebs et al. 1978) and red-winged blackbirds (*Agelaius phoeniceus*, Yasukawa 1981) have also shown that repertoires are more effective than a single song type in deterring intruders. Such a result is perhaps more surprising, though, in the case of the starling, which defends only a very small area around the nest hole, where the song appears to be directed at the female, and where males are attracted by the song. Catchpole (1982) predicted that in species such as the European starling which have highly complex song structure speaker replacement experiments should have no significant effect on the response of males. Nonetheless, if song complexity carries some information about male quality it is reasonable that other males should take heed of it, even if it is not primarily directed at them.

There is some evidence that starlings continue to learn new song phrases beyond the first year of life (Feare 1984, Adret-Hausberger et al. 1989) and age may therefore be the aspect of male quality that is conveyed by song complexity. The age of the singer may also be important information for a female choosing a mate (Manning 1985) but unfortunately too few females entered nest-boxes to determine whether they showed any preference for complex song. Further work will be necessary to determine what role female choice plays in shaping starling song.

Acknowledgements

We thank T. Winquist and M. Clarke for their comments on the manuscript and L. Robidoux, C. Tessier, and J. Templeton for their assistance. This study was supported by a Natural Sciences and Engineering Research Council grant to R. E. Lemon.

References

Adret-Hausberger M, Guttinger HR, Merkel FW (1989) Individualgeschichte und gesangsauspragung beim star (*Sturnus vulgaris*) in einar kolonie. J Ornithol 130:149-160

Adret-Hausberger M, Jenkins P (1988) Complex organization of the warbling song in the European starling *Sturnus vulgaris*. Behaviour 103:138-156

Alatalo RV, Lundberg A, Bjorkland M (1982) Can the song of male birds attract other males? An experiment with the pied flycatcher *Ficedula hypoleuca*. Bird Behaviour 4:42-45

Catchpole CK (1980) Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour 74:149-166

Catchpole CK (1982) The evolution of bird sounds in relation to mating and spacing behavior. In: Acoustic communication in birds. Vol. 1, Kroodsma DE, Miller EH (eds.). Academic Press, New York, pp. 297-319.

Cuthill I, Hindmarsh A (1985) Increase in starling song activity with removal of mate. Anim Behav 33:326-328

Darwin C (1871) The descent of man and selection in relation to sex. Murray, London

Eens M, Pinxten R, Verheyen RF (1989) Temporal and sequential organisation of song bouts in the starling. Ardea 77:75-86

Eriksson D, Wallin L (1986) Male bird song attracts females - a field experiment. Behav Ecol Sociobiol 19:297-299

Falls JB (1978) Bird song and territorial behaviour. In: Krames L, Pliner P, Alloway T (eds) Aggression, dominance and individual spacing in the study of communication and affect, vol 4. Plenum, New York, pp 61-89

Falls JB (1988) Does song deter territorial intrusion in white-throated sparrows (*Zonotrichia albicollis*)? Can J Zool 66:206-211

Feare CJ (1984) The Starling. Oxford, Oxford University Press

Gibson RM (1989) Field playback of male display attracts females in lek breeding sage grouse. Behav Ecol Sociobiol 24:439-443

Goransson G, Hogstedt G, Karlsson J, Kallander H, Ulfstrand S (1974) Sangensroll for revirhallandet hos naktergal *Luscinia luscinia* nagra experiment med playbackteknik. Var Fagelvarld 33:201-209

Hilden O (1965) Habitat selection in birds. A review. Ann Zool Fenn 2:53-75

Howard E (1920) Territory in bird life. Murray, London.

Krebs JR (1977) Song and territory in the great tit. In: Evolutionary ecology, Stonehouse B, Perrins C (eds). MacMillan, New York, pp 47-62

Krebs JR, Ashcroft R, Webber MI, (1978) Song repertoires and territory defence in the great tit. Nature 271:539-542

Manning JT (1985) Choosy females and correlates of male age. J Theor Biol 116:349-354

Nottebohm F (1972) The origins of vocal learning. Am Nat 106:116-140

Peek FW (1972) An experimental study of the territorial function of vocal and visual display in the male red-winged blackbird (*Agelaius phoeniceus*). Anim Behav 20:112-118

Persson B (1971) Habitat selection and nesting of a south Swedish whitethroat *Sylvia communis* Lath. population. Ornis Scan 2:119-126

Smith DG (1979) Male singing ability and territory integrity in red-winged blackbirds (*Agelaius phoeniceus*). Behaviour 68:191-206

Stutchbury BJ, Robertson RJ (1986) A simple trap for catching birds in nest boxes. J Field Ornithol 57:64-65

Svardson G (1949) Competition and habitat selection in birds. Oikos 1:157-174

Verheyen R (1980) Breeding strategies of the starling. In: Bird problems in agriculture, Wright EN, Ingliss IR, Feare CJ (eds.). British Crop Protection Council, Croydon, pp. 69-83

Yasukawa K (1981) Song repertoires in the red-winged blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. Anim Behav 29:114-125

CHAPTER 2

Extended song learning in wild European starlings

ABSTRACT

The songs of wild adult European starlings, *Sturnus vulgaris*, were recorded over successive years to determine whether repertoire size and composition changed between years. Repertoire-size estimates increased between the first and last year of recording for five of seven males that were at least 2 years old when first recorded. All seven birds showed extensive changes in the composition of their repertoires. Many phrase types were dropped from the repertoire, and others were modified. All birds added many new phrase types to their repertoires between years. These results indicate that extended song learning occurs in adult starlings, even in birds that are at least 4 years old, and that repertoire size is correlated with age in this species. The influence of song repertoire size on male-male competition and possibly female mate choice may be related to its value as an indicator of male age.

INTRODUCTION

It appears probable that the advertisement songs of all oscine songbirds (Passeriformes, suborder Passeri) are acquired by hearing and copying the songs of conspecifics (Kroodsma 1982; Slater 1989). It has been generally believed that exposure to conspecific song must occur during a 'sensitive period' during the first year of life, and that once acquired these songs are not substantially modified during the rest of an individual's life (Thorpe 1961; Marler & Tamura 1964; Nottebohm 1970; Catchpole 1979). In recent years, however, evidence has accumulated to show that a number of social and environmental factors can influence the timing of song learning (Kroodsma 1982; Slater 1989). There is also considerable variation between species in the timing of song learning (Slater 1983), and even between different categories of song within a species (Byers & Kroodsma 1992; Lemon et al. 1993).

In a number of species, the ability to learn new songs seems to persist beyond the first breeding season. This has been best documented in the domestic canary, *Serinus canaria*, where individuals drop some song phrase types from their repertoire, modify others, and add new phrase types, such that their repertoire in the subsequent breeding season is larger and substantially modified from the previous year (Nottebohm & Nottebohm 1978; Nottebohm et al. 1986).

European starlings, *Sturnus vulgaris*, have also been shown to be capable of learning new song phrases at least during their second calendar year. Böhner et al. (1990) demonstrated that captive starlings were capable of learning new song phrases between 11 and 12 months of age. Eens et al. (1992a) showed that yearling starlings had much smaller repertoires than did older birds, and that the range of repertoire sizes recorded for six yearlings did not overlap the range for 19 older males. Finally, Eens et al. (1992b) showed that three captive yearlings increased their repertoires markedly in the next season. Thus the accumulated evidence to date indicates that starlings increase their song phrase repertoires substantially between their first and second breeding seasons.

It is not clear, though, whether the ability to learn new song phrases persists in older starlings. Adret-Hausberger et al. (1990) reported that two of three older starlings (at least 4 years of age when first recorded) added new phrase types to their repertoires in the next year. In addition, recordings of one other bird in its second and third calendar years suggested that it had dropped most of the phrases from its original repertoire and had added a larger number of new phrases. Eens et al. (1992b), however, reported that males older than 1 year did not show a consistent trend toward increasing their repertoire size, and found that both yearlings and older birds retained almost all of their original repertoire into the next breeding season.

In this paper we present the results of a study of song learning in wild starlings, in which recordings were made of individual males in successive breeding seasons. We show that starlings that were at least 2 years old when first recorded subsequently modified their repertoires extensively, and in most cases also increased the size of their repertoire. These changes in repertoire composition and size indicate that starlings continue to learn new phrase types after their second calendar year. We consider how this extended song learning period may affect the operation of sexual selection on repertoire size.

METHODS

Study Areas and Field Recordings

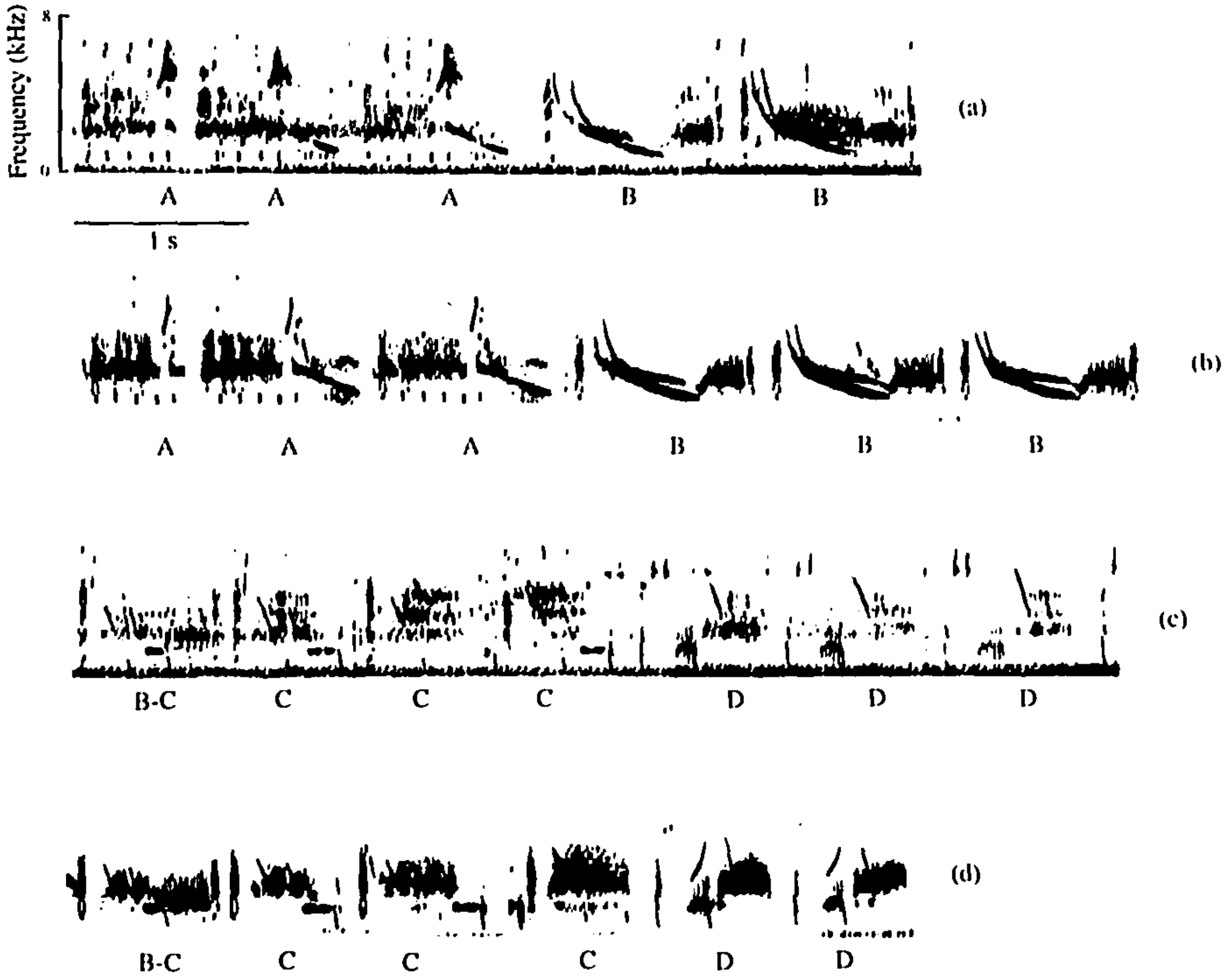
This study was conducted on the western section of the island of Montreal, Quebec, Canada. The first study area was the property of Macdonald College of McGill University at Ste Anne de Bellevue; the second study area was Cap St Jacques Regional Park in Pierrefonds. The two areas are separated by a distance of at least 3 km. As part of a larger study on the function of starling song, males were captured, measured and banded with standard aluminum bands and coloured plastic bands for individual recognition. The birds were aged when first captured as yearlings or older birds based on the length of their throat hackle feathers (Pyle et al. 1987). All song recordings were made during the breeding season (April - June) between 1989 and 1992. Most recordings were made before the birds were paired or during song bouts that preceded copulations, although some males continued to sing regularly after this stage and some additional recordings were obtained at this time. Song recordings stage and some additional recordings were obtained at this time. Song recordings were made with Sony WM-D6C cassette-recorders and Sennheiser MD 211 U microphones mounted in Dan Gibson parabolas. Of the seven birds studied most intensively, two nested within 100 m or less of each other in 2 of the 3 years in which they were both recorded. None of the other five birds nested near any of the others.

Song Analysis and Terminology

Spectrograms were printed for all song analysed using a Kay 7800 Digital Sona-graph and a 7900 Sona-graph Printer. The organization of starling song has been described in some detail by Adret-Hausberger & Jenkins (1988) and Eens et al. (1989, 1991b), but there has not been complete agreement on the categories or the terminology used to describe this complex song. Starling song is composed of many distinct units which are repeated once, twice, or several times before the next unit is introduced (Fig. 1); we refer to these units as 'phrases'. Phrases are often repeated two or more times before the next 'phrase type' is introduced; we refer to one or more consecutive repetitions of a particular phrase type as a 'phrase group'. The units of starling song that we label as phrases have been referred to as 'motifs' (Adret-Hausberger & Jenkins 1988) or 'song types' (Eens et al. 1989, 1991b), but these terms have also been used to identify the categories of acoustically similar units (phrase types), and even the consecutive repetitions of similar units (phrase groups). In order to avoid confusion over which meaning is intended we prefer to use the more specific terminology outlined above. Although this terminology deviates from what has been used in other descriptions of starling song, it is consistent with terms commonly used for descriptions of complex song in other species.

A complete starling song usually includes four relatively distinct sections. It begins with one to many phrases of moderate volume which are interspersed with pauses of 1 s or more. These phrases are often rather simple pure toned 'whistles', but they may also be harsh, more structurally complex, and often include heterospecific imitations. In the second section, the song accelerates into a series of complex phrases which frequently incorporate heterospecific imitations, are of

Figure 1. Spectrogram of a section of song from male 3 in 1991 (a,c) and a corresponding section of song from the same male in 1992 (b,d) illustrating the typical structure of starling song with most phrase types being repeated several times (a phrase group) before the next phrase type is introduced. Most of the phrase types in this section of song have been retained between years and are sung in the same order. Phrase type D was modified in 1992 by the addition of an ascending note between 3 and 5 kHz.


Frequency (kHz)
8
0
1 s
A
A
A
B
B
(a)
A
A
A
B
B
B
(b)
B-C
C
C
C
D
D
D
(c)
B-C
C
C
C
D
D
(d)

relatively low amplitude, and have only short pauses between them. This section is normally followed by phrases which are characterised by having a rapid series of clicks running through the phrase at the same time as other sounds are being produced. These phrases only occasionally include heterospecific imitations, are usually as soft as or even softer in volume than the preceding complex phrases, and often have no distinct temporal gaps between the units. The song sequence is typically completed by a fourth section in which the phrases include at least some high frequency sounds (6-10 kHz) and are the loudest phrases in the typical sequence. These phrases rarely include heterospecific imitations but may include some rapid clicks. The songs of an individual starling usually follow a more or less set sequence, with the majority of phrase types followed by a single predictable phrase type in most or all cases (Adret-Hausberger & Jenkins 1988; Eens et al. 1989). However, a song may end at any point in this sequence, or occasionally a bird may revert to a phrase type already sung and repeat part of the song sequence.

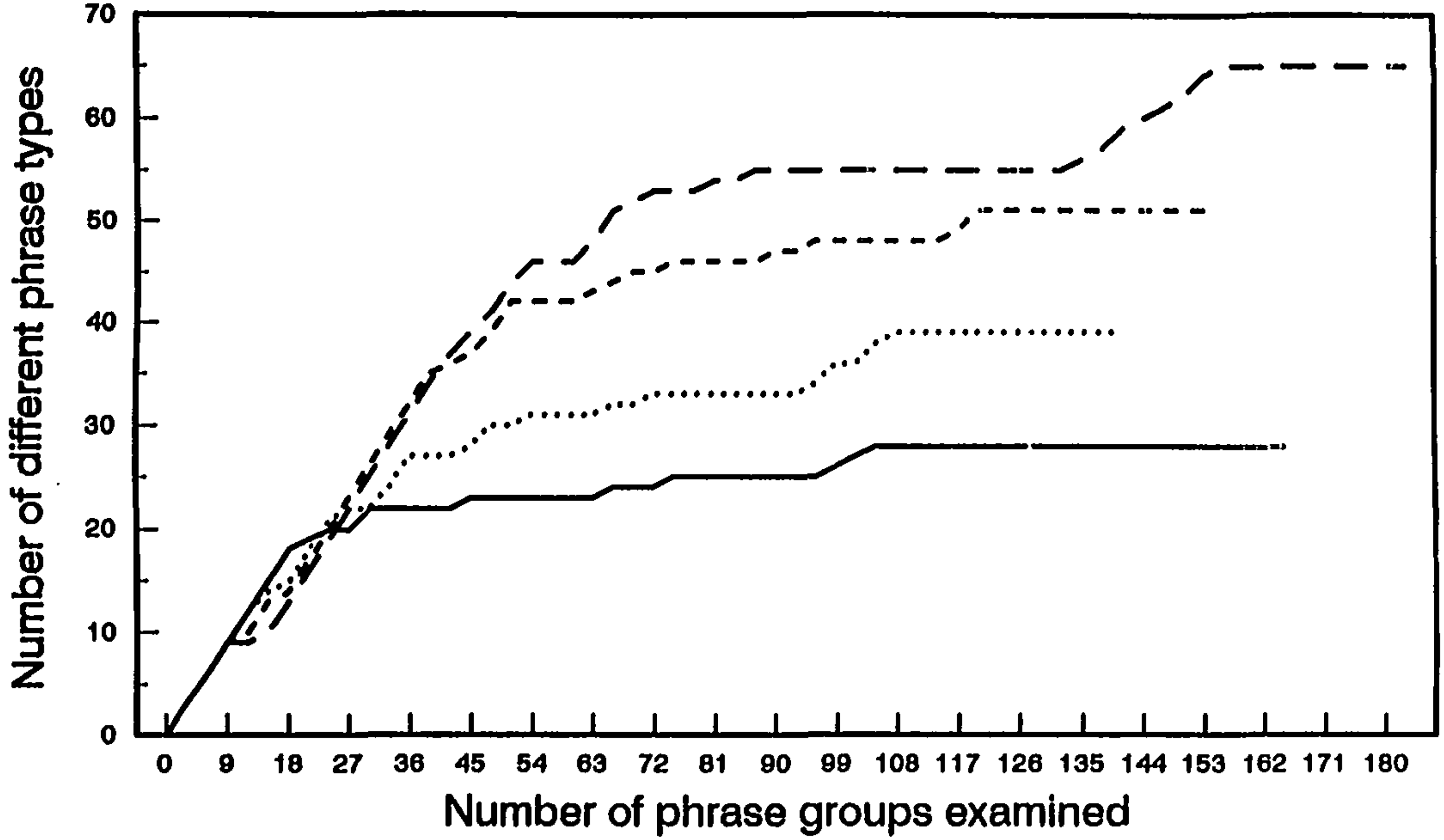
For each individual starling in a given year one of us (D.J.M.) classified the phrases into types based on visual inspection of the spectrograms and then plotted the cumulative number of phrase types encountered against the number of phrase groups examined. Such a plot typically rises steeply at first, because the stereotypy of individual song sequences results in a rapid presentation of new phrase types and few repetitions of phrase groups within a song. After examination of the first complete song, however, many of the phrase types in subsequent songs will have been previously encountered, and the plot will rise less steeply and gradually level off towards an asymptote as the curve approaches the bird's phrase type repertoire (Fig. 2). It is difficult to obtain the complete repertoire of an individual because new phrase types may still be identified in some cases after 300 or more phrases have been examined (Eens et al. 1991b). It is not necessary though, to obtain every phrase type in order to arrive at a meaningful estimate of its repertoire size. Due to the stereotyped sequences of phrase types within songs, a large proportion of an individual's repertoire is normally obtained in the first three or four songs analysed, and because of the large individual differences in repertoire size (which range from 21 to 68 phrase types; Eens et al. 1992a, 1992b), differences between individuals become apparent well before the complete repertoire is obtained. We established a criterion of 90 phrase groups as the minimum sample of song to be analysed from each individual in each recording season to produce a useful estimate of repertoire size; birds that did not meet this criterion were excluded from the analysis. Based on a mean of 2.2 repetitions of a phrase type per phrase group (Eens et al. 1991b), this criterion is equal to approximately 200 'motifs' (Adret-Hausberger & Jenkins 1988) or 'song types' (Eens et al. 1989). We estimate that on average approximately 85% of an individual's repertoire will have been obtained at this point. It is not sufficient, however, to simply establish a minimum criterion, as comparisons based on different amounts of analysed song will still be biased to a certain degree. This is because repertoire size estimates derived from analysis of larger samples of song will still tend to be higher than estimates derived from smaller samples, regardless of whether there are actual differences in repertoire sizes. Therefore, all comparisons of repertoire-size estimates are based on identical sample sizes of analysed song. For estimates of repertoire size for the same individual in different years this level of comparison is the smallest number of phrase groups obtained in any of the years under consideration. The number of phrase groups actually used for between-year comparisons of repertoire size ranged from 97 to 129.

RESULTS

Changes in Repertoire Size

Repertoire size estimates were obtained for 2 or more years for seven individuals, all of which were at least 2 years old when first recorded. Five of these birds showed an increase in estimated repertoire size between the first and last years that they were recorded, and these increases ranged from six to 14 phrase types (Fig. 3). Two other birds showed small decreases in their repertoire estimate of one and four phrase types. Overall, however, there was a significant increase in the repertoire size estimates (paired *t*-test, $t = 2.606$, one-tailed $P < 0.025$).

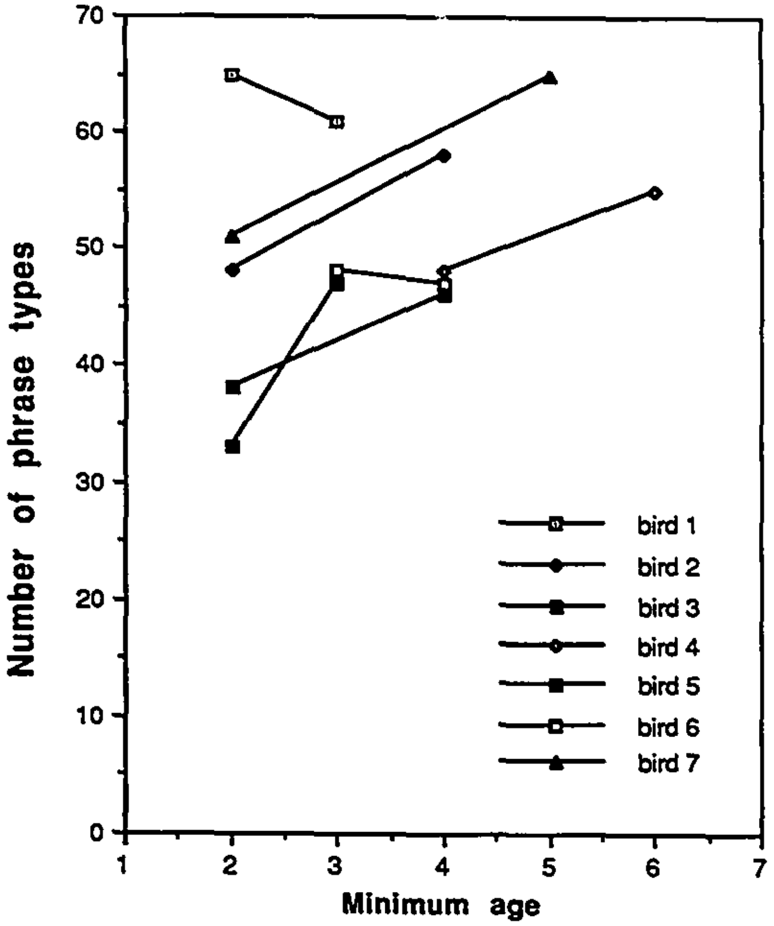
Figure 2. Plots of the cumulative number of phrase types identified against the number of phrase groups analysed for individual male starlings. Differences between birds with low and high repertoire sizes become obvious before 90 phrase groups have been analysed, even though in some cases the complete repertoire may not be obtained until more than 150 phrase groups have been analysed. The plots presented here represent the birds for which the greatest amount of song was analysed in each of the four quartiles of the range of estimated repertoire sizes.



70
60
50
40
30
20
10
0
Number of different phrase types
0
9
18
27
36
45
54
63
72
81
90
99
108
117
126
135
144
153
162
171
180
Number of phrase groups examined

In addition to those individuals that were recorded in more than one season, we obtained a number of recordings from known-age birds. Repertoire size estimates for nine yearlings were on average much lower than those for older males (yearlings: mean = 33.9; older males: $N = 19$, mean = 46.6, $t = 4.06$, $df = 26$, $P < 0.001$, comparisons based on 96 phrase groups for all birds). Five of these yearlings had repertoire estimates of 24 to 32 phrase types, lower than the estimates for any older male. However, unlike Eens et al. (1992a), we found that four birds aged as yearlings had repertoire estimates of 35 to 47 phrase types, within the range of older birds. It is possible that one or more of these birds was incorrectly aged, although this cannot be proven. The distribution of throat hackle measurements in our population is bimodal with a minimum at 12 mm, but with no gap between the two groups. This suggests that there will be a few individuals with 'borderline' measurements that will be incorrectly aged using this criterion. It is very likely, though, that at least two of these individuals (with throat hackles less than 10 mm in length) were indeed yearlings. The repertoire of one of these birds was unusual in the large number of introductory phrase types (whistles or more complex sounds, typically delivered with pauses of at least 0.5 s between phrases) it contained, but the other components of its repertoire were not more diverse than in other yearlings with low total repertoire estimates. The second undoubted yearling had a repertoire of 35 phrase types, near the lower limit for repertoire size among the older males. Finally, one bird that was banded as a yearling was first recorded when it was 3 years old, and it then had a repertoire estimate of 53 phrase types, somewhat higher than the mean for older males. Interestingly, among males that were at least 2 years old there was no correlation between their throat hackle length and their estimated repertoire size in 100 phrase groups ($r = -0.279$, $N = 15$, $P > 0.05$).

Figure 3. Repertoire size estimates for male starlings in their first and last year of recording. Repertoire size estimates are based on the same number of analysed phrase groups for the first and last year for each individual, but the amount of song analysed varies for different individuals.


Number of phrase types
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
Minimum age
bird 1
bird 2
bird 3
bird 4
bird 5
bird 6
bird 7

Changes in Repertoire Composition

As well as increasing the number of phrase types in their repertoire, the older males that were recorded in more than one year also showed major changes in the composition of their repertoire (Table I). We compared all the phrase types identified in an individual's repertoire with those recorded in the following year and classified them as 'retained' (identical in appearance in the two years), 'modified' (similar in appearance but with addition or deletion of notes or a shift in frequency), or 'new' (not similar to a phrase type recorded in the previous year). Although there was considerable variation between individuals, on average only 43.5% of the first year's repertoire was retained unchanged into the following year. Another 23% was modified to some degree. The remaining third of the original repertoire was not identified in the second year's recordings (Fig. 4). However, about 37% of the second-year phrase types had not been seen in the previous year's recordings, indicating that a very substantial number of new phrases had been learned (Fig. 4). The number of new phrase types considerably exceeded the average increase in estimated repertoire size. In fact, even those individuals that showed slight decreases in their estimated repertoire between years had many new phrase types in their repertoires the second year. Of course, these numbers must be viewed with caution as the complete repertoire was probably not obtained for all birds in each year. Undoubtedly, a few of the phrase types that were apparently missing in the second-year repertoire actually were present but simply not recorded; and similarly, some phrase types that were apparently new in the second year had probably been missed the preceding year. However, considering the rather large number of phrase groups analysed in determining repertoire composition (mean = 127.4 phrase groups per year) and the large number of phrase types identified in these samples (over 60 phrase types in seven of the samples), the number of phrase types that were missed must be quite small, and cannot account for the large number of phrase types that were apparently new or dropped between years.

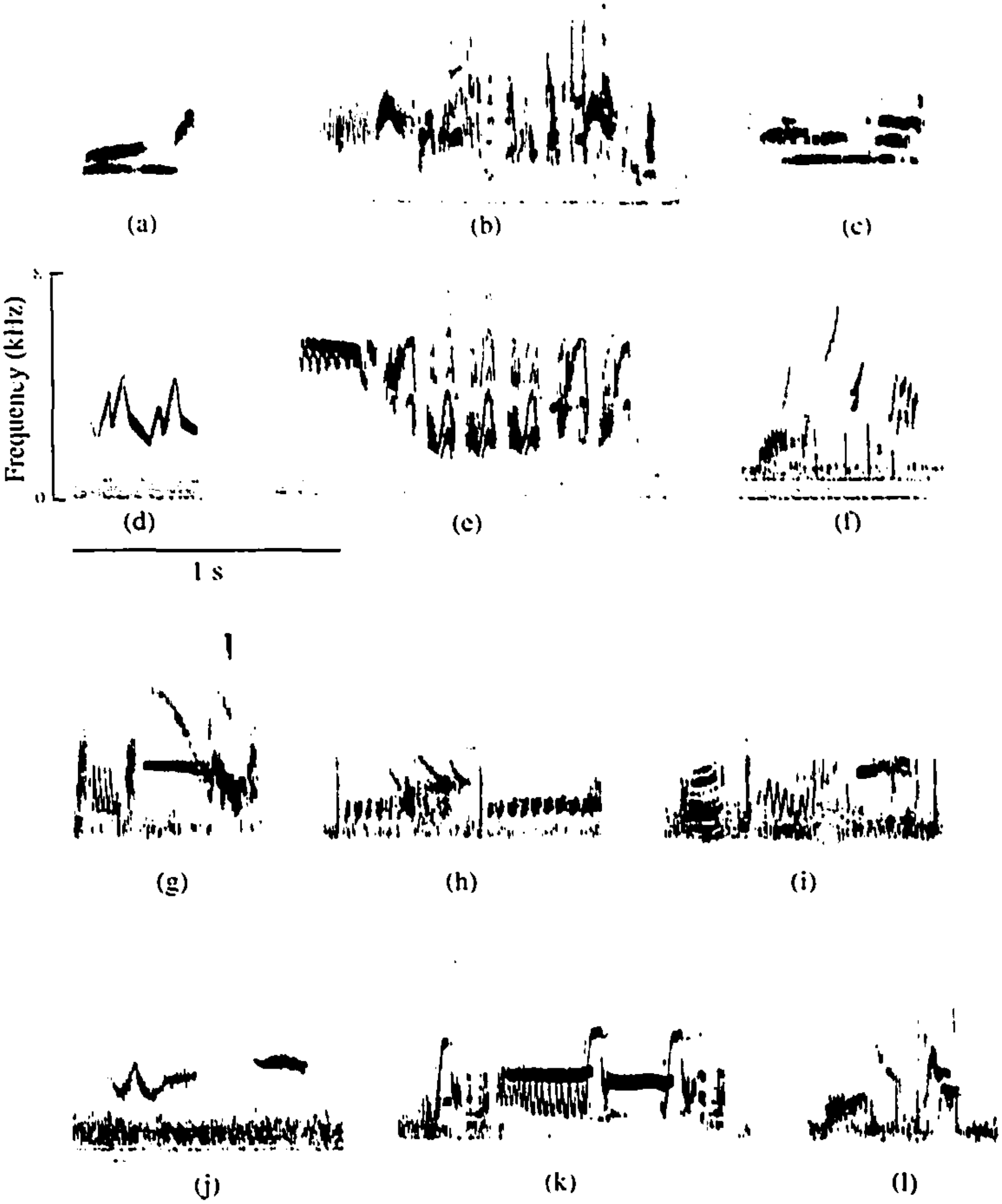
Table I. Between-year changes in the composition of the phrase type repertoires of seven adult male starlings

Bird	Years recorded	Phrase types identified in first year	Phrase groups analysed in first year	Phrase types 'dropped'	Phrase types modified	Phrase types same as previous year	'New' phrase types	Phrase types identified in second year	Phrase groups analysed in second year
1	1991-1992	65	126	24	9	32	20	61	123
2	1990-1991	48	119	14	8	26	17	52	129
2	1991-1992	52	129	19	7	25	28	60	136
3	1990-1991	38	102	11	11	16	36	63	138
3	1991-1992	63	138	29	10	24	13	47	107
4	1990-1992*	49	97	25	12	12	32	56	105
5	1990-1991	35	111	17	12	6	27	47	102
6	1990-1991	50	120	12	4	35	10	48	118
7	1989-1990	51	153	17	18	18	23	64	142
7	1990-1991	64	142	19	15	28	20	65	183
7	1991-1992	65	183	16	25	23	16	65	129

Note that because differing amounts of song were analysed in each year the values in this table for the number of phrase types identified are not unbiased estimates of repertoire size.

* Comparison after 2 years.

Figure 4. (a-f) Spectrograms of examples of phrase types apparently dropped from the repertoire of male 7 between 1989 and 1990. (g-l) Examples of phrase types apparently added to the repertoire of male 2 between 1991 and 1992.


(a)
(b)
(c)
Frequency (kHz)
0
(d)
(e)
(f)
1 s
(g)
(h)
(i)
(j)
(k)
(l)

DISCUSSION

The European starling is one of only five species of passerine birds for which there is evidence that individuals increase their song repertoire size after their first breeding season. The other species are the red-winged blackbird *Agelaius phoeniceus* (Marler et al. 1972; Yasukawa et al. 1981), the island canary (Nottebohm & Nottebohm 1978), the yellow warbler *Dendroica petechia* (Cosens & Sealy 1986) and the northern mockingbird *Mimus polyglottos* (Derrickson 1987). Our results indicate that in starlings, as in canaries (Nottebohm et al. 1986), this increase in repertoire size continues even after their second breeding season; it is not clear whether or not this is also true in the other species. These five species are not very closely related, having traditionally been placed in four or five separate families (American Ornithologists' Union 1983), suggesting that extended song learning resulting in increases in repertoire size could be a more widespread phenomenon than has been previously recognized. It is important to note that all five species have moderately large to very large repertoires of song or phrase types. It has been shown in a number of species with smaller repertoire sizes that individuals do not increase their repertoires after their first year. This is true even in several species where extended song learning does occur, but in these cases it apparently results only in a replacement of some old song types with new ones (e.g. saddleback, *Philesturnus carunculatus*: Jenkins 1977; great tit, *Parus major*: MacGregor & Krebs 1982, 1989; American redstart, *Setophaga ruticilla*: Lemon et al. 1993). However, among species that have large repertoires the only species known not to increase their repertoires with age appear to be restricted to the genus *Acrocephalus* (*A. palustris*: Dowsett-Lemaire 1979; *A. schoenobaenus*: Catchpole 1980; *A. arundinaceus*: Catchpole 1986). Thus, it would be interesting to know whether other large repertoire species also increase their repertoire size with age.

It is not clear from our data when starlings stop increasing their repertoire size. Among birds that were at least 3 years old there were both increases and decreases in estimated repertoire sizes in the following seasons. It seems likely that there is some limit to repertoire size, as none of the birds in this sample possessed more than 65 phrase types, even if that level was reached or approached before the final year of recordings.

The degree to which repertoire composition was altered between years indicates that learning continues to have an important effect on the repertoires of even very old birds and those that have already acquired extensive repertoires. The combination of frequent modification of old phrase types, dropping of phrase types, and acquisition of many new phrase types is a pattern that seems very similar to the extensive repertoire changes reported in the domestic canary (Nottebohm & Nottebohm 1978). The new phrase types acquired by adult starlings did not differ in any obvious way from the phrase types that were dropped from their repertoires (Fig. 4). The large degree of turnover in repertoire composition may be an incidental consequence of the birds retaining the ability to learn new phrase types later in life, and the new phrase types that are acquired are not necessarily superior in any sense to those that have been dropped. This extended learning period might be favoured because it makes it possible for males to continue to increase their repertoires. The fact that most birds learned 20-30 new phrase types each year but repertoire sizes increased at a much slower rate indicates that smaller repertoires are not simply the result of there being insufficient time available to learn enough phrases. It seems likely that there are other factors limiting the repertoire size of younger birds. It is possible that there might be a constraint on the capacity of song memory which changes with age, perhaps through greater investment in the brain nuclei responsible for song memory as the bird ages. The song memory capacity would presumably have an upper limit (which might vary somewhat between individuals) such that the repertoire of even old birds does not exceed 60-70 phrase types.

We consider the changes in repertoire size and composition we observed among birds that were several years old to be evidence of continued song learning, but this does necessarily indicate that the new phrase types were memorized at this time. It is theoretically possible that all of the many phrase types sung throughout the life of an individual are memorized during the first year of life but are not regularly produced until many years later, although this phenomenon does not seem to have been documented in any species. However, even if this scenario were correct, the incorporation of these phrase types into the crystallized song and the maintenance of these phrase types in the repertoire can be considered to be stages of the song learning process as well (Nottebohm et al. 1986), and these stages are still occurring when the birds are several years old.

Our findings of significant repertoire increases in starlings after their second breeding season and substantial between-year repertoire changes in birds of all ages are quite different from the results of Eens et al. (1992b). There are several possible reasons that might help to explain some of these differences. First, it is likely that the birds recorded by Eens et al. were older on average than the birds we studied. Their five captive males were all at least 4 years old when first recorded, whereas most of our birds had a minimum age of 2 years. Thus, it is more likely that their birds had already reached their individual repertoire size limits. Certainly two of their older birds (one captive and one wild) which already had repertoires of 66 and 67 phrase types, very close to the maximum recorded for any starling, would not have been expected to show major increases in subsequent years. Four of their older captive males, however, had repertoires considerably below the observed maximum and, although there is likely to be individual variation in the maximum repertoire, it is less convincing that these birds had reached their maximum potential repertoire size. It is possible that these birds were affected in some way by being in captivity, either through general stress or physiological constraints on their potential for learning. It is more likely though, that the major effect of being in captivity was that the opportunity for social interaction and the variety of potential song tutors was limited. In several species social interactions play an important role in determining the timing of song learning, and the choice of song tutors (Kroodsma & Pickert 1984; Petrinovich & Baptista 1987; Slater 1989). The captive males studied by Eens et al. (1992b) were housed with a relatively small number of other individuals from whom they could potentially learn, and remained with basically the same birds from one year to the next. As well, the yearling males Eens et al. studied did not learn equally from all males with which they were housed; rather each yearling had learned most of the attributable phrases in its repertoire from a single tutor with which it had been housed in its fledgling season. This suggests that early social interactions may have influenced the choice of song tutors, and this might further reduce the effective pool of potential song tutors. In contrast, wild starlings are highly social birds that interact with many other individuals during their extended singing season, and the population of birds that they interact with undergoes a large degree of turnover between years. Thus, compared to wild birds, the captives studied by Eens et al. (1992b) would have experienced much the same pool of potential phrase types from year to year. This might help explain why the older males did not continue to increase their repertoire, and also could explain why none of their captive birds showed the same degree of repertoire modification as the wild birds in our study, as there would be little exposure to novel phrase types from year to year.

The ongoing process of song learning in the European starling results in a correlation between repertoire size and the age of the individual, with little overlap in the repertoire sizes of yearlings and older males and continuing repertoire size increases even among males that are at least 2 years old. Repertoire size in starlings is likely to be strongly influenced by sexual selection. We have shown experimentally that repertoire size can affect intra-specific competition for breeding resources; playback of 'complex' song, which includes a larger number of phrase types, is more effective than 'simple' song in deterring males from entering a nest box (Mountjoy & Lemon 1991). A correlation between repertoire size and pairing success in starlings has also been reported (Eens et al. 1991), which suggests that females may use repertoire size as a cue for mate choice. In both intra- and inter-sexual contexts, repertoire size can convey information about the age of the singer and therefore about those relevant characteristics of the individual that are also correlated with age. These characteristics might include condition, competitive experience, reproductive experience and genetic quality. Determining the relative importance of these characteristics will be difficult, but could offer important insights into the evolution of song repertoires.

ACKNOWLEDGEMENTS

We thank Dorothy Howard and Jennifer Templeton for assistance in the field, and Amy Valachovic and Jennifer Hunter for help in printing out sonagrams. Beth Kwavnick, George Lozano, Stephane Perreault, M. Beecher, M. West and an anonymous referee provided useful comments on the manuscript. This work was supported by an NSERC operating grant to R.E.L.

REFERENCES

Adret-Hausberger, M., Güttinger, H.-R. & Merkel, F. W. 1990. Individual life history and song repertoire changes in a colony of starlings (*Sturnus vulgaris*). Ethology, 84, 265-280.

Adret-Hausberger, M. & Jenkins, P. 1988. Complex organization of the warbling song in the European starling *Sturnus vulgaris*. Behaviour, 107, 138-156.

American Ornithologists' Union. 1983. Check-list of North American birds, 6th edn. Washington, D.C.: American Ornithologists' Union.

Böhner, J., Chaiken, M., Ball, G.F. & Marler, P. 1990. Song acquisition in photosensitive and photorefractory male European starlings. Horm. Behav., 24, 582-594.

Byers, B.E. & Kroodsma, D.E. 1992. Development of two song categories by chestnut-sided warblers. Anim. Behav., 44, 799-810.

Catchpole, C.K. 1979. Vocal Communication in Birds. London: Edward Arnold.

Catchpole, C.K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour, 74, 149-166.

Catchpole, C.K. 1986. Song repertoires and reproductive success in the great reed warbler *Acrocephalus arundinaceus*. Behav. Ecol. Sociobiol., 19, 439-445.

Cosens, S.E. & Sealy, S.G. 1986. Age-related variation in song repertoire size and repertoire sharing of yellow warblers (*Dendroica petechia*). Can. J. Zool., 64, 1926-1929.

Dowsett-Lemaire, F. 1979. The imitative range of the marsh warbler *Acrocephalus palustris*, with special reference to imitations of African birds. Ibis, 121, 453-468.

Eens, M., Pinxten, R. & Verheyen, R.F. 1989. Temporal and sequential organisation of song bouts in the European starling. Ardea, 77, 75-86.

Eens, M., Pinxten, R. & Verheyen, R.F. 1991a. Male song as a cue for mate choice in the European starling. Behaviour, 116, 210-238.

Eens, M., Pinxten, R. & Verheyen, R.F. 1991b. Organization of song in the European starling: species-specificity and individual differences. Belg.J.Zool., 121, 257-278.

Eens, M., Pinxten, R. & Verheyen, R.F. 1992a. No overlap in song repertoire size between yearling and older European starlings, *Sturnus vulgaris*. Ibis, 134, 72-76.

Eens, M., Pinxten, R. & Verheyen, R.F. 1992b. Song learning in captive European starlings, *Sturnus vulgaris*. Anim. Behav., 44, 1131-1143.

Kroodsma, D.E. 1982. Learning and the ontogeny of sound signals in birds. In: Acoustic Communication in Birds. (Ed. by D. E. Kroodsma, E. H. Miller & H. Ouellet), pp. 1-23. London: Academic Press.

Kroodsma, D.E. & Pickert, R. 1984. Sensitive phases for song learning: effects of social interaction and individual variation. Anim. Behav., 32, 389-394.

Lemon, R.E., Perreault, S. & Weary, D.M. 1993. Dual strategies of song development in American redstarts (*Setophaga ruticilla*). Anim. Behav., 47, 317-329.

Marler, P., Mundinger, P., Waser, M.S. & Lutjen, A. 1972. Effects of acoustical stimulation and deprivation on song development in red-winged blackbirds (*Agelaius phoeniceus*). Anim. Behav., 20, 586-606.

Marler, P. & Tamura, M. 1964. Culturally transmitted patterns of vocal behaviour in sparrows. Science, 146, 1483-1486.

McGregor, P.K. & Krebs, J.R. 1982. Song types in a population of great tits (*Parus major*): their distribution, abundance and acquisition by individuals. Behaviour, 79, 126-152.

McGregor, P.K. & Krebs, J.R. 1989. Song learning in adult great tits (*Parus major*): effects of neighbours. Behaviour, 108, 139-159.

Mountjoy, D.J. & Lemon, R.E. 1991. Song as an attractant for male and female European starlings, and the influence of song complexity on their response. Behav. Ecol. Sociobiol., 28, 97-100.

Nottebohm, F. 1970. Ontogeny of bird song. Science, 167, 950-956.

Nottebohm, F. & Nottebohm, M.E. 1978. Relationship between song repertoire and age in the canary *Serinus canarius*. Z. Tierpsychol., 46, 298-305.

Nottebohm, F., Nottebohm, M.E., & Crane, L. 1986. Developmental and seasonal changes in canary song and their relation to changes in the anatomy of song-control nuclei. Behav. Neur. Biol., 46, 445-471.

Petrinovich, L. & Baptista, L.F. 1987. Song development in the white-crowned sparrow: modification of learned song. Anim. Behav., 35, 961-974.

Pyle, P., Howell, S.N.G., Yunick, R.P. & D. F. DeSante. 1987. Identification Guide to North American Passerines. Bolinas, California: Slate Creek Press.

Slater, P.J.B. 1983. Bird song learning: theme and variations. In: Perspectives in Ornithology (Ed. by A.H. Brush & G.A. Clark, Jr.), pp.475-511. Cambridge: Cambridge University Press.

Slater, P.J.B. 1989. Bird song learning: causes and consequences. Ethol. Ecol. Evol. 1, 19-46.

Thorpe, W.H. 1961. Bird Song. Cambridge: Cambridge University Press.

CHAPTER 3

Female choice for complex song in the European starling: a field experiment

Summary. Male European starlings *Sturnus vulgaris* sing long complex songs that appear to be important in the courtship of females but which also influence competitive interactions between males. We tested the hypothesis that females choose mates on the basis of the complexity of their songs, rather than on the quality of the territories the males defended. In order to determine whether certain territories were preferred over others, the first set of birds to settle in the experimental nest-boxes was removed and a second set allowed to settle. Consistent preferences for certain nest-boxes were indicated by correlations between the settlement patterns of the first and second sets of birds. However, males with the most complex song did not necessarily occupy the most preferred nest-sites. The length of time required for males to acquire mates was negatively correlated with the complexity of male song. This relationship remained significant when nest-site preference was statistically controlled, indicating that female starlings chose males with complex song rather than those that defended preferred nest-sites. Song complexity in European starlings increases with age, and the evolution of song complexity in this species appears to be most consistent with an age-indicator model of sexual selection, rather than a Fisherian model of runaway selection.

INTRODUCTION

Among certain bird species the males possess either a large repertoire of song types or sing long songs that are composed of many different phrase types. Various hypotheses have been offered over the years to explain why these species have such elaborate songs while others possess much simpler songs, but there is as yet no consensus on their relative importance. For simplicity, these hypotheses can be divided into two categories based on whether they suggest inter-sexual selection or intra-sexual selection as the dominant force favouring the evolution of song complexity. Early authors discussing the function of complex song in the context of sexual selection (Darwin 1871, Nottebohm 1972) suggested that female choice might favour males with more "beautiful" song or larger repertoires. However, the first field study of the function of song complexity (Howard 1974) revealed that in the northern mockingbird (*Mimus polyglottos*) repertoire size was correlated with territory rank as well as with female choice (pairing date). Partial correlations suggested that territory rank was more important than song in determining pairing date, and when territory rank was held constant the partial correlation between repertoire size and pairing date was not significant.

The effect of song complexity on territorial interactions has subsequently been demonstrated experimentally by song playback studies which have shown that a repertoire of song types or more complex song is more effective than a single song type or simpler song in deterring other males from intruding on a territory (Krebs et al. 1978, Yasukawa 1981, Mountjoy and Lemon 1991). Attempts to demonstrate an effect of song repertoires on female choice have often utilized the technique of implanting females with oestradiol to enhance their willingness to give copulation solicitation displays in response to certain stimuli (Searcy and Marler 1981). Many such studies on species that possess song repertoires have consistently found that females in laboratory conditions respond more to playback of larger repertoires (reviewed by Searcy 1992). The interpretation of these results has been complicated though, by the finding that implanted females respond more to repertoires even in two species where careful field studies have been unable to detect any influence of repertoires on female choice (McGregor et al. 1981; Searcy 1984).

The only species for which there is clear evidence of a female preference for males with larger song repertoires in the field, which is not confounded by choice of high quality territories, is the sedge warbler (*Acrocephalus schoenobaenus*) (Catchpole 1980). Catchpole found that repertoire size had a strong negative correlation with the date on which male sedge warblers became paired, suggesting that females preferred to mate with males with more varied song. To test whether this correlation resulted from a tendency for high repertoire males to occupy the territories on which females prefer to settle, Catchpole calculated a partial correlation between repertoire size and pairing date, while holding constant the order of male arrival (assuming that the first males to settle would claim the best territories). The partial correlation between pairing date and repertoire size remained highly significant, providing the best evidence to date of female choice for males with large song repertoires. However, this study leaves unanswered the question of why females should prefer to mate with large repertoire males. The comparative evidence for *Acrocephalus* suggests that large repertoires are more important for female choice in monogamous species with complex songs such as the sedge warbler than in polygynous species with simpler songs such as the great reed warbler (*A. arundinaceus*) and the aquatic warbler (*A. paludicola*) (Catchpole 1980, 1986). This evidence suggests that song may be being used to assess male quality (Catchpole 1982), but no aspect of male quality has yet been found to be correlated with song repertoire size in this genus.

In order to further examine the potential use of song complexity by females as a means of assessing male quality we have studied the European starling (*Sturnus vulgaris*). There are a number of reasons for suspecting that repertoire size might influence female choice in this species. The structure of the song (long, complex, and not highly stereotyped) is of the form that has been hypothesized to function in inter-sexual selection (Catchpole 1982). Most of the singing activity of male starlings appears to be directed at females (Eens et al. 1990, 1993; pers. obs.) and song output drops after pairing, but increases again if the female is removed (Cuthill and Hindmarsh 1985). Furthermore, copulations in this species are normally preceded by singing by the male (Eens and Pinxten 1990; pers. obs.).

A correlation between male pairing success and repertoire size has, in fact, been reported for this species (Eens et al. 1991), but territory quality was not measured or controlled in this study. Although starlings only defend the nest site and its immediate vicinity (Feare 1984), and the nest-boxes used by Eens et al. were all of the same design, nest-site preferences of starlings have been shown to be influenced by factors such as the orientation and height of the cavity (Verheyen 1980) and it is possible that factors such as this might have influenced the pairing decisions of females in their study. Furthermore, the demonstration that male starlings are less likely to intrude into an experimental 'territory' at which song of greater complexity is played back (Mountjoy and Lemon 1991) suggests that male song characteristics influence competition for preferred nest sites. Thus song complexity and territory quality may be correlated in starlings as they are in a number of other species (Howard 1974; Yasukawa et al. 1980; Catchpole 1986).

We conducted an experiment in which the first set of starlings that settled in a series of nest boxes was removed and a second set was allowed to settle. If there are preferences for certain nest-boxes there should be a correlation between the settlement patterns of the birds in the two rounds of the experiment. This information about nest site preferences can then be used to separate the potential influences of nest site quality and male repertoire size on the pairing decisions of female starlings.

METHODS

This study was carried out at Sainte Anne de Bellevue at the western end of Montreal Island, Quebec, Canada. Most of the nest-boxes were on the grounds of the Macdonald College Farm and other adjacent property associated with the Macdonald Campus of McGill University. Forty nest-boxes were erected on 15 and 16 April 1990. These boxes were surveyed daily to note the presence of birds and to record the song of males whenever possible. The surveys were carried out in the morning and the starting point of the surveys was rotated among three different points on the route to avoid having certain boxes always visited early in the morning and others late. Boxes were opened and inspected on at least a weekly basis to record the presence and amount of bird droppings, nesting material, and eggs as an indication of the occupancy status. Male starlings started carrying nesting material into nest boxes shortly after they began entering them, even if they did not necessarily become established residents. Thus the amount of material in a box served as a useful indicator of the amount of activity at the box, and in some cases it could reveal that males were visiting a box even though little or no activity had been detected on the daily surveys. Shortly after completion of the first clutches and the beginning of incubation we started to capture and remove nesting birds (beginning with the male of the pair, if possible). After the pair was captured all contents of the box were removed and the entrance hole was blocked off. Some birds were taken into captivity and the remainder was released at a site approximately 40 km to the NE. Boxes that were not occupied were sealed beginning on 5 May. All possible nesting pairs, and some apparent pairs that had not begun egg-laying, were removed by 11 May. Four boxes were left closed because one or both birds could not be captured, and an additional four were left closed, or the second round data were discarded, because the males that had been removed returned to the same box. All other boxes were opened again on 12 May for the second round of the experiment and they were again surveyed daily, the songs of males were recorded, and the contents of the boxes were checked every six days.

A number of variables were used to describe settlement patterns. SURVEY is the number of days on which a starling was observed at or close to a nest-box. NEST CHECK is the sum of the scores assigned for the nest-box contents in three nest checks, with the contents being scored on a scale from 0 (completely empty) to 9 (a complete lined nest). FIRST OBSERVED is the earliest date on which a starling was observed at the box, while FIRST CLAIM is the date of the earliest observation of a bird which persistently occupied the box.

Other relevant variables that were recorded were FIRST EGG (the date on which the first egg was laid in a nest) and DELAY (the number of days between the date when a nest-box was claimed and the date when the first egg was laid). For boxes where birds were removed before a first egg was actually laid it was conservatively assumed that the first egg would have been laid on the day after the first round of the experiment ended.

The length of the irridescent portion of the throat hackle feathers (MHACKLE) was noted for all males captured. These feathers are shorter in yearling males than in older birds (Pyle et al. 1987). They are also erected when males are singing vigorously, and so might have an influence on female choice.

Spectrograms were printed for all song analyzed using a Kay 7800 Digital Sona-graph^{R} and a 7900 Sona-graph^{R} printer. Starling song is composed of many phrases which may be repeated once, twice or many times before the next phrase type ('song type' in the terminology of Eens et al. 1989) is introduced; one or more consecutive repetitions of a particular phrase type is referred to as a phrase group. We estimated the repertoire size (REPERTOIRE) of individual males by determining the number of phrase types identified in a large sample of song. The criterion for an adequate sample size was set *a priori* at 90 phrase groups (equivalent on average to about 200 phrases). A sample of this size should contain approximately 85% of an individual's repertoire (Chapter 2). In fact, all individuals that met the 90 phrase group criterion had at least 92 phrase groups available for analysis, so this slightly higher sample size was actually used for comparisons between males. Although not all of a male's repertoire will usually have been obtained by this point, a sufficiently large proportion will have been identified to be able to distinguish between individuals of differing total repertoire sizes. Starlings have repertoires that vary greatly in size between individuals in a population, ranging from 21 to 68 phrase types (Eens et al. 1992a, 1992b). Thus, when the cumulative number of phrase types identified is plotted against the number of phrases examined, differences between high and low repertoire individuals become apparent well before the complete repertoire has been obtained (Chapter 2, see also figures in Eens et al. 1991).

RESULTS

Starlings were observed at or within a few metres of all 40 of the nest-boxes during the first round of the experiment, and 90% of the boxes had males apparently in residence for a period of several days at least. The four variables describing settlement patterns (SURVEY, NEST CHECK, FIRST OBSERVED and FIRST CLAIM) were all significantly correlated with each other in the first round of the experiment, but the strength of these correlations varied (Table 1). Correlations between FIRST OBSERVED and the other variables were consistently lower than the other correlations, suggesting that it was a poorer measure of settlement than the other variables.

The existence of consistent preferences for certain nest-boxes is indicated by highly significant correlations between the first and second round values of NEST CHECK (r = 0.697, Bonferroni adjusted $P < 0.0001$, n = 32) and SURVEY scores (r = 0.523, Bonferroni adjusted P = 0.002, n = 32). FIRST CLAIM dates were not significantly correlated after adjustment for multiple tests (r = 0.350, Bonferroni adjusted P = 0.148, n = 32), again suggesting that the measures based on a date of observation were less reliable because birds might not be present at the box at the time they were surveyed. NEST CHECK scores were therefore used as the primary measure of site preferences because they allowed for the detection of activity that might have been missed during the daily surveys.

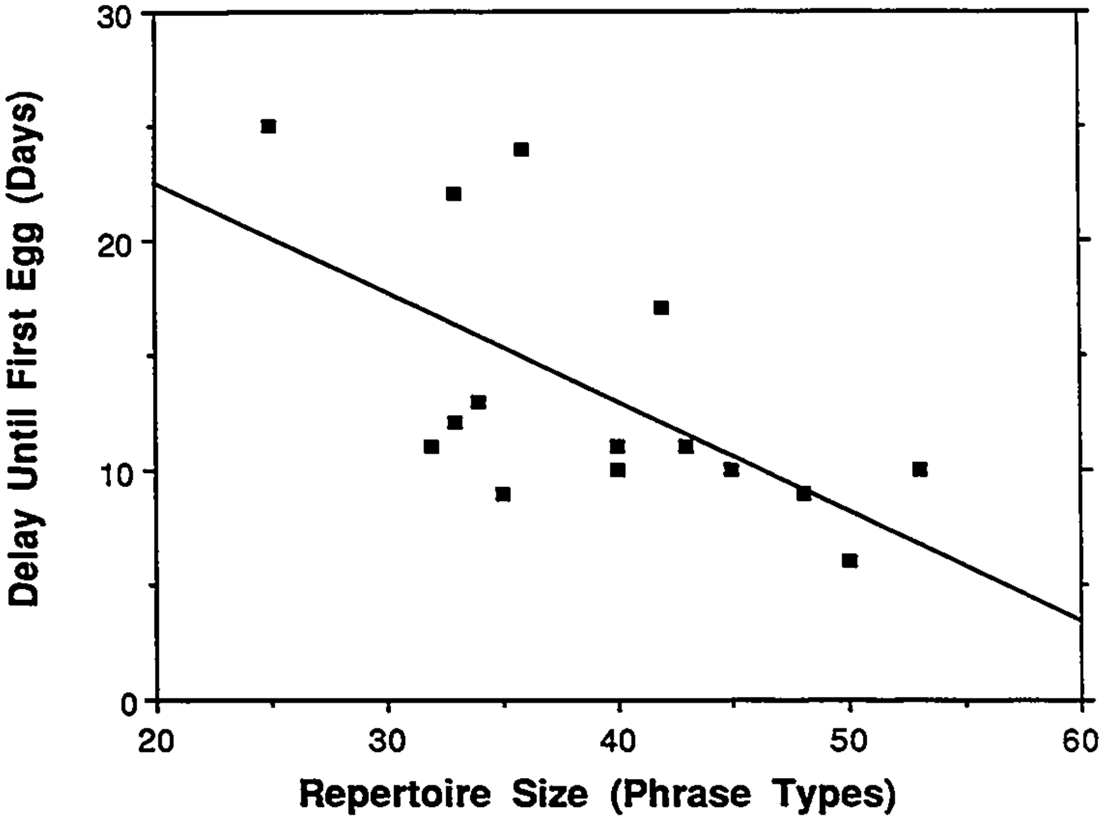
To test whether males with larger repertoires occupied the most preferred nest-boxes we calculated correlations between the repertoire sizes of males recorded in one round and the NEST CHECK scores of the other round. The NEST CHECK scores of the same round were not used because they are not independent of the behaviour of the male. There was no significant correlation between these variables in either round (REPERTOIRE round 1 versus NEST CHECK round 2, r = 0.425, n = 11, P = 0.192; REPERTOIRE round 2 versus NEST CHECK round 1,
r = -0.357, n = 7, P = 0.432).

If females prefer males with large repertoires there should be a negative correlation between REPERTOIRE and DELAY. As predicted, there was a highly significant correlation in the first round of the experiment (Fig. 1). Although there was little indication that large repertoire males defended the most preferred boxes, a partial correlation was calculated to confirm that this relationship did not depend on nest-box preferences. Using NEST CHECK scores from the second round of the experiment as

Table 1. Matrix of Pearson correlation coefficients (above diagonal) and Bonferroni adjusted probability values (below diagonal) for measures of initial settlement, before removals. Sample size is 40 for all correlations

	NEST CHECK	SURVEY	FIRST OBSERVED	FIRST CLAIM
NEST CHECK	-	0.820	-0.413	-0.732
SURVEY	<0.0001	-	-0.649	-0.759
FIRST OBSERVED	0.0483	<0.0001	-	0.490
FIRST CLAIM	<0.0001	<0.0001	0.0080	-

Fig. 1. Size of song phrase repertoire versus the delay (in days) between the date a nest box was claimed and the date when the first egg was laid for the first round of the removal experiment (r = -0.625, n = 15, one-tailed P = 0.006).


30
20
10
0
20
30
40
50
60
Delay Until First Egg (Days)
Repertoire Size (Phrase Types)

the measure of preference, repertoire size was still found to be significantly correlated with DELAY when site preferences were controlled for ($r_{12.3}$ = -0.672, n = 11, one-tailed P = 0.012). Furthermore, the correlation between NEST CHECK scores from the second round and DELAY was marginally non-significant (r = -0.432, n = 15, one-tailed P = 0.054). In the second round of the experiment considerably fewer boxes were occupied, and no correlation was found between male repertoire size and female settlement (REPERTOIRE versus DELAY, r = 0.456, n = 7, P = 0.303).

For the first round of the experiment, we also examined whether male hackle length affected female mating decisions. However, MHACKLE was not significantly correlated with DELAY (r = 0.296, n = 18, P = 0.233). Furthermore, the relationship between REPERTOIRE and DELAY when MHACKLE was controlled in a partial correlation remained significant ($r_{12.3}$ = -0.643, n = 12, one-tailed P = 0.012).

DISCUSSION

The highly significant correlations between NEST CHECK and SURVEY scores from the first and second rounds of the experiment indicate that consistent preferences for certain nest-sites exist, even though all of the nest-boxes were of the same design. However, the most preferred sites were not generally occupied by males with more complex song. This result may in part reflect the fact that in this study the nest-boxes were not erected until after the return of some spring migrants. In unmanipulated situations, where older males are more likely to remain on the breeding grounds throughout the year than are younger males, or arrive earlier in the spring (Verheyen 1980, Feare 1984), it is likely that older males will occupy the most preferred sites before the return of the younger birds. As older males tend to have larger repertoires (Eens et al. 1992a, Chapter 2) this could result in a correlation between repertoire size and nest-site quality in natural populations.

The negative correlation between repertoire size and DELAY in the first round of the experiment indicates a female preference for mating with males that have more complex song. This preference apparently overrides any possible preference for particular nest-sites, as the measures of site preference were not significantly correlated with DELAY. If the preferences for particular nest-boxes indicated by the consistent pattern of settlement in the two rounds of the experiment reflect real differences in the quality of nest-sites, then choosing males with more complex song rather than choosing on the basis of nest-site quality may have imposed a cost on those females. It is uncertain whether this potential cost of obtaining a lower quality nest-site is outweighed by benefits resulting from mating with a large repertoire male. However, if there is a correlation between male repertoire size and preferred nest sites in natural populations, as discussed above, then this cost may not be typical.

The failure to obtain a similar correlation between repertoire size and DELAY in the second round of the experiment may have been largely due to the small sample size, but the relationship was also strongly influenced by two unusual data points. In these two cases the males with the smallest repertoire sizes had exceptionally short delays between claiming a box and the day when the first egg was laid. DELAY was only 4 days in these two cases, two days less than the shortest DELAY in the first round of the experiment. It seems possible that these females might have been paired to other males previously, and this may have facilitated their rapid initiation of laying after settling with the experimental males.

This is only the second field study to demonstrate a correlation between repertoire size and female preferences after controlling for possible effects of territory quality. However, in the first study, on sedge warblers (Catchpole 1980), no correlation was found between repertoire size and any measure of male quality. Repertoire size does not seem to be correlated with age in sedge warblers or other members of the genus that have been studied (Dowsett-Lemaire 1979, Catchpole 1986). Thus, there is no convincing explanation as to why females should prefer to mate with male sedge warblers with larger repertoires. In starlings, however, song repertoires are larger in older birds and thus serve as an indicator of male age. It has been suggested that females may benefit from choosing older males because these males have demonstrated their survival ability and are likely to be of higher than average genetic quality (Trivers 1972, Manning 1985). Older males may also be better parents as a result of accumulated breeding experience improving the ability of a bird to perform specific parental duties, or because increased foraging efficiency allows a male to devote more time to parental care (Curio 1983, Desrochers 1992). Also, life history theory predicts that if mortality increases with age, then older birds should invest more in their current broods than should younger birds (Curio 1983). Thus, there are several reasons why females might benefit by choosing older males as mates, and age-correlated repertoires could act as a cue that makes such choices possible.

Although the evidence regarding starling song repertoires is consistent with the age indicator model of sexual selection (Manning 1985), it is difficult to rule out the possibility that a Fisherian process (Fisher 1958) involving female choice for an arbitrary character might be at least in part responsible for the evolution of song complexity. There are, however, several features of this system that make it appear unlikely that it can be explained by a Fisherian model. First, song complexity is not arbitrary with respect to age, and as noted above, age may be correlated with various aspects of male quality. Second, although there may well be some underlying genetic variation which influences an individual's repertoire size, the fact that repertoire size increases with age indicates that there is not a strong correlation between the potential genetic variation and the expression of the trait. This will make it difficult for a strong genetic covariance to be established between the trait and the female preference, as is required in most Fisherian models (Borgia 1987, Lande 1987). Third, the finding that females did not obtain the most preferred nest-sites by choosing males with large repertoires suggests that there may be significant direct costs associated with mate choice which would limit the conditions under which Fisherian models could operate (Harvey and Bradbury 1991). Finally, increased song complexity reduces the probability that an intruding male will enter a nest-box (Mountjoy and Lemon 1991). It seems unlikely that an arbitrary trait evolved through a Fisherian process would be used to resolve important competitive interactions if real asymmetries exist between the individuals (Baker 1986). For these reasons, it is unlikely that a Fisherian model is applicable. Instead, it appears that the most likely explanation for the evolution of song complexity in the European starling is the age indicator model.

ACKNOWLEDGEMENTS

We thank Dorothy Howard and Jennifer Templeton for assistance in the field and George Lozano for comments on an earlier draft. This study was supported by a Natural Sciences and Engineering Research Council grant to R.E. Lemon.

REFERENCES

Baker MC (1986) Sexual selection and size of repertoire in songbirds. In: Ouellet H (ed) Proc XIX Int Congr Ornithol 1:1358-1365.

Borgia G (1987) A critical review of sexual selection models. In: Bradbury JW, Andersson MB (eds) Sexual selection: testing the alternatives. John Wiley & Sons, Chichester pp 55-66

Catchpole CK (1980) Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour 74:149-166

Catchpole CK (1982) The evolution of bird sound in relation to mating and spacing behaviour. In: Kroodsma DE, Miller EH (eds) Acoustic communication in birds, Vol. 1. Academic Press, London pp 297-319

Catchpole CK (1986) Song repertoires and reproductive success in the great reed warbler *Acrocephalus arundinaceus*. Behav Ecol Sociobiol 19:439-445

Curio E (1983) Why do young birds reproduce less well? Ibis 125:400-404

Cuthill I, Hindmarsh AM (1985) Increase in starling song activity with removal of mate. Anim Behav 33:326-328

Darwin C (1871) The descent of man and selection in relation to sex. John Murray, London

Desrochers A (1992) Age and foraging success in European blackbirds: variation between and within individuals. Anim Behav 43:885-894

Dowsett-Lemaire F (1979) The imitative range of the marsh warbler *Acrocephalus palustris*, with special reference to imitations of African birds. Ibis 121:453-468

Eens M, Pinxten R (1990) Extra-pair courtship in the starling *Sturnus vulgaris*. Ibis 132:618-619.

Eens M, Pinxten R, Verheyen RF (1989) Temporal and sequential organisation of song bouts in the European starling. Ardea 77:75-86

Eens M, Pinxten R, Verheyen RF (1990) On the function of singing and wing-waving in the European starling *Sturnus vulgaris*. Bird Study 37:48-52

Eens M, Pinxten R, Verheyen RF (1991) Male song as a cue for mate choice in the European starling. Behaviour 116:210-238

Eens M, Pinxten R, Verheyen RF (1992a) No overlap in song repertoire size between yearling and older European starlings, *Sturnus vulgaris*. Ibis 134:72-76

Eens M, Pinxten R, Verheyen RF (1992b) Song learning in captive European starlings, *Sturnus vulgaris*. Anim Behav 44:1131-1143

Eens M, Pinxten R, Verheyen RF (1993) Function of the song and song repertoire in the European starling (*Sturnus vulgaris*): an aviary experiment. Behaviour 125:51-66

Feare CJ (1984) The starling. Oxford University Press, Oxford.

Fisher RA (1958) The genetical theory of natural selection. Dover Publ. Inc., New York.

Harvey PH, Bradbury JW (1991) Sexual selection. In: Krebs JR, Davies NB (eds) Behavioural Ecology. Blackwell Scientific Publications, London pp 203-233

Howard RD (1974) The influence of sexual selection and interspecific competition on mockingbird song (*Mimus polyglottos*). Evolution 28:428-438

Krebs JR, Ashcroft R, Webber MI (1978) Song repertoires and territory defence in the great tit. Nature 271:539-542

Lande R (1987) Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. In: Bradbury JW, Andersson MB (eds) Sexual selection: testing the alternatives. John Wiley & Sons, Chichester pp 83-94

Manning JT (1985) Choosy females and correlates of male age. J Theor Biol 116:349-446

McGregor PK, Krebs JR, Perrins CM (1981) Song repertoires and lifetime reproductive success in the great tit (*Parus major*). Am Nat 118:149-159

Mountjoy DJ, Lemon RE (1991) Song as an attractant for male and female European starlings, and the influence of song complexity on their response. Behav Ecol Sociobiol 28:97-100

Nottebohm F (1972) The origins of vocal learning. Am Nat 106:116-140

Pyle P, Howell SNG, Yunick RP, DeSante DF (1987) Identification guide to North American passerines. Slate Creek Press, Bolinas CA

Searcy WA (1984) Song repertoire size and female preferences in song sparrows. Behav Ecol Sociobiol 14:281-286

Searcy WA (1992) Song repertoire and mate choice in birds. Am Zool 32:71-80

Searcy WA, Marler P (1981) A test for responsiveness to song structure and programming in female sparrows. Science 213:926-928

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man, 1871-1971. Aldine Press, Chicago, pp 136-179

Verheyen RF (1980) Breeding strategies of the starling. In: Wright EN, Inglis IR, Feare CJ (eds) Bird problems in agriculture. British Crop Protection Council, Croydon, pp 69-82

Yasukawa K (1981) Song repertoires in the red-winged blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. Anim Behav 29:114-125

Yasukawa K, Blank JL, Patterson CB (1980) Song repertoires and sexual selection in the red-winged blackbird. Behav Ecol Sociobiol 7:233-238

CHAPTER 4

Male song complexity and parental care in the European Starling

ABSTRACT

We tested the hypothesis that female European Starlings (*Sturnus vulgaris*) that choose to mate with males that have large song phrase repertoires benefit by obtaining older and more experienced mates that will provide better parental care. Contrary to the hypothesis, males with large repertoires did not spend more time incubating nor did they make more feeding trips to the nestlings than did males with small repertoires. The possibility that females can use some male trait other than song as an indicator of future parental care is suggested by the fact that, in pairs with biparental care, there is a positive correlation between the nestling feeding rates of males and females. The possibility that the benefit of mating with large repertoire males is that these males are of higher genetic quality is discussed.

INTRODUCTION

It is accepted that selection should favour females able to choose males that will provide high levels of parental care (Maynard Smith 1987). However, it is not clear in many cases how well females will be able to assess the expected contribution of the male at the time when they select their mates. If males provide resources to females only before mating, such as the food provided by male scorpionflies (*Panorpa* spp., Thornhill 1981), then reliable assessment of male investment is possible. Similarly, the territories defended by many male birds can be assessed by the females prior to mating, although certain aspects of a territory may change during the breeding season in ways that are not easily predictable at the time of mating. In situations where males normally provide post-mating parental care, it will be more difficult for females to assess this contribution in advance. Nonetheless, if the level of care varies between males and affects female reproductive success, then females should discriminate between males on this basis if there are any useful predictors available (Searcy 1979).

The most reliable predictors of future parental care may be those behaviours that are most similar to the activities actually performed by the male after mating. For example, courtship feeding rates may be well correlated with incubation feeding and nestling feeding rates because the behaviours involved are all very similar and courtship feeding may be a good test of the male's ability to procure food in general. Courtship feeding rates have been found to be correlated with later male investment in Common Terns (*Sterna hirundo*, Nisbet 1973; Wiggins and Morris 1986) and Herring Gulls (*Larus argentatus*, Niebuhr 1981), but not in Pied Flycatchers (*Ficedula hypoleuca*, Lifjeld and Slagsvold 1986).

Less directly related characteristics may also serve as indicators of the quality of parental care in some species. A number of studies of fishes have found that females choose to mate with larger males, and that larger males in these species provide superior care for eggs (e.g. Downhower and Brown 1980; Bisazza and Marconato 1988; Côte and Hunte 1989). Courtship rate is another trait that has been found to be positively correlated with levels of parental care. Nestling feeding rates in Red-winged Blackbirds (*Agelaius phoeniceus*, Eckert and Weatherhead 1987) and egg survival in Bicolor Damselfish (*Stegastes partitus*, Knapp and Kovach 1991) are higher for males that court most actively. Traits such as body size or courtship rates could be reliable indicators of future male investment if they reflect an individual's energy reserves, and if an individual's energy reserves influence the level of parental investment. It is less clear though, whether other traits that do not obviously reflect energy reserves could also be used by females to select a mate of high parental quality. Hoelzer (1989) has developed a model that suggests that the evolution of epigamic traits which advertise non-heritable variation in parental quality is possible, but the reliability of the signal is an assumption of the model and not a result. However, two studies have produced results that suggest that such a system of mate choice may be feasible. Norris (1990a, 1990b) found that female Great Tits (*Parus major*) appear to prefer males that have wider breast stripes, and that those males had heavier fledglings and were more likely to mob a human intruder at the nest. Hill (1991) found that the rate of male feeding visits to incubating females was correlated with the male's plumage brightness, a trait which is preferred by females (Hill 1990), and suggested that this might indicate higher nestling feeding rates as well.

In this study we examine the possibility that female European Starlings (*Sturnus vulgaris*) use male song complexity as an indicator of future parental care. Male European Starlings sing long complex songs composed of many different phrase types, and the repertoires of individual males vary between 21 and 68 phrase types (Eens et al. 1992a, 1992b). The phrase type repertoires of individual starlings increase with age (Eens et al. 1992a, Chapter 2) and females prefer to mate with males that have large repertoires (Chapter 3), thus older and more experienced males are preferred as mates. Searcy and Andersson (1986) suggested that in species where repertoire size increases with age females might choose to mate with males with large repertoires because such males will be more experienced mates that will contribute more parental care. The quality of male care may be particularly important in the case of starlings, as males in this species typically play a larger role in the nesting activities than do the males of most passerine species. Male starlings not only make almost as many feeding visits to nestlings as do females, but they also contribute roughly 20-30% of the total incubation time (Kessel 1957, Feare 1984). There is, however, considerable variation in male behaviour (Feare 1984), and if females can use song complexity as an indicator of future male contributions they might realize substantial benefits by choosing mates on this basis.

METHODS

Field Methods

This study was conducted during the breeding seasons (March-June) of 1989 through 1991 on the western end of the island of Montreal, Quebec, Canada. The specific areas used were Cap St. Jacques Regional Park in Pierrefonds and the grounds of the Macdonald campus of McGill University in Ste. Anne de Bellevue and adjacent associated properties. All birds considered here nested in nestboxes erected for the purpose of our studies. Recordings of the songs of males occupying the boxes were made opportunistically throughout the breeding season, but particularly in mid-April to early May when males were advertising for mates or singing prior to copulations. Recordings were made with Sony WM-D6C cassette recorders and Sennheiser MD 211 U microphones mounted in Dan Gibson parabolas. Birds were captured in their nest-boxes, usually during early incubation, with the aid of a long collapsible aluminum pole which could be inserted into the entrance hole of the box to block it before the birds could exit. Captured birds were weighed, measured and marked with a standard aluminum band and a combination of coloured plastic leg bands for individual identification. Many of the females were also marked on their foreheads with white non-toxic paint to facilitate separation of the sexes during nest-watches. No nest watches were carried out later in the same day on which one of the birds in a pair was captured in order to allow the birds time to adjust after being handled. All nest watches, both during incubation and nestling stages, were of 1 h duration, and were conducted between 0530 and 1240 hours. In most cases nests were observed by a person positioned approximately 50-100 m from the nest using a Bushnell Spacemaster 15-45X spotting scope. A few nests were observed through 10X Bausch and Lomb or Zeiss binoculars from shorter distances using a car as a blind. During the incubation stage the amount of time spent inside the nest-box by the male and by the female was recorded. During the nestling stage the number of visits made by each sex to the box was recorded. We excluded those few occasions where the bird returned after having left the box but had remained in the immediate vicinity and could not have gathered any additional food. No systematic attempt was made to quantify the number of food items or determine the prey types brought to the nest.

Song Analysis

Spectrograms were printed for all song analysed using a Kay 7800 Digital Sona-graph and a 7900 Sona-graph Printer. Starling song is composed of many distinct units which are given once, twice, or several times before the next acoustically different unit is introduced. We refer to these units as 'phrases' and to one or more consecutive repetitions of a particular 'phrase type' as a 'phrase group'. The units that we refer to as phrases have also been called 'motifs' (Adret-Hausberger & Jenkins 1988) or 'song types' (Eens et al. 1989). For each starling in a given year one of us (D. J. M.) classified the phrases into types based on visual inspection of the spectrograms and then plotted the cumulative number of different phrase types encountered against the number of phrase groups examined. Such a plot typically rises steeply at first but after examination of one or two complete songs it gradually levels off as the curve approaches the bird's phrase type repertoire (see Eens et al. 1991a; Chapter 2, for examples). It is difficult to obtain the complete repertoire of an individual because new phrase types may still be identified in some cases after 300 or more phrases have been examined (Eens et al. 1991b), but it is not necessary to obtain every phrase type in order to arrive at a meaningful estimate of its repertoire size. Due to the rather stereotyped sequences of phrase types within songs, a large proportion of an individual's repertoire is normally obtained in the first three or four songs analysed, and because of the large individual differences in repertoire size (which range from 21 to 68 phrase types; Eens et al. 1992a, 1992b), differences among individuals become apparent well before the complete repertoire is obtained. We established an *a priori* criterion of 90 phrase groups as the minimum sample of song to be analysed from each individual to produce a useful estimate of repertoire size; birds that did not meet this criterion were excluded from the analysis. We estimate that on average approximately 85% of an individual's repertoire will have been obtained at this point. It is important though that comparisons between individuals are based on the same amount of analysed song to avoid sample size biases. At least 93 phrase groups were available for each male that met the 90 phrase group minimum, and this slightly higher number was used for all repertoire size estimates presented here.

RESULTS

Incubation behaviour

During the incubation watches males spent on average 21.3 min per hour (SD = 13.6, n = 18 males) in the nest box compared to 31.8 min per hour (SD = 11.8, n = 18 females) for females. Male contribution to incubation was quite variable; two males were not observed to incubate at all, while one male spent on average over 45 min in the nest box during watches. At nests where male contribution to incubation was low females appeared to attempt to compensate by increasing the time they spent in the nest box as the average incubation time of females showed a strong negative correlation with the average incubation time of males ($r_s = -0.865$, n = 18 nests, $P < 0.00001$). However, this compensation was not complete as the average total incubation time by both sexes was still positively correlated with the average male incubation time ($r_s = 0.503$, n = 18, $P < 0.05$), although not with average female incubation time ($r_s = -0.067$, n = 18, $P > 0.5$). Males with larger song phrase repertoires did not contribute more to incubation than did males with low repertoires;

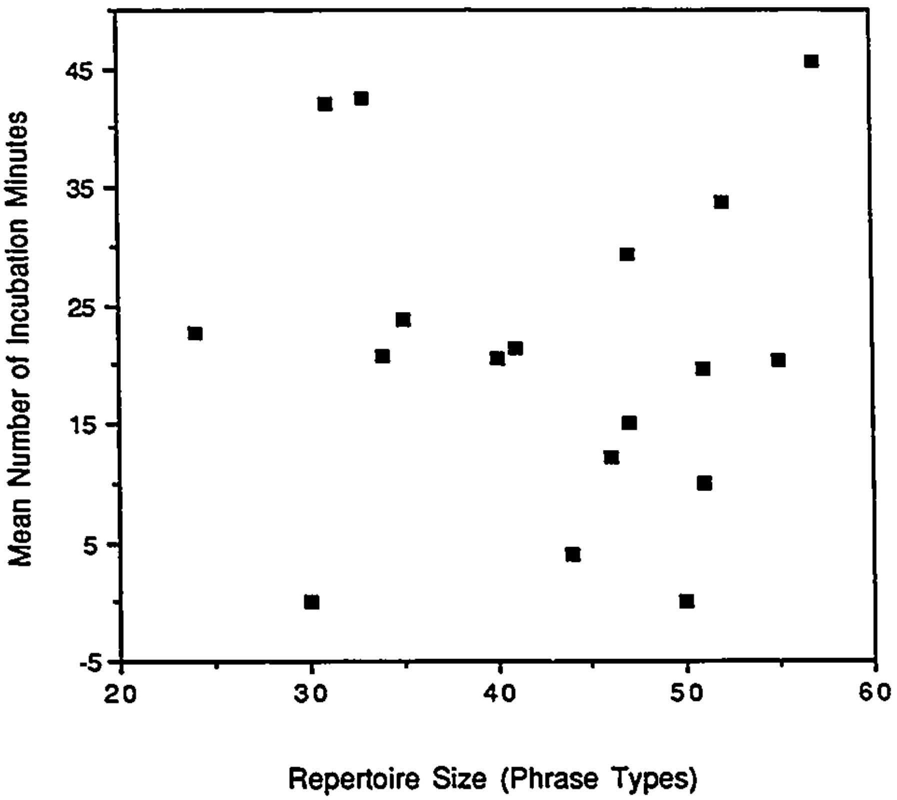
the average male incubation time was uncorrelated with their repertoire size estimates (Fig. 1, $r_s = -0.059$, $n = 18$, $P > 0.8$) and both low repertoire males (< 35 phrase types) and high repertoire males (> 45 phrase types) had average incubation times ranging from 0 to > 40 min per hour.

Nestling feeding

The percentage of total feeding visits to nestlings made by males ranged from 0 to 87.5%, with an average of 46.2% for 15 males. The numbers of feeding visits made by males and by females were not correlated (Fig. 2; $r_s = -0.143$, $n = 15$, $P > 0.6$), but this fact was due to the influence of those cases in which only one bird fed during one or more nest watches and that bird compensated by making more feeding visits than normal. There were two cases where the male was never observed to feed and one case where the female did not feed during one nest watch. If only those pairs in which both birds fed during all nest watches are included, there was a significant positive correlation between the numbers of male and female feeding visits ($r_s = 0.611$, $n = 12$ pairs, $P = 0.035$).

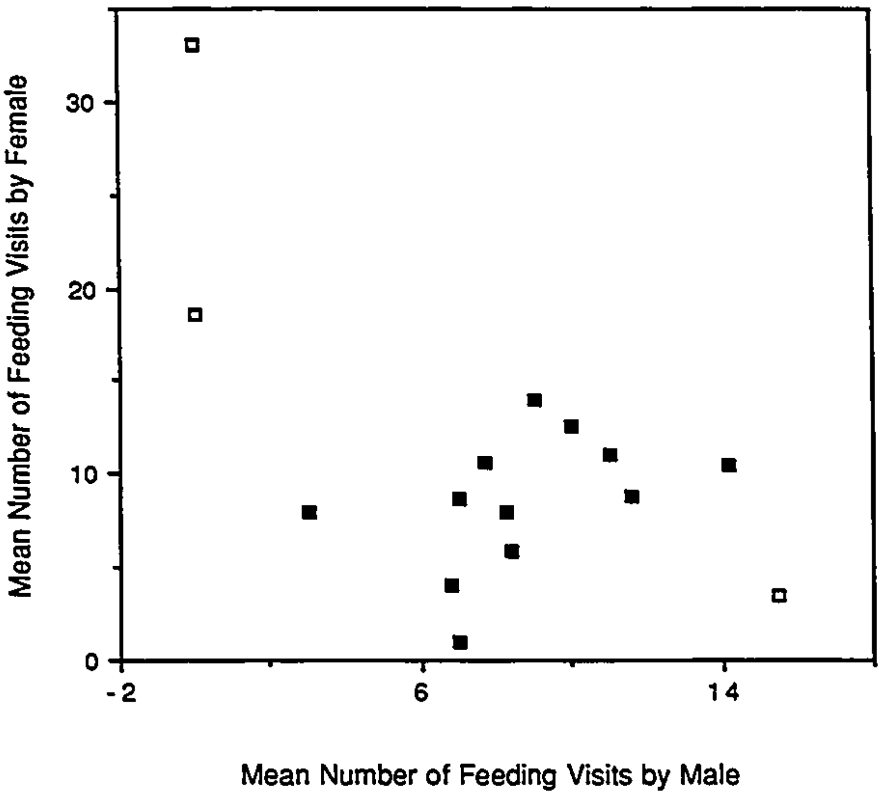
The positive correlation between male and female feeding visits might result from several causes. These include factors that might influence the numbers of feeding trips made by both males and females, such as brood size or nestling age which could affect the total food requirements of the young, or prey availability and distance to foraging sites which affect foraging behaviour. In such situations it may be desirable to examine male contribution to feeding as a proportion of the total number of feeding visits as this will remove the influence of those factors that affect the number of feeding visits made by both sexes. Alternatively, the correlation between the numbers of male and female feeding visits might result from an assortative pairing of birds with similar parental abilities. If this were the case then differences among males in the proportion of the total feeding trips which are made by males would be expected to be slight and the variation in the number of feeding trips made would be more relevant to

FIG. 1. The relationship between estimated male song phrase repertoire size and the mean number of minutes per hour that they spent incubating.



Mean Number of Incubation Minutes
45
35
25
15
5
-5
20
30
40
50
60
Repertoire Size (Phrase Types)

FIG. 2. The relationship between the mean number of feeding visits per hour to nestlings by females and by males. Filled squares represent nests with biparental care, open squares represent nests where only one bird fed nestlings during at least one nest watch.



Mean Number of Feeding Visits by Female
30
20
10
0
-2
6
14
Mean Number of Feeding Visits by Male

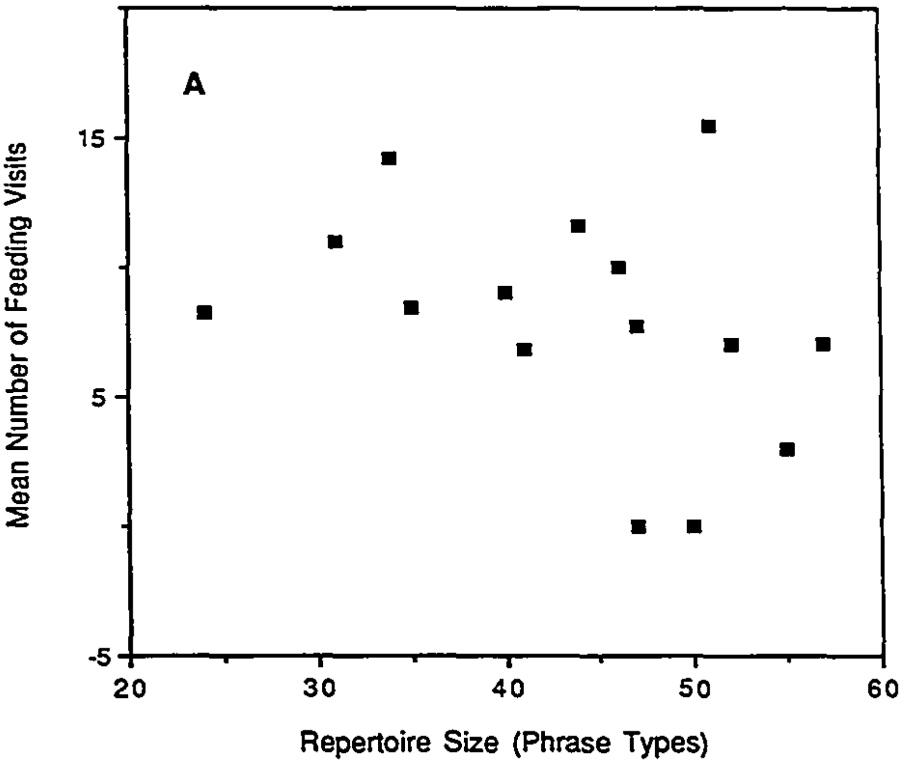
the question of differences in male parental quality. As we cannot readily distinguish between these possibilities we have analysed data on nestling feeding using both the proportion of trips made by the male and the absolute numbers of trips made.

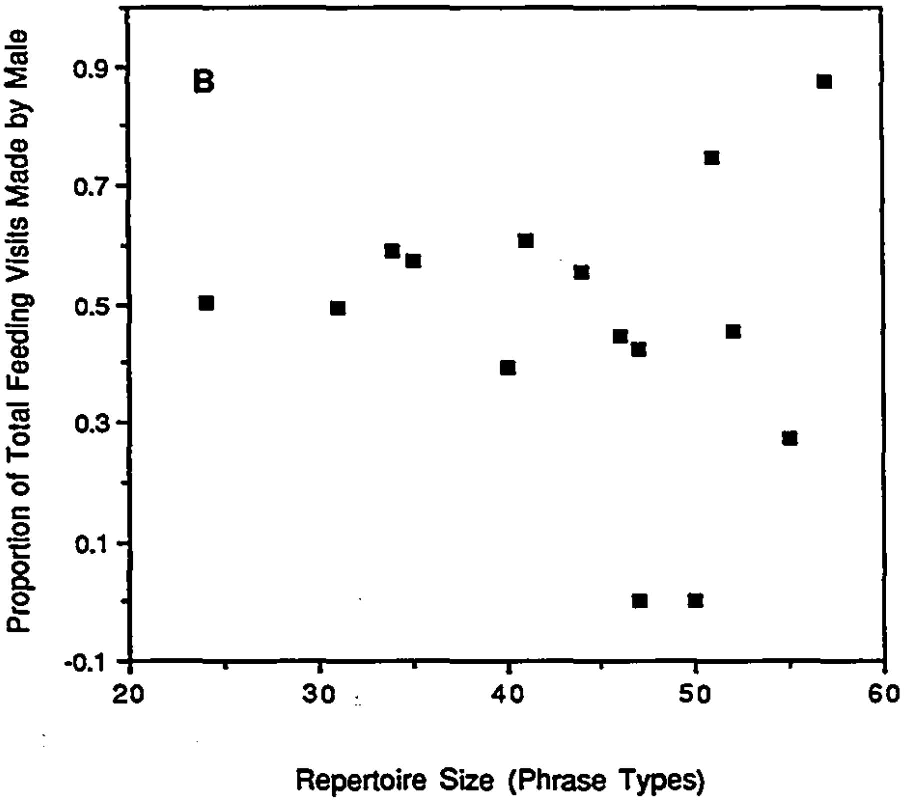
Neither the mean number of feeding trips nor the proportion of the total number that were made by the male was correlated with male song repertoire size (Fig. 3; number: $r_s = -0.443$, $n = 15$ males, $P = 0.098$; proportion: $r_s = -0.124$, $n = 15$, $P > 0.65$). The trend, at least for the absolute number of feeding trips, was for males with larger repertoires to make fewer visits than males with small repertoires, although the individual male that made the greatest number of feeding trips did have a relatively large repertoire.

DISCUSSION

We failed to find any support for the hypothesis that male starlings with large phrase repertoires provide higher levels of paternal care, and thus this potential benefit cannot explain the female preference for such males (Chapter 3). This result is perhaps surprising because male starlings make a relatively large contribution to parental care, and if this care influences female fitness it would seem to be an obvious basis for female mate choice. In fact, the males in the population we studied appeared to make a greater contribution, especially in incubation, than has been noted in some other studies. In European populations it has been found that males perform about 25-30% of incubation (Walraff 1953; Feare 1984), whereas we found that males contributed about 40% of total incubation time. Tinbergen (1981) found that both sexes made roughly the same number of nestling feeding visits and Wright and Cuthill (1989) found no significant sex difference in visitation rate, similar to our finding that males made about 46% of the total feeding visits. However, Wright and Cuthill (1990) reported that males fed nestlings less often than females did, and Feare (1984) found that males were responsible for only about 30% of the visits with food.

FIG. 3. The relationship between estimated male song phrase repertoire size and (a) the mean number of feeding visits per hour to nestlings by the males; (b) the mean proportion of the total feeding visits to nestlings that were made by the males.


A
Mean Number of Feeding Visits
15
5
-5
20
30
40
50
60
Repertoire Size (Phrase Types)


B
Proportion of Total Feeding Visits Made by Male
0.9
0.7
0.5
0.3
0.1
-0.1
20
30
40
50
60
Repertoire Size (Phrase Types)

The lack of a relationship between repertoire size and the level of male parental care parallels the results of Wright and Cuthill (1992), who found that male visitation rates to nestlings were not related to a number of male traits including several measures of body size and one song feature, the proportion of time males spent singing. It may in fact be difficult for female starlings to assess at the time of mating the probable level of parental care that will be supplied by males, even though such predictors have been found in other bird species. Traits that indicate future levels of parental care in other species may include song features. The song-rate of male Stonechats (*Saxicola torquata*) has been found to be positively correlated with the degree of participation in nest defence and nestling feeding (Greig-Smith 1982), although it is not known if song rate is actually used by females when assessing potential mates.

One factor that may act against any positive correlation between repertoire size and paternal care in European Starlings is the occurrence of occasional polygyny in this species (Feare 1984, Pinxten et al. 1989). Males with large repertoires are more likely to become polygynous (Eens et al. 1991b) and polygynous males often do not feed nestlings at secondary nests (Feare 1984) and may help less at primary nests (Pinxten and Eens 1990). Polygyny did not appear to be common in our study population, but one nest at which the male did not feed nestlings and spent little time incubating was a secondary nest, although the primary nest had been preyed upon before incubation began at the secondary nest. One other male that did not incubate or feed nestlings was infrequently seen in the vicinity of that nest and may also have been polygynous. However, given the low incidence of known polygyny it seems unlikely that this would have much effect on levels of parental care except for perhaps accounting for the non-significant negative trend in the relationship between repertoire size and nestling feeding.

Despite the lack of success in identifying any male characteristics that are correlated with the level of parental care, it is still possible that some such trait is available to females. This possibility is suggested by the positive correlation between the nestling feeding rates of males and females at those nests with biparental care, which may be due in part to assortative mating of birds with similar levels of parental care. Although we cannot from our results readily distinguish between the possibility of assortative mating and those factors associated with the brood or nest site that might evoke similar levels of care from both parents, assortative mating has been suggested by another study. Wright and Cuthill (1990) found positive correlations between male and female visitation rates in two of three years of their study (although not quite significant in one of the years). They argued that because of their experimental standardization of the broods, the uniformity of the nest sites, and the fact that starlings do not defend feeding territories, the correlations were more likely to be due to assortative mating than to factors associated with the brood or nest site.

The finding that phrase repertoire size is not related to male participation in incubation or nestling feeding rates leaves unresolved the question of why female starlings prefer to mate with large repertoire males (Chapter 3). It is possible that such males provide some other parental care benefits such as more effective nest defence that were not measured in this study, but there is no clear reason why large repertoire males should invest more in one aspect of parental care when they do not contribute more to other forms. Another potential benefit that females might gain from mating with large repertoire males is a high quality nest site. This seems unlikely to be the primary basis for the preference because in a field experiment females chose large repertoire males even though these males did not occupy more preferred nestboxes (Chapter 3). In a natural situation it is more likely that older males with more complex song will occupy the most preferred sites, as older males are the first to claim nest sites (Verheyen 1980), but there is no obvious reason to suspect that females cannot assess site quality independently and therefore must rely on male repertoire size as an indicator for this purpose.

Alternatively, females may gain no direct benefit from pairing with males which have large repertoires. If complex song evolved through a Fisherian process of sexual selection (Fisher 1958), then the only advantage to the female would be the mating advantage gained by her male offspring. However, there are several reasons for doubting this scenario. The fact that repertoire size increases with age (Eens et al.

1992a, Chapter 2) indicates that the correlation between genetic variation for the trait and its expression will be weak, thereby reducing the genetic covariance between female preference and the male trait that is important in this model. Furthermore, the influence of song complexity in intra-male competition (Mountjoy and Lemon 1991) suggests that the trait is not arbitrary as is expected in a Fisherian model but rather reflects some aspect of male quality.

The hypothesis that appears to be most consistent with the evidence regarding the evolution of song complexity in starlings is the age indicator model of sexual selection. This model suggests that females gain genetic benefits for their offspring by mating with older males, which will be of higher than average genetic quality because they have survived exposure to natural selection which has removed inferior members of their age class (Trivers 1972, Manning 1985). Although there is some doubt as to whether there is sufficient genetic variation in overall fitness to benefit females that choose males on this basis, recurrent deleterious mutations may provide sufficient variation for the operation of such a model (Charlesworth 1987). While the possibility that the phrase repertoires of starlings serve as a viability indicator in this manner is an intriguing one, obtaining convincing evidence regarding the genetic fitness of male starlings and their offspring is likely to be a difficult task.

ACKNOWLEDGEMENTS

We thank Dorothy Howard and Jennifer Templeton for assistance in the field, Amy Valachovic and Jennifer Hunter for help in printing out sonagrams, and George Lozano for comments on an earlier manuscript. This study was supported by a Natural Sciences and Engineering Research Council of Canada grant to R. E. Lemon.

REFERENCES

Adret-Hausberger, M., and Jenkins, P. 1988. Complex organization of the warbling song in the European starling Sturnus vulgaris. Behaviour **107**: 138-156.

Bisazza, A., and Marconato, A. 1988. Female mate choice, male-male competition and parental care in the river bullhead, Cottus gobio L. (Pisces, Cottidae). Anim. Behav. **36**: 1352-1360.

Charlesworth, B. 1987. The heritability of fitness. In Sexual selection: testing the alternatives. Edited by J. W. Bradbury and M. B. Andersson. John Wiley and Sons, Chichester. pp. 21-40.

Côte, I. M., and Hunte, W. 1989. Male and female mate choice in the redlip blenny: why bigger is better. Anim. Behav. **38**: 78-88.

Downhower, J. F., and Brown, L. 1980. Mate preferences of female mottled sculpins, Cottus bairdi. Anim. Behav. **28**: 728-734.

Eckert, C. G., and Weatherhead, P. J. 1987. Male characteristics, parental quality and the study of mate choice in the red-winged blackbird (Agelaius phoeniceus). Behav. Ecol. Sociobiol. **20**: 35-42.

Eens, M., Pinxten, R., and Verheyen, R. F. 1989. Temporal and sequential organisation of song bouts in the European starling. Ardea **77**: 75-86.

Eens, M., Pinxten, R., and Verheyen, R. F. 1991a. Male song as a cue for mate choice in the European starling. Behaviour **116**: 210-238.

Eens, M., Pinxten, R., and Verheyen, R. F. 1991b. Organization of song in the European starling: species-specificity and individual differences. Belg. J. Zool. **121**: 257-278.

Eens, M., Pinxten, R., and Verheyen, R. F. 1992a. No overlap in song repertoire size between yearling and older European starlings, Sturnus vulgaris. Ibis **134**: 72-76.

Eens, M., Pinxten, R., and Verheyen, R. F. 1992b. Song learning in captive European starlings, Sturnus vulgaris. Anim. Behav. **44**: 1131-1143.

Feare, C. 1984. The starling. Oxford University Press, Oxford.

Fisher, R. A. 1958. The genetical theory of natural selection. Dover Publications, New York.

Greig-Smith, P. W. 1982. Song-rates and parental care by individual male stonechats (Saxicola torquata). Anim. Behav. **30**: 245-252.

Hill, G. E. 1990. Female house finches prefer colourful males: sexual selection for a condition-dependent trait. Anim. Behav. **40**: 563-572.

Hill, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. Nature **350**: 337-339.

Hoelzer, G. A. 1989. The good parent process of sexual selection. Anim. Behav. 38: 1067-1078.

Kessel, B. 1957. A study of the breeding biology of the European Starling in North America. Am. Mid. Nat. 58: 257-331.

Knapp, R. A., and Kovach, J.T. 1991. Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus*. Behav. Ecol. 2: 295-300.

Lifjeld, J. T., and T. Slagsvold. 1986. The function of courtship feeding during incubation in the Pied Flycatcher *Ficedula hypoleuca*. Anim. Behav. 34: 1441-1453.

Manning, J. T. 1985. Choosy females and correlates of male age. J. Theor. Biol. **116:** 349-354.

Maynard Smith, J. 1987. Sexual selection - a classification of models. *In* Sexual selection: testing the alternatives. *Edited by* J. W. Bradbury and M. B. Andersson. John Wiley and Sons, Chichester. pp. 9-20.

Mountjoy, D. J., and Lemon, R. E. 1991. Song as an attractant for male and female European starlings, and the influence of song complexity on their response. Behav. Ecol. Sociobiol. 28: 97-100.

Niebuhr, V. 1981. An investigation of courtship feeding in Herring Gulls *Larus argentatus*. Ibis 123: 218-223.

Nisbet, I. C. T. 1973. Courtship feeding, egg-size and breeding success in Common Terns. Nature, **241:** 141-142.

Norris, K. J. 1990a. Female choice and the evolution of the conspicuous plumage coloration of monogamous male great tits. Behav. Ecol. Sociobiol **26:** 129-138.

Norris, K. J. 1990b. Female choice and the quality of parental care in the great tit *Parus major*. Behav. Ecol. Sociobiol **27:** 275-281.

Pinxten, R., and Eens, M. Polygyny in the European starling: effect on female reproductive success. Anim. Behav. **40**: 1035-1047.

Pinxten, R., Eens, M., and Verheyen, R. F. 1989. Polygyny in the European starling. Behaviour **111**: 234-256.

Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to Red-winged Blackbirds (Agelaius phoeniceus). Am. Nat. **114**: 77-100.

Searcy, W. A., and Andersson, M. 1986. Sexual selection and the evolution of song. Ann. Rev. Ecol. Syst. 17: 507-533.

Thornhill, R. 1981. Panorpa (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive efforts. Ann. Rev. Ecol. Syst. **12**: 355-386.

Tinbergen, J. M. 1981. Foraging decisions in Starlings (Sturnus vulgaris L.). Ardea **69**: 1-67.

Trivers, R. L. 1972. Parental investment and sexual selection. In Sexual selection and the descent of man, 1871-1971. Edited by B. Campbell. Aldine Press, Chicago. pp. 136-179.

Verheyen, R. F. 1980. Breeding strategies of the starling. In Bird problems in agriculture. Edited by R. I. Ingliss and C. J. Feare. British Crop Protection Council, Croydon. pp. 69-83.

Wallraff, H. G. 1953. Beobachtungen zur brutbiologie des Stares (Sturnus v. vulgaris L.) in Nürnberg. J. Ornithol. **94**: 36-67.

Wiggins, D.A., and Morris, R. D. 1986. Criteria for female choice of mates: courtship feeding and parental care in the Common Tern. Am. Nat. 128: 126-129.

Wright, J. and Cuthill, I. 1989. Manipulation of sex differences in parental care. Behav. Ecol. Sociobiol. 25: 171-181.

Wright, J. and Cuthill, I. 1990. Manipulation of sex differences in parental care: the effect of brood size. Anim. Behav. 40: 462-471.

Wright, J. and Cuthill, I. 1992. Monogamy in the European starling. Behaviour 120: 262-285.

GENERAL CONCLUSIONS

This thesis has highlighted some of the complexity involved in studying sexually selected traits. The song of the European Starling serves not just one but several distinctly different functions. First, Chapter 1 demonstrated a role for male song in intersexual selection by showing that song in itself is an effective attractant for female starlings. This simple attraction of females would presumably facilitate the pairing of males that sing and should be a potent force favouring the evolution of song. However, it is not clear that the extreme complexity of starling song has any particular relevance to this function of female attraction. The same basic function is suggested to apply to the much simpler songs of a great many other passerine species (Kroodsma and Byers 1991), and characteristics such as the volume of the song or its distinctness from the vocalisations of other species may be more relevant to female attraction than how many phrase types it contains.

The complexity of a male's song is relevant though in the second intersexual function of song discussed here, the assessment of a potential mate. Chapter 3 demonstrates that males with more complex song acquire mates more rapidly than do males with smaller repertoires. This may be the most important advantage to song complexity, as song in this species does seem to be directed primarily at females (Eens et al. 1993). However, Chapter 1 showed that song complexity also plays a potentially important role in intrasexual selection as well. Complex song was more effective than simple song in inhibiting males from entering a nest-box at which song was broadcast, and thus may have a significant influence on competition for nest-sites. Although male interactions involving song appear to be relatively uncommon (Eens et al. 1993, pers. obs.), if these interactions can potentially result in the loss of a nest-site to a competitor (and possibly forfeiting the opportunity to breed in that season), then intrasexual competition could also be an important force favouring the evolution of song complexity, even if such interactions occur at a low frequency.

This influence of repertoire size on the behaviour of intruding males occurs despite the fact that starling song in itself does not deter other males from approaching. Males were, in fact, attracted to playback of starling song. These results may seem contradictory initially, but it is important to bear in mind the distinction between the attraction and assessment functions of bird song. For both males and females, song by itself advertises the presence of a conspecific male. Females may be attracted if they are searching for a mate, while males may respond to the song because the singing male may be in possession of a suitable nesting cavity which could be usurped. After approaching the singer, the listener is able to judge the complexity of the song, and to use that information to make some assessment of the singer as a potential mate or competitor.

Chapter 2 indicates that one aspect of a male's quality that can be assessed by attending to the complexity of a starling's song is the age of the singer. Repertoire size continues to increase in this species even after an individual's second breeding season. If competitive ability increases with age this could explain the response of males to song complexity. For females, there are several potential aspects of quality that might be expected to correlate with age. One possibility that has been suggested is that older males may be better parents (Krebs and Kroodsma 1980, Searcy and Andersson 1986). I examined this possibility in Chapter 4 and did not find any evidence that male starlings with larger repertoires contribute any more to incubation or to nestling feeding. This result indicates that female starlings do not appear to gain material benefits by choosing males with more complex song.

If mate choice for material benefits can be eliminated in this case, then other hypotheses for the evolution of sexually selected traits through female choice must be considered as possible explanations. The major alternatives are Fisherian runaway selection and various 'good genes' models of sexual selection (Bradbury and Andersson 1987). Fisherian runaway selection does not appear to be a likely explanation for the evolution of song complexity in starlings for several reasons. First, the use of song complexity in intrasexual interactions suggests that it is not an arbitrary character but is likely to reflect some aspect of male quality. Second, the increase in repertoire size with age indicates that variation in song complexity will not be strongly linked to any potential genetic variation in the trait, thus making it difficult for genetic covariance to develop between the trait and the female preference. Third, females are likely to experience direct costs as a result of choosing males on the basis of repertoire size, including the costs involved in assessing males and the costs of missed opportunities, such as not choosing males that have superior nest sites. These costs will limit the conditions under which Fisherian sexual selection can operate (Harvey and Bradbury 1991).

A possible alternative to Fisherian sexual selection is the age-indicator model (Manning 1985). This model suggests that older males are preferred because they have demonstrated their superior fitness through their longevity, and will contribute their high quality genes to their offspring. The preference of female starlings for males with complex song is consistent with this model, but determining whether the offspring of these males actually do have higher fitness is likely to be difficult. No one study will resolve the intense debate surrounding the various models of sexual selection, but the results of this thesis suggest that further serious consideration of good genes models is warranted, and in particular the age-indicator model.

REFERENCES

Bradbury, J. W., and M. B. Andersson. 1987. Sexual selection: testing the alternatives. John Wiley and Sons, Chichester.

Eens, M., R. Pinxten, and R. F. Verheyen. 1993. Function of the song and song repertoire in the European starling (*Sturnus vulgaris*): an aviary experiment. Behaviour 125: 51-66.

Harvey, P. H., and J. W. Bradbury. 1991. Sexual selection. Pp. 203-233 in J. R. Krebs and N. B. Davies (eds.) Behavioural Ecology. Blackwell Scientific Publications, London.

Krebs, J. R., and D. E. Kroodsma. 1980. Repertoires and geographical variation in bird song. Adv. Study Behav. 11: 143-177.

Kroodsma, D. E., and B. E. Byers. 1991. The function(s) of bird song. Am. Zool. 31: 318-328.

Manning, J. T. 1985. Choosy females and the correlates of male age. J. Theor. Biol. 116: 349-354.

Searcy, W. A., and M. B. Andersson. 1986. Sexual selection and the evolution of song. Ann. Rev. Ecol. Syst. 17: 507-533.