

THE UNIVERSITY OF CALGARY

SONG DIALECTS AND MATE CHOICE BY WHITE-CROWNED SPARROWS,
ZONOTRICHIA LEUCOPHRYS

BY

GLEN DEAN CHILTON

A DISSERTATION

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA

MARCH, 1993

© GLEN DEAN CHILTON 1993



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

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 0-315-83115-4

Name GLEN CHILTON

Dissertation Abstracts International is arranged by broad, general subject categories. Please select the one subject which most nearly describes the content of your dissertation. Enter the corresponding four-digit code in the spaces provided.

ZOOLOGY

SUBJECT TERM

0472

SUBJECT CODE

U·M·I

Subject Categories

THE HUMANITIES AND SOCIAL SCIENCES

COMMUNICATIONS AND THE ARTS

Architecture 0729
Art History 0377
Cinema 0900
Dance 0378
Fine Arts 0357
Information Science 0723
Journalism 0391
Library Science 0399
Mass Communications 0708
Music 0413
Speech Communication 0459
Theater 0465

EDUCATION

General 0515
Administration 0514
Adult and Continuing 0516
Agricultural 0517
Art 0273
Bilingual and Multicultural 0282
Business 0688
Community College 0275
Curriculum and Instruction 0727
Early Childhood 0518
Elementary 0524
Finance 0277
Guidance and Counseling 0519
Health 0680
Higher 0745
History of 0520
Home Economics 0278
Industrial 0521
Language and Literature 0279
Mathematics 0280
Music 0522
Philosophy of 0998
Physical 0523

Psychology 0525
Reading 0535
Religious 0527
Sciences 0714
Secondary 0533
Social Sciences 0534
Sociology of 0340
Special 0529
Teacher Training 0530
Technology 0710
Tests and Measurements 0288
Vocational 0747

LANGUAGE, LITERATURE AND LINGUISTICS

Language
General 0679
Ancient 0289
Linguistics 0290
Modern 0291
Literature
General 0401
Classical 0294
Comparative 0295
Medieval 0297
Modern 0298
African 0316
American 0591
Asian 0305
Canadian (English) 0352
Canadian (French) 0355
English 0593
Germanic 0311
Latin American 0312
Middle Eastern 0315
Romance 0313
Slavic and East European 0314

PHILOSOPHY, RELIGION AND THEOLOGY

Philosophy 0422
Religion
General 0318
Biblical Studies 0321
Clergy 0319
History of 0320
Philosophy of 0322
Theology 0469

SOCIAL SCIENCES

American Studies 0323
Anthropology
Archaeology 0324
Cultural 0326
Physical 0327
Business Administration
General 0310
Accounting 0272
Banking 0770
Management 0454
Marketing 0338
Canadian Studies 0385
Economics
General 0501
Agricultural 0503
Commerce-Business 0505
Finance 0508
History 0509
Labor 0510
Theory 0511
Folklore 0358
Geography 0366
Gerontology 0351
History
General 0578

Ancient 0579
Medieval 0581
Modern 0582
Black 0328
African 0331
Asia, Australia and Oceania 0332
Canadian 0334
European 0335
Latin American 0336
Middle Eastern 0333
United States 0337
History of Science 0585
Law 0398
Political Science
General 0615
International Law and
Relations 0616
Public Administration 0617
Recreation 0814
Social Work 0452
Sociology
General 0626
Criminology and Penology 0627
Demography 0938
Ethnic and Racial Studies 0631
Individual and Family
Studies 0628
Industrial and Labor
Relations 0629
Public and Social Welfare 0630
Social Structure and
Development 0700
Theory and Methods 0344
Transportation 0709
Urban and Regional Planning 0999
Women's Studies 0453

THE SCIENCES AND ENGINEERING

BIOLOGICAL SCIENCES

Agriculture
General 0473
Agronomy 0285
Animal Culture and
Nutrition 0475
Animal Pathology 0476
Food Science and
Technology 0359
Forestry and Wildlife 0478
Plant Culture 0479
Plant Pathology 0480
Plant Physiology 0817
Range Management 0777
Wood Technology 0746
Biology
General 0306
Anatomy 0287
Biostatistics 0308
Botany 0309
Cell 0379
Ecology 0329
Entomology 0353
Genetics 0369
Limnology 0793
Microbiology 0410
Molecular 0307
Neuroscience 0317
Oceanography 0416
Physiology 0433
Radiation 0821
Veterinary Science 0778
Zoology 0472
Biophysics
General 0786
Medical 0760

EARTH SCIENCES

Biogeochemistry 0425
Geochemistry 0996

Geodesy 0370
Geology 0372
Geophysics 0373
Hydrology 0388
Mineralogy 0411
Paleobotany 0345
Paleoecology 0426
Paleontology 0418
Paleozoology 0985
Palynology 0427
Physical Geography 0368
Physical Oceanography 0415

HEALTH AND ENVIRONMENTAL SCIENCES

Environmental Sciences 0768
Health Sciences
General 0566
Audiology 0300
Chemotherapy 0992
Dentistry 0567
Education 0350
Hospital Management 0769
Human Development 0758
Immunology 0982
Medicine and Surgery 0564
Mental Health 0347
Nursing 0569
Nutrition 0570
Obstetrics and Gynecology 0380
Occupational Health and
Therapy 0354
Ophthalmology 0381
Pathology 0571
Pharmacology 0419
Pharmacy 0572
Physical Therapy 0382
Public Health 0573
Radiology 0574
Recreation 0575

Speech Pathology 0460
Toxicology 0383
Home Economics 0386

PHYSICAL SCIENCES

Pure Sciences
Chemistry
General 0485
Agricultural 0749
Analytical 0486
Biochemistry 0487
Inorganic 0488
Nuclear 0738
Organic 0490
Pharmaceutical 0491
Physical 0494
Polymer 0495
Radiation 0754
Mathematics 0405
Physics
General 0605
Acoustics 0986
Astronomy and
Astrophysics 0606
Atmospheric Science 0608
Atomic 0748
Electronics and Electricity 0607
Elementary Particles and
High Energy 0798
Fluid and Plasma 0759
Molecular 0609
Nuclear 0610
Optics 0752
Radiation 0756
Solid State 0611
Statistics 0463
Applied Sciences
Applied Mechanics 0346
Computer Science 0984

Engineering
General 0537
Aerospace 0538
Agricultural 0539
Automotive 0540
Biomedical 0541
Chemical 0542
Civil 0543
Electronics and Electrical 0544
Heat and Thermodynamics 0548
Hydraulic 0545
Industrial 0546
Marine 0547
Materials Science 0794
Mechanical 0548
Metallurgy 0743
Mining 0551
Nuclear 0552
Packaging 0549
Petroleum 0765
Sanitary and Municipal 0554
System Science 0790
Geotechnology 0428
Operations Research 0796
Plastics Technology 0795
Textile Technology 0994

PSYCHOLOGY

General 0621
Behavioral 0384
Clinical 0622
Developmental 0620
Experimental 0623
Industrial 0624
Personality 0625
Physiological 0989
Psychobiology 0349
Psychometrics 0632
Social 0451



Nom _____

Dissertation Abstracts International est organisé en catégories de sujets. Veuillez s.v.p. choisir le sujet qui décrit le mieux votre thèse et inscrivez le code numérique approprié dans l'espace réservé ci-dessous.



SUJET

CODE DE SUJET

Catégories par sujets

HUMANITÉS ET SCIENCES SOCIALES

COMMUNICATIONS ET LES ARTS

Architecture	0729
Beaux-arts	0357
Bibliothéconomie	0399
Cinéma	0900
Communication verbale	0459
Communications	0708
Danse	0378
Histoire de l'art	0377
Journalisme	0391
Musique	0413
Sciences de l'information	0723
Théâtre	0465

ÉDUCATION

Généralités	515
Administration	0514
Art	0273
Collèges communautaires	0275
Commerce	0688
Économie domestique	0278
Éducation permanente	0516
Éducation préscolaire	0518
Éducation sanitaire	0680
Enseignement agricole	0517
Enseignement bilingue et multiculturel	0282
Enseignement industriel	0521
Enseignement primaire	0524
Enseignement professionnel	0747
Enseignement religieux	0527
Enseignement secondaire	0533
Enseignement spécial	0529
Enseignement supérieur	0745
Évaluation	0288
Finances	0277
Formation des enseignants	0530
Histoire de l'éducation	0520
Langues et littérature	0279

Lecture	0535
Mathématiques	0280
Musique	0522
Orientation et consultation	0519
Philosophie de l'éducation	0998
Physique	0523
Programmes d'études et enseignement	0727
Psychologie	0525
Sciences	0714
Sciences sociales	0534
Sociologie de l'éducation	0340
Technologie	0710

LANGUE, LITTÉRATURE ET LINGUISTIQUE

Langues	
Généralités	0679
Anciennes	0289
Linguistique	0290
Modernes	0291
Littérature	
Généralités	0401
Anciennes	0294
Comparée	0295
Médiévale	0297
Moderne	0298
Africaine	0316
Américaine	0591
Anglaise	0593
Asiatique	0305
Canadienne (Anglaise)	0352
Canadienne (Française)	0355
Germanique	0311
Latino-américaine	0312
Moyen-orientale	0315
Romane	0313
Slave et est-européenne	0314

PHILOSOPHIE, RELIGION ET THÉOLOGIE

Philosophie	0422
Religion	
Généralités	0318
Clergé	0319
Études bibliques	0321
Histoire des religions	0320
Philosophie de la religion	0322
Théologie	0469
SCIENCES SOCIALES	
Anthropologie	
Archéologie	0324
Culturelle	0326
Physique	0327
Droit	0398
Économie	
Généralités	0501
Commerce-Affaires	0505
Économie agricole	0503
Économie du travail	0510
Finances	0508
Histoire	0509
Théorie	0511
Études américaines	0323
Études canadiennes	0385
Études féministes	0453
Folklore	0358
Géographie	0366
Gérontologie	0351
Gestion des affaires	
Généralités	0310
Administration	0454
Banques	0770
Comptabilité	0272
Marketing	0338
Histoire	
Histoire générale	0578

Ancienne	0579
Médiévale	0581
Moderne	0582
Histoire des noirs	0328
Africaine	0331
Canadienne	0334
États-Unis	0337
Européenne	0335
Moyen-orientale	0333
Latino-américaine	0336
Asie, Australie et Océanie	0332
Histoire des sciences	0585
Loisirs	0814
Planification urbaine et régionale	0999
Science politique	
Généralités	0615
Administration publique	0617
Droit et relations internationales	0616
Sociologie	
Généralités	0626
Aide et bien-être social	0630
Criminologie et établissements pénitentiaires	0627
Démographie	0938
Études de l'individu et de la famille	0628
Études des relations interethniques et des relations raciales	0631
Structure et développement social	0700
Théorie et méthodes	0344
Travail et relations industrielles	0629
Transports	0709
Travail social	0452

SCIENCES ET INGÉNIERIE

SCIENCES BIOLOGIQUES

Agriculture	
Généralités	0473
Agronomie	0285
Alimentation et technologie alimentaire	0359
Culture	0479
Élevage et alimentation	0475
Exploitation des pâturages	0777
Pathologie animale	0476
Pathologie végétale	0480
Physiologie végétale	0817
Sylviculture et faune	0478
Technologie du bois	0746
Biologie	
Généralités	0306
Anatomie	0287
Biologie (Statistiques)	0308
Biologie moléculaire	0307
Botanique	0309
Cellule	0379
Écologie	0329
Entomologie	0353
Génétique	0369
Limnologie	0793
Microbiologie	0410
Neurologie	0317
Océanographie	0416
Physiologie	0433
Radiation	0821
Science vétérinaire	0778
Zoologie	0472
Biophysique	
Généralités	0786
Médicale	0760

Géologie	0372
Géophysique	0373
Hydrologie	0388
Minéralogie	0411
Océanographie physique	0415
Paléobotanique	0345
Paléocéologie	0426
Paléontologie	0418
Paléozoologie	0985
Palynologie	0427

SCIENCES DE LA SANTÉ ET DE L'ENVIRONNEMENT

Économie domestique	0386
Sciences de l'environnement	0768
Sciences de la santé	
Généralités	0566
Administration des hôpitaux	0769
Alimentation et nutrition	0570
Audiologie	0300
Chimiothérapie	0992
Dentisterie	0567
Développement humain	0758
Enseignement	0350
Immunologie	0982
Loisirs	0575
Médecine du travail et thérapie	0354
Médecine et chirurgie	0564
Obstétrique et gynécologie	0380
Ophtalmologie	0381
Orthophonie	0460
Pathologie	0571
Pharmacie	0572
Pharmacologie	0419
Physiothérapie	0382
Radiologie	0574
Santé mentale	0347
Santé publique	0573
Soins infirmiers	0569
Toxicologie	0383

SCIENCES PHYSIQUES

Sciences Pures	
Chimie	
Généralités	0485
Biochimie	0487
Chimie agricole	0749
Chimie analytique	0486
Chimie minérale	0488
Chimie nucléaire	0738
Chimie organique	0490
Chimie pharmaceutique	0491
Physique	0494
Polymères	0495
Radiation	0754
Mathématiques	0405
Physique	
Généralités	0605
Acoustique	0986
Astronomie et astrophysique	0606
Électronique et électricité	0607
Fluides et plasma	0759
Météorologie	0608
Optique	0752
Particules (Physique nucléaire)	0798
Physique atomique	0748
Physique de l'état solide	0611
Physique moléculaire	0609
Physique nucléaire	0610
Radiation	0756
Statistiques	0463
Sciences Appliquées Et Technologie	
Informatique	0984
Ingénierie	
Généralités	0537
Agriculture	0539
Automobile	0540

Biomédicale	0541
Chaleur et thermodynamique	0348
Conditionnement (Emballage)	0549
Génie aérospatial	0538
Génie chimique	0542
Génie civil	0543
Génie électronique et électrique	0544
Génie industriel	0546
Génie mécanique	0548
Génie nucléaire	0552
Ingénierie des systèmes	0790
Mécanique navale	0547
Métallurgie	0743
Science des matériaux	0794
Technique du pétrole	0765
Technique minière	0551
Techniques sanitaires et municipales	0554
Technologie hydraulique	0545
Mécanique appliquée	0346
Géotechnologie	0428
Matériaux plastiques (Technologie)	0795
Recherche opérationnelle	0796
Textiles et tissus (Technologie)	0794

PSYCHOLOGIE

Généralités	0621
Personnalité	0625
Psychobiologie	0349
Psychologie clinique	0622
Psychologie du comportement	0384
Psychologie du développement	0620
Psychologie expérimentale	0623
Psychologie industrielle	0624
Psychologie physiologique	0989
Psychologie sociale	0451
Psychométrie	0632

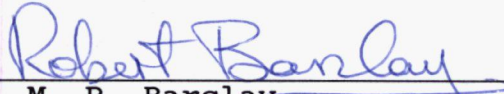


THE UNIVERSITY OF CALGARY
FACULTY OF GRADUATE STUDIES

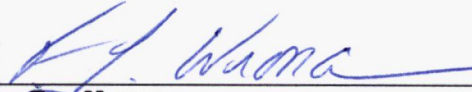
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a dissertation entitled "Song Dialects and Mate Choice by White-crowned Sparrows, Zonotrichia leucophrys", submitted by Glen Dean Chilton in partial fulfillment of the degree of Doctor of Philosophy.



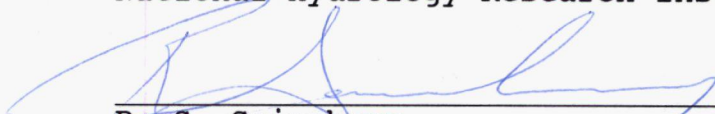
M. R. Lein, Supervisor
Department of Biological Sciences



R. M. R. Barclay
Department of Biological Sciences



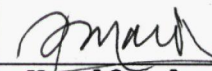
F. J. Wrona
National Hydrology Research Institute



R. S. Sainsbury
Department of Psychology



M. McDonald-Pavelka
Department of Anthropology



P. Handford, External Examiner,
University of Western Ontario

Date 1993-04-19

ABSTRACT

The songs of male White-crowned Sparrows (Zonotrichia leucophrys) show dialectal variation. It has been suggested that behavioral responses to this variation may decrease gene flow across boundaries between dialect populations. Females may discriminate against foreign singers when choosing from among potential mates.

Previous studies of dialect discrimination by female White-crowned Sparrows have produced conflicting results. Most have considered populations far from dialect boundaries. However, discrimination must operate at dialect boundaries if it is to reduce gene flow.

Two subspecies of White-crowned Sparrow (Z. l. oriantha and Z. l. gambelii), whose males sing distinctive songs in allopatry, intergrade in s.w. Alberta. Near the midpoint of the intergrade zone, the oriantha and gambelii song types are equally common. The early experiences and mate choice decisions of females in this mixed-dialect population are likely similar to those of females living near the boundaries between dialect populations. I studied mate choice behavior in this mixed dialect population to help resolve the conflict in earlier studies.

My field studies showed that females were no more

likely to choose different mates of the same song type in successive years than expected by chance. Further, despite earlier suggestions of paternal influence, an individual female was no more likely to choose mates of the same song type as her father than expected by chance. Females did not limit themselves to mates of a single song type.

Captive female White-crowned Sparrows, treated with estradiol, respond to song playback with a stereotyped copulation-solicitation display. As a group, females from the mixed-dialect population did not respond more strongly to either song type. Further, individuals did not respond more strongly to the song type of their chosen mate.

Captive females from the mixed-dialect population, treated with testosterone, were more likely to sing the oriantha song type than were males in nature. Females sang the same song type as their current mates more often than expected by chance. Perhaps females learn, and have the potential to perform, the song type of their first chosen mate, regardless of the song types of subsequent mates.

These results suggest that early experience with more than one song type prevents females in this mixed-dialect population from forming an irrevocable commitment to either. Discrimination by females is unlikely to reduce gene flow across dialect boundaries.

ACKNOWLEDGMENTS

In my early correspondence with Dr. M. Ross Lein, he asked me to consider the unique opportunities and challenges of the study of White-crowned Sparrows. The experience certainly has proven challenging. I would like to thank my thesis supervisor, Dr. Lein, for the professional challenge, support, and inspiration.

Results of this research are more meaningful as a result of the input from members of my thesis committee. I owe thanks to Dr. R. M. R. Barclay, Dr. R. S. Sainsbury, and Dr. F. J. Wrona. Dr. R. E. Owen and Dr. H. I. Rosenberg provided further challenge as additional members of my candidacy committee. Dr. M. Pavelka and Dr. P. Handford were gracious enough to serve on my dissertation defence committee.

Dr. John C. Wingfield of the University of Washington provided invaluable input regarding experimental protocol involving hormonal manipulation.

Funding for this study was provided by: the Frank M. Chapman Memorial Fund of the American Museum of Natural History; Sigma Xi's Grant-in-Aid of Research; a Student Research Award (Carnes Award) from the American Ornithologists' Union; an E. Alexander Bergstrom Award from

the Association of Field Ornithologists; a Thesis Research Grant from the University of Calgary Research Grants Committee; Taverner Award from the Society of Canadian Ornithologists; an NSERC Post-graduate Scholarship; and an NSERC Operating Grant to MRL. Results of a portion of this research were presented at a joint meeting of the American Ornithologists' Union and Cooper Ornithological Society (1990) and funding for travel was provided by the American Ornithologists' Union (Marcia Brady Tucker Travel Award), and the University of Calgary (Graduate Student Conference Travel Grant). I gratefully acknowledge the help of each agency.

This research would not have been possible without the dedicated efforts and camaraderie of many field assistants. I owe thanks to Jennifer Copping, Sharon Dechesne, Cathy Esser, Jocelyn Dilay, Robyn Maerz, Gail MacCrimmon, Leslie Metherell, Melody Michel, David Prescott, Paul Reinhardt, Christine Selbstaedt, Rena Vandenbos, and Robert Walker.

I am grateful to Fortress Mountain Skiing Inc. for access to the study area, and to the personnel of the Kananaskis Centre of Environmental Research for logistic support.

The contribution made to my personal and professional life by my lab mates cannot be overstated. Endless thanks

to Kevin Cash, L. Scott Johnson, David Prescott, Robert Walker, and their dear wives. Each has left their mark. Myra Wiebe and Matt Evans helped to keep me smiling.

There is all the world of difference between being treated like a family member, and actually being a family member. To Tim, Maryel, David, Kevin, and Sylvia Volk, I am the latter. Many thanks for Sunday dinners, clean clothes, and for Lisa.

I came to Calgary in search of wisdom, and found a wife. Does anyone deserve as much love and respect as I get from Lisa? We both seem to be bigger people together than either one could be alone. I cannot remember life before her, and cannot imagine life without her.

As a result of education and employment, my brothers and I have spent almost all of our adult lives apart. On those wonderful occasions when we are together, I find it hard to believe that we share only 50 % of our genes. Thanks to Reagan and Ross for showing their love in countless ways. You're good lads.

It would be unfair for a Mother to ask her sons to aim high unless she was willing to aim at the same target. My Mother has shown her sons the potential of the human spirit, and the responsibilities of those blessed with potential. Thanks Mum.

TABLE OF CONTENTS

	PAGE
APPROVAL PAGE	ii
ABSTRACT	iii
ACKNOWLEDGMENTS	v
TABLE OF CONTENTS	viii
LIST OF TABLES	xi
LIST OF FIGURES	xiii
RATIONALE AND GENERAL OBJECTIVES	1
LITERATURE REVIEW	3
Songbirds and Bird Song	3
Definitions	3
Functions of Bird Song	4
Ontogeny of Bird Song	5
Learning for Performance and Discrimination ..	14
Song Dialects	16
Definitions	16
Origin of Song Dialects	20
Maintenance of Song Dialect Boundaries	24
Proposed Functions of Song Dialects	26
Mate Selection and Song Dialects	33
General Biology of White-crowned Sparrows	39
SPECIFIC OBJECTIVES	44

MATERIALS AND METHODS	47
Study Areas and Populations	47
Fortress Mountain	47
Clearwater River	55
Field Techniques	58
Capture and Banding	58
Song Recording	61
Laboratory Techniques	62
Housing of Captive Birds	62
Estradiol Experiments	63
Testosterone Experiments	74
Song Analysis	75
Statistical Analysis	81
RESULTS	83
Consistency of Mate Choice by Song Type	83
Comparison of Songs of Fathers and Mates	86
Estradiol Experiments	89
Testosterone Experiments	95
Integration of Testosterone and Estradiol	
Experiments	109
DISCUSSION	111
Gene Flow Across Dialect Boundaries	111
Consistency of Mate Choice by Song Type	114
Comparison of Songs of Fathers and Mates	116

Estradiol Experiments	119
Testosterone Experiments	125
Integration of Results of Testosterone and Estradiol Experiments	145
Significance of Findings	147
LITERATURE CITED	153

LIST OF TABLES

TABLE	TITLE	PAGE
1.	Comparison of song types of mates of female White-crowned Sparrows in successive breeding seasons. <u>or.</u> indicates <u>oriantha</u> ; <u>ga.</u> indicates <u>gambelii</u> . Numbers in parentheses represent the comparison of song types of the first two mates of each female only	85
2.	Comparison of song types of fathers of individual female White-crowned Sparrows to those of their mates. Numbers in parentheses represent females in their first breeding season only	88
3.	Comparison of the number of copulation-solicitation displays, weighted for intensity of response, given by female White-crowned Sparrows from Fortress Mountain in response to the playback of the same conspecific song type in the first and fourth trials	90
4.	The number of copulation-solicitation displays, weighted for intensity of response, given by captive female White-crowned Sparrows taken from Fortress Mountain in 1988 and 1989 in response to the playback of three conspecific male song types. The song type of the mate of each subject is also given	92
5.	The number of copulation-solicitation displays, weighted for intensity of response, given by captive female White-crowned Sparrows taken from Clearwater River in 1989 in response to the playback of three conspecific male songs. The song type of the mate of each female is known or assumed to be the <u>gambelii</u> type	94
6.	Complex syllables and trills of captive female White-crowned Sparrows taken from Fortress Mountain between 1985 and 1989, treated with testosterone, and the song types of their mates. "?" indicates that complex syllable or trill was not judged without ambiguity. Two additional females were judged to have produced no complex syllable or trill	96

7. Distribution of complex syllables and trill types of banded male White-crowned Sparrows at Fortress Mountain, 1984 to 1988, and of captive female White-crowned Sparrows taken from Fortress Mountain, 1985 to 1989..... 103
8. Complex syllables and trills of female White-crowned Sparrows taken from Fortress Mountain between 1984 and 1989, and the song type of their mates..... 105
9. Comparison of extent of matching of complex syllables of female White-crowned Sparrows taken captive before and after egg-laying with the complex syllables of their mates. The first two rows represent matching of complex syllables, while the last two rows represent pairs mismatched by complex syllable type..... 107
10. Complex syllables and trills of songs of captive female White-crowned Sparrows taken from Clearwater River in 1989. Song type of their mates were known or assumed to be gambelii. CR-gambelii indicates a variant of the gambelii complex syllable common among male White-crowned Sparrows in the Clearwater River region. "?" indicates that the complex syllable or trill was not judged without ambiguity..... 108
11. Complex syllable types of songs of captive female White-crowned Sparrows taken from Fortress Mountain in 1988 and 1989, and the number of copulation-solicitation displays, weighted for intensity of response, given by those females in response to the playback of conspecific gambelii and oriantha male song. "?" indicates that the female's complex syllable was not judged without ambiguity..... 110

LIST OF FIGURES

FIGURE	TITLE	PAGE
1.	Audiospectrograms of songs of male White-crowned Sparrows recorded at Fortress Mountain. A - C. Songs typical of <u>Z. l. gambelii</u> . D - F. Songs typical of <u>Z. l. oriantha</u> . An audiospectrogram is a graphic representation of an audio event, encoding frequency (Y-axis) and duration (X-axis).....	49
2.	Audiospectrograms of "hybrid" songs of male White-crowned Sparrows recorded at Fortress Mountain.....	53
3.	Audiospectrograms of songs of male White-crowned Sparrows recorded at Clearwater River. A. <u>gambelii</u> song with a variant complex syllable. B - D. Songs identical to the <u>gambelii</u> songs heard at Fortress Mountain.....	56
4.	Audiospectrograms of <u>gambelii</u> songs of male White-crowned Sparrows used in playback to estradiol-treated captive female White-crowned Sparrows.....	66
5.	Audiospectrograms of <u>oriantha</u> songs of male White-crowned Sparrows used in playback to estradiol-treated captive female White-crowned Sparrows.....	68
6.	Audiospectrograms of songs of male White-crowned Sparrows from the Cypress Hills used in playback to estradiol-treated captive female White-crowned Sparrows.....	70
7.	Audiospectrograms of complex syllables of male White-crowned Sparrows used in categorizing the songs of testosterone-treated female White-crowned Sparrows. A. syllable typical of <u>gambelii</u> songs. B. syllable typical of <u>oriantha</u> songs. C. <u>gambelii</u> syllable variant from Clearwater River.....	77
8.	Audiospectrograms of trills of male White-crowned Sparrows used in categorizing the songs of testosterone-treated female White-crowned Sparrows. A. trill typical of <u>gambelii</u> songs. B. trill typical of <u>oriantha</u> songs.....	79

9. Audiospectrograms of songs of six captive female White-crowned Sparrows, treated with testosterone.
A - C. Complex syllables categorized as gambelii.
D - F. Complex syllables and trills categorized as oriantha. The downward-sweeping note at the beginning of songs A and C are artifacts resulting from voice-activated recording..... 97
10. Audiospectrogram of song of captive female White-crowned Sparrow, banded PK/W. The downward-sweeping note at the beginning of the song is an artifact resulting from voice-activated recording..... 100

RATIONALE AND GENERAL OBJECTIVES

The songs of male White-crowned Sparrows (Zonotrichia leucophrys), like those of many other species of songbird, show dialectal variation. Despite intensive study and extensive debate, the possible function of these song dialects has been a point of contention among behavioral ecologists. For instance, it is unclear what impact, if any, dialectal variation has on the choice of mates by female White-crowned Sparrows. The behavioral responses of females to males singing foreign dialects may limit the flow of genes across dialect boundaries (Marler and Tamura 1962; Nottebohm 1969, 1970; Baker 1983).

The objective of this study was to examine the influence of early experience with two distinctive song types on the subsequent mate choice decisions of female White-crowned Sparrows. The study population was located near the middle of the intergrade zone between the subspecies Z. l. oriantha and Z. l. gambelii. While each male sings only one song type, two songs were commonly heard at this location. Most previous studies of mate choice and dialects of White-crowned Sparrows (e.g., Baker et al. 1981a; Baker 1982; Baptista and Morton 1982) have investigated populations dominated by a single song type.

If behavioral responses to song dialects are to

isolate breeding populations, discrimination by females must operate at dialect boundaries where males singing foreign songs are most likely to be encountered (Baker and Mewaldt 1978). The early experiences of female White-crowned Sparrows in a mixed-dialect population may be similar to those of females born at or near dialect boundaries. Further, adult females in the mixed-dialect population will choose from among potential mates of more than one song type, which may be similar to the choices made by females at dialect boundaries. If so, then results of the current study may do more to resolve the debate concerning gene flow and dialect boundaries than have previous studies of single-song populations.

The current field studies were designed to: 1) determine whether the songs of males chosen as mates in successive breeding seasons by an individual female are of the same type more often than expected by chance; and 2) determine whether early experience with the paternal song type predisposes a female to choose, as mates, males who sing that song type.

Laboratory studies involving females from the mixed-dialect population were designed to: 1) document the behavioral responses of females to the playback of male songs of different dialects; and 2) compare the songs given by testosterone-treated females to the songs of their

chosen mates.

LITERATURE REVIEW

Songbirds and Bird Song

Definitions

The term "songbird" is a common colloquialism used to describe those passerine species whose syrinx is equipped with complex intrinsic musculature (Konishi 1985). In some classification schemes (e.g., Van Tyne and Berger 1971), these species constitute the suborder Passeres of the order Passeriformes.

Avian vocalizations are of two types: songs and calls. Songs are generally longer, louder, and more elaborate than calls, and are usually given by sexually mature males during the breeding season (Nottebohm 1975; Konishi 1985). While songs are often produced spontaneously, calls are usually given in response to specific stimuli and in specific situations (Nottebohm 1975; Konishi 1985). Even though the vocalizations of some non-passerine species have many of the features of songs, Konishi (1985) suggested that the term "bird song" be reserved for the complex vocalizations of passerines.

Functions of Bird Song

Although song may serve different functions in different species, the two principal functions of the songs of territorial males discussed most frequently are to attract potential mates (Wasserman 1977; Catchpole 1980, 1983; Ericksson and Wallin 1986; Temrin 1986) and to repel rival males (Baptista 1982; Catchpole 1983). The response of females to the unique features of songs of males of her species may serve as an isolating mechanism, preventing hybridization (Searcy et al. 1981; Baptista 1982; Payne 1986). Song may also stimulate development of reproductive organs (Baptista 1982) and synchronize reproductive behaviors of mates (Wasserman 1977; Morton et al. 1985). Song can provide information about the singer, including individual identity, deme membership, territorial and sexual status, and the probability of behaving sexually or aggressively (Emlen 1972; Brooks and Falls 1975a, b; Shields 1985).

In the majority of songbird species, females sing infrequently or not at all (Kern and King 1972; Baptista et al. in press). In those species in which singing by females is common, it may help solidify the pair bond or stimulate the breeding activity of the male (Kern and King 1972). In a number of species in which females sing

infrequently in the wild, they can be induced to sing via treatment with exogenous testosterone (e.g., White-crowned Sparrow [Kern and King 1972]; Chaffinch [Fringilla coelebs] [Kling and Stevenson-Hinde 1977]; Materials and Methods). Female Song Sparrows (Melospiza melodia) sing when interacting with female intruders, suggesting that song is a consequence of the high levels of male sex hormones that accompany such interactions (Arcese et al. 1988).

Ontogeny of Bird Song

Discussion of the theoretical consequences of avian vocal dialects requires an understanding of the ontogeny of song. In this regard, the most thoroughly-studied species is the White-crowned Sparrow (reviewed by Marler 1970a; Nottebohm 1970; Konishi 1978, 1985; Petrinovich 1985, 1988a; DeWolfe et al. 1989), and the following discussion pertains specifically to this species, except where noted.

In the first few months of his life, a young male White-crowned Sparrow hears the species-specific song of his father and other adult males. The memory of this song is retained by the young male for several months, apparently without any specific rehearsal, before producing a copy of that song the following spring (Marler and Peters 1982). In some cases, males begin to sing when a little

over 100 days of age. Initially the song is a quiet and fragmented version of the full adult song, and is termed "subsong". Nottebohm (1970) and Marler (1990) suggested the term "plastic song" to describe the version given following subsong which has most of the species' characteristics, but lacks the fine detail and stability of full song. Males "crystallize" a song with all the species-specific attributes at about 200 days. Typically each adult male White-crowned Sparrow has a single song pattern which is repeated throughout the breeding season with only minor variation. Having crystallized in the first breeding season, an individual's song is not likely to change in form thereafter (Nottebohm 1970, 1975; but see Kroodsma et al. 1985; and below).

Timing of the ontogeny of song of the nuttalli subspecies of White-crowned Sparrow is different from that of other subspecies. Z. l. nuttalli is non-migratory, and juveniles may begin to establish breeding territories as early as September of their first year (DeWolfe et al. 1989). Unlike members of migratory subspecies which apparently postpone subsong until the following spring, many Z. l. nuttalli young-of-the-year enter subsong in July, and may sing crystallized song as early as late September (DeWolfe et al. 1989).

In many non-songbird species, the acquisition of

species-specific vocalizations is independent of auditory experience (Konishi 1978). With the exception of interspecific brood parasites, male songbirds of all species studied to date must be able to hear and imitate the songs of conspecific adults to develop normal song. A bird isolated from tutors a few days after hatching, but able to hear its own voice, develops a song consisting of pure and sustained tones with some traits characteristic of the species (e.g., pitch and duration), but lacking fine detail.

If a young male is to acquire the species-specific song, he must be able to hear his own first renditions. If a male is deafened experimentally after exposure to song, but before he starts singing, he is likely to produce a song similar to that of a deafened naive subject. Deafening has little effect on song produced after the adult pattern of singing has become established (Konishi 1978).

For many species of songbirds, song learning is restricted to a period early in the individual's life. This "sensitive period" has been likened to the critical period for imprinting (Nottebohm 1970). Acoustic experience in the first ten days of life has proven to have little influence over subsequent behavior, and so this ten-day period generally defines the lower limit of the

sensitive period (Marler 1970a, b). In order to determine the upper limit, Marler (1970a) and Cunningham and Baker (1983) tutored captive White-crowned Sparrows (Z. l. nuttalli) with songs on audio tapes. "Normal song development" only occurred in those subjects exposed to conspecific song between 10 and 50 days of age (Marler 1970a), suggesting closure of the sensitive period at about 50 days of age (Cunningham and Baker 1983).

The sensitive phase of the White-crowned Sparrow may not be as brief as suggested by the studies above. Baptista and Petrinovich (1986) confirmed that males older than 50 days of age would not learn songs from audio tapes, but would copy the songs of live tutors well beyond this age. In a review of dialectal song variation (see below) and population structure of the Puget Sound subspecies (Z. l. pugetensis), Heinemann (1981) concluded that juvenile White-crowned Sparrows were not learning the fine details of song during the first 50 days of life, but rather during premigratory dispersal, while on the wintering ground, or even during territory establishment the following spring.

Like White-crowned Sparrows, Nightingales (Luscinia megarhychos) (Hultsch and Kopp 1989), Song Sparrows (Marler and Peters 1987), and Swamp Sparrows (Melospiza georgiana) (Marler and Peters 1988a) tend to imitate songs heard in the first 50 days of life in preference to those heard

later. The sensitive period of other species of songbirds may be considerably longer. Dittus and Lemon (1969) exposed young Northern Cardinals (Cardinalis cardinalis) to taped song of one type at 6 weeks of age, and to taped song of a second type at 22 weeks and 36 weeks. Several subjects produced song patterns most similar to those of the latter exposures.

Closure of the sensitive period with the onset of crystallized song has been described in such final terms as the "absolute irreversibility in song learning" (Konishi 1978). Even so, closure may not be as complete as once suspected. Male White-crowned Sparrows in their first breeding season have been observed to sing as many as four different song types early in the season, before settling on a single type and singing it to the exclusion of others thereafter (Baptista 1985a; DeWolfe et al. 1989; M. R. Lein, unpublished data; unpublished observations).

Timing of closure of the sensitive period may be influenced by the environment. Birds that hatch late in the breeding season probably receive less exposure to adult song than birds hatched earlier. Captive male Marsh Wrens (Cistothorus palustris) exposed to a photoperiod simulating a late season hatch were more likely to learn songs during the following spring than were those raised under conditions simulating an early season hatch (Kroodsma and

Pickert 1980). An environmentally-determined sensitive phase of this sort would allow dispersing juveniles some flexibility in learning a local song type after dispersal (Kroodsma and Pickert 1980). Similarly, captive male Zebra Finches (Taeniopygia guttata) whose auditory experience was restricted during the sensitive phase for song learning (35 to 65 days after hatching) were able to reproduce songs heard earlier or later (Slater et al. 1988)

The learning of song seems universal among songbirds. Even so, some species seem able to learn conspecific songs only. Captive male Swamp Sparrows will not learn the song of the closely-related and sympatric Song Sparrow from audio tape, even if Song Sparrow song elements are arranged in a temporal pattern typical of Swamp Sparrows (Marler and Peters 1977). This innate learning preference is apparently based on both syllable structure and temporal organization of phrases (Marler and Peters 1988b). Young Swamp Sparrows are able to discriminate between conspecific and allospecific songs on first exposure, and before the onset of their own adult song (Dooling and Searcy 1980).

Marler and Tamura (1964) were unable to teach young White-crowned Sparrows the taped songs of either Song Sparrows or Harris's Sparrows (Zonotrichia querula). While a young captive bird exposed only to the taped songs of an alien species is likely to produce a song most like that of

a social isolate (Marler and Tamura 1964), a live model may sometimes override this innate filter. Baptista (1985a) provided captive naive male White-crowned Sparrows with live, interacting Song Sparrow and Dark-eyed Junco (Junco hyemalis) tutors. Even though they were able to hear the songs of adult White-crowned Sparrows housed nearby, subjects learned only the songs of their interacting allospecific tutors.

In trying to interpret and integrate the role of acoustic experience and preference for conspecific song, some authors have described the song memory with reference to a "template" (e.g., Konishi 1978; Petrinovich 1988a). While the individual is sensitive to learning, an innate song template can filter out allospecific song as an inappropriate stimulus. At this time, the template crudely defines a limited number of song attributes. Experience refines the innate template, adding detail, including dialectal nuances (see below). As the young male begins to practice its song, it matches its own output to the refined template. As seen above, this template can be circumvented in some circumstances.

Most of the tenets of the species-specific sensory template hypothesis are based on experiments involving tutoring with audio tape. Because many subjects have shown themselves able to learn the songs of live allospecific

tutors, Baptista and Petrinovich (1984) and Petrinovich (1988a) have suggested that the hypothesis may have little applicability to birds learning songs in the wild.

Given that young songbirds must learn their species-specific song, the identity of the tutor can have profound implications for the study of song variation and population structure (Heinemann 1981). In Darwin's finches (Geospiza spp.) (Bowman 1979; Millington and Price 1985), and Bengalese Finches (Lonchura striata var. domestica) (Dietrich 1980), young birds seem to learn the song of their father in preference to the song of unrelated adults. In contrast, young Bobolinks (Dolichonyx oryzivorus) (Avery and Oring 1977), Saddlebacks (Philesturnus carunculatus rufaster) (Jenkins 1977), Indigo Buntings (Passerina cyanea) (Payne et al. 1987), and Corn Buntings (Miliaria calandra) (McGregor et al. 1988) seem inclined to learn the songs of unrelated adults. Slater et al. (1988) demonstrated that young male Zebra Finches learned their father's songs, but Eales (1989) showed that an interacting tutor could override the influence of early experience with the paternal song type.

Petrinovich (1988b) compared the songs of father-son pairs of White-crowned Sparrows (Z. l. nuttalli), and found no greater similarity between fathers and their sons than between sons and neighboring males. Further, there was no

particular similarity between the songs of male siblings. Baptista and Morton (1988) also found that the songs of adult Z. l. oriantha were no more similar to their fathers than to their neighbors. In contrast, Lein, Chilton and Walker (unpublished ms) found that most male White-crowned Sparrows in a zone of overlap between Z. l. oriantha and Z. l. gambelii sang their fathers' song type in preference to the other common song type. In this species, it seems as though general song characteristics may be learned from the father, while fine details are learned from unrelated individuals.

Treisman (1978) has suggested that song learning, song dialects (see below), and kin association may interact in a selectively meaningful way. Establishing a breeding territory among related individuals may serve to genetically isolate a breeding population. If genetic isolation is a profitable condition, there may be a selective advantage to both singer and listener to recognize their relatedness. If young males learn the peculiarities of their fathers' songs, they may be selected to settle next to kin by referring to the local song type, and to be less aggressive to others singing the same song type, as potential relatives (Treisman 1978). Trainer (1980) counters this theoretical treatment with results from experiments on White-crowned Sparrows, Song Sparrows,

and Northern Cardinals. In each species, males respond more aggressively to the playback of songs of their own dialect than to the playback of a different dialect, contrary to the predictions of Treisman's kin association model.

Our understanding of the ontogeny of songs of females is fragmentary, and where contrary evidence is not available, the process is assumed to be similar to the song development of males (Kroodsma et al. 1985). Kling and Stevenson-Hinde (1977) have provided evidence for parallels in the development of song in male and female Chaffinches.

When young captive female White-crowned Sparrows were tutored with conspecific song from audio tapes, their songs showed far less fidelity to the tutor's version than did the songs of their male counterparts (Cunningham and Baker 1983). Baptista and Petrinovich (1986) suggested that song learning by females may require more subtle cues, not yet identified and not available to captives.

Learning for Performance and Discrimination

McGregor and Avery (1986) emphasized the distinction between learning for performance and learning for discrimination. With regard to bird song, the former concerns the learning of songs to be performed by

territorial males in inter- and intra-sexual context. Experimental hormonal manipulation shows that females are clearly capable of learning songs for performance, even if they do not routinely perform those songs. The latter concerns the learning of songs by females for use in mate choice decisions, and by males for use in discriminating between the songs of familiar holders of neighboring territories, and strangers as potential usurpers.

The learning of songs for performance seems limited to a sensitive period early in life. In contrast, learning for discrimination probably continues throughout life, as individuals learn the subtle differences of songs of new mates and new neighbors each year. This difference raises the possibility that different mechanisms are responsible for these learning processes, including the hormonal control and the brain centres involved (McGregor and Avery 1986). McGregor and Avery (1986) predicted that differences in the sensitive periods of performance and discrimination learning will prove to be a general phenomenon among songbirds.

Song Dialects

Definitions

In many species of songbirds, the territorial songs of males show variation across the species' range. Males in different regions may produce songs with qualitative differences in a single note, a group of notes, or the entire song (Thielcke 1969), or in the rate of presentation of songs (e.g., Carolina Wren, Thryothorus ludovicianus, Borror 1956). Although not all species have been studied in sufficient detail, Mundinger (1982) suggested that variation in song is likely the typical state, rather than the exception.

The differences in songs of birds of different regions were first likened to the dialectal differences in human languages by Barrington (1773). Even though there is not a single accepted definition of the term dialect, it is now generally used in a more restricted sense than by Barrington.

Thielcke (1969) suggested that the term dialect be used to describe only those "vocal variants with a mosaic distribution". This definition implies that the song type shared by members of a particular population is delineated from other dialects by dialect boundaries (Mundinger 1982).

One song type is not replaced by another as a cline (Cunningham and Baker 1983; Wiens 1982). The variation in song observed between dialect populations should be considerably greater than the variation over a similar distance within a dialect population (Brenowitz 1985). The researcher will be able to distinguish between dialectal variation and clinal variation in the songs of a species only through extensive sampling across the transition zone. Thielcke (1969) suggests that 20 recording locations should be the minimum number to make the distinction.

Although the dialect boundary is a key component in the definition of dialects used by most researchers, it need not be a sharp boundary. Dialects may be separated by a "mixed zone" in which both dialect types are heard (Thielcke 1969).

The dialect boundary is not an explicit component of the definition of the term dialect used by all researchers. With reference to the Rufous-collared Sparrow (Zonotrichia capensis) Nottebohm (1969) defined dialects as "song differences between neighboring populations, or between populations of potentially interbreeding individuals". Dialectal variation is distinguished from "geographic variation" which represents "differences over long distances and between populations which normally do not mix" (Nottebohm 1969). Orejuela and Morton (1975) used

these distinctions in describing the dialects of White-crowned Sparrows (Z. l. oriantha).

However, distance is probably a poor criterion in the definition of song dialects. In some cases, a song is relatively invariant among populations hundreds of kilometers apart (e.g., Brown-headed Cowbird, Molothrus ater obscurus, Fleischer and Rothstein 1988). In other cases, several dialects have been described in a few square kilometers (e.g., Chaffinch, Baptista 1990). In White-crowned Sparrows, the size of dialect populations varies among subspecies (Baptista and King 1980).

Most territorial male White-crowned Sparrows in a region share one or more song features that differ discretely from those of males in adjacent populations (Cunningham and Baker 1983; Slater 1986, 1989; Baker 1987). Therefore the term "dialect" seems suitable in most cases for describing the unique song patterns characteristic of adjacent breeding populations of this species (Marler and Tamura 1964; Orejuela and Morton 1975; Mundinger 1982). The exception may be some Z. l. gambelii populations in which song types are not necessarily distributed in a mosaic pattern (DeWolfe et al. 1974; Austen and Handford 1991).

The term dialect has been applied to the songs of many species of bird, including Chaffinches (Marler 1952),

White-crowned Sparrows (Marler and Tamura 1962), Rufous-collared Sparrows (Nottebohm 1969), Northern Cardinals (Lemon 1971; Anderson and Conner 1985), Vesper Sparrows (Pooecetes gramineus) (Kroodsma 1972), Splendid Sunbirds, (Nectarinia coccinigaster) (Grimes 1974), Bobolinks (Avery and Oring 1977), Saddlebacks (Jenkins 1977), Corn Buntings (McGregor 1980; Pellerin 1982), Starlings (Sturnus vulgaris) (Adret-Hausberger 1982), Yellowhammers (Emberiza citrinella) (Møller 1982), Indigo Buntings (Payne 1983a), Village Indigobirds (Vidua chalybeata) (Payne 1985), Short-toed Tree Creepers (Certhia brachydactyla) (Thielcke and Wüstenberg 1985), Brown-headed Cowbirds (Fleischer and Rothstein 1988), and Yellow-rumped Caciques (Cacicus cela vitellinus) (Trainer 1989), and the calls of other species, including Pine Grosbeaks (Pinicola enucleator) (Adkisson 1981), Bobwhite Quail (Colinus virginianus) (Bailey and Baker 1982), and Black-capped Chickadees (Parus atricapillus) (Ficken et al. 1985). The term "dialect" has also been applied to the sounds of humpback whales (Megaptera novaeangliae) (Winn and Winn 1978), Gunnison's prairie dogs (Cynomys gunnisoni zuniensis) (Slobodchikoff and Coast 1980), cricket frogs (Acris crepitans) (Capranica et al. 1973), and honey bees (Apis mellifera) (Gould 1982).

Variation in the territorial songs of males has not been demonstrated for all species, and Thielcke (1969)

cites the Willow Tit (Parus montanus), Chiffchaff (Phylloscopus collybita), and Traill's Flycatcher (Empidonax traillii) as species without "geographic variation". Whitney (1989) found "striking similarity of song" in Wood Thrushes (Hylocichla mustelina) recorded in South Carolina and New York state.

Some authors describe song variation within dialect groups, labeled "subdialects" (Baptista 1975), "song neighborhoods" (Goodfellow and Slater 1986), or "microgeographic variation" (Trainer 1983). In the San Francisco Bay area of California, White-crowned Sparrow (Z. l. nuttalli) song dialects are distinguished on the basis of terminal syllables (Baptista 1975). Within a dialect, small groups of neighboring males produce songs with shared introductory phrases (Baptista 1985a). However, in the same subspecies, Trainer (1983) was unable to provide substantiating evidence of similarity of song at this level.

Origin of Song Dialects

A number of hypotheses have been proposed to explain the origin of vocal dialects. The first involves variation in the sound transmission properties of different habitats selecting for variation in species-specific song.

Dialectal variation in the song of the Northern Cardinal appears to be related to differences in vegetation density, such that each local song is best suited for long-distance communication with least distortion by the canopy foliage (Anderson and Conner 1985). Similarly, dialects of Darwin's Finches are characterized by frequencies and amplitudes that facilitate sound transmission with greatest integrity in particular habitats (Bowman 1979).

While the song dialect boundaries of Rufous-collared Sparrows are congruent with borders between vegetation types (Handford 1981, 1988; Loughheed et al. 1989; but see Handford and Loughheed 1991), neither Baptista (1977) nor Austen and Handford (1991) were able to find a correlation between habitat type and song type in the closely-related White-crowned Sparrow (Z. l. pugetensis and Z. l. gambelii respectively). Similarly, sound propagation properties appear to be of minor importance in establishing the song dialects of Yellowhammers (Møller 1982), and the dialects of Bobolinks seem to vary on a much smaller scale than differences in their breeding habitat (Avery and Oring 1977).

Song learning can be incorporated into this hypothesis of the origin of song dialects. The environment may act as an "acoustic filter", such that birds hear and learn those elements that transmit with least distortion (Hansen 1979).

The learning of songs in habitats with different sound-transmission properties could promote song variation between populations (Hansen 1979).

The second hypothesis for the origin of vocal dialects involves the demographics of small populations. Geographic isolation may facilitate dialect formation in two ways, both of which are behavioral analogs of genetic events. First, populations may be founded by a small number of individuals, bringing with them only a small portion of the genetic variability of the parent population, and could, by chance, differ significantly from it (Wilson and Bossert 1971). This phenomenon is known as the "founder effect", and its behavioral equivalent is the limited vocal repertoire of population founders. A small number of founders might bring with them only a small portion of song variation found in the parent population. By chance, vocal attributes of subsequent generations of the parent and offspring populations could differ substantially.

Second, the copying errors that may occasionally arise in song learning could be passed to following generations, and these variants could become increasingly common over time (Payne 1981). Examples of imperfect song learning are given by James (1976), Eberhardt and Baptista (1977), and Baker and Jenkins (1987). "Genetic drift" refers to chance fluctuation in allelic composition resulting from random

assortment of gametes in a small population (Hartl 1981). Its behavioral equivalent is the potential impact of a single tutor, whose odd song resulted from a copying error, on the songs produced by members of a small population in subsequent generations.

In summary, geographic variation in song is likely to arise when young birds learn the songs of older members of the population, imitation is not always perfect, and individuals tend to settle to breed in the same area as the adults they have chosen as tutors (Whitney 1989; Thielcke 1992).

The interaction of song learning and the geographic isolation of small populations has been used to explain the origin of vocal dialects of northern elephant seals (Mirounga angustirostris) (LeBoeuf and Petrinovich 1974), Song Sparrows (Eberhardt and Baptista 1977), and Pine Grosbeaks (Adkisson 1981). A computer simulation, using biologically realistic parameters, was designed to test the idea that dialects arise from song learning and copying errors. With an error rate of 10%, annual mortality of 10% to 40%, and an interacting population of 100 males, the results suggested that copying errors are unlikely to account for the origin of large dialect groups as seen in White-crowned Sparrows (Goodfellow and Slater 1986).

Maintenance of Song Dialect Boundaries

As described above, the period between ten and 50 days of life is often cited as the sensitive period for song learning by White-crowned Sparrows. Since the 50-day limit corresponds to a period of fidelity to the natal area, Baker et al. (1982a) and Cunningham and Baker (1983) concluded that White-crowned Sparrows should be predisposed to learn and perform their natal dialect. If young do not disperse far from their place of origin, the integrity of dialect boundaries will be preserved (Konishi 1965). If, however, the sensitive period for song learning is considerably longer than 50 days, as proposed by Baptista and Petrinovich (1986), and if songs are learned after dispersal from the natal area from resident territorial males, then dialect boundaries might be preserved regardless of dispersal distance.

Cunningham et al. (1987) considered the microgeographic song variation of White-crowned Sparrows (Z. l. nuttalli) in an effort to distinguish between predispersal and postdispersal song learning. In the former situation, sons should sing the same song types as their father, while in the latter, birds in their first breeding season should sing songs more similar to those of their territorial neighbors. Cunningham et al. (1987)

concluded that the pattern of song differences observed was most consistent with song learning before dispersal.

In another study of non-migratory Z. l. nuttalli, DeWolfe et al. (1989) found that major dispersal movements of young males may precede the earliest crystallized songs by two months. Unlike Cunningham et al. (1987), DeWolfe et al. (1989) found small "subdialect groups", consisting of small groups of neighboring males sharing a common song. The lab and field studies of DeWolfe and coworkers found that young males match the song type of their neighbors, suggesting that neighbors influence the song development of immature males attempting to establish territories. Baptista (1985b) claims that the accumulated evidence shows that young White-crowned Sparrows are capable of learning and performing songs heard after dispersal from their natal area, and that matching neighbor's songs may be selectively advantageous.

Evidence of post-dispersal song learning is less contested in studies of another songbird species. Young male Saddlebacks, seeking to establish a breeding territory some distance from their natal region, clearly conform to the local song pattern, perpetuating the existing dialect system (Jenkins 1977).

Proposed Functions of Song Dialects

Bird song dialects appear to be a consequence of vocal learning. Behavioral ecologists are split in their opinion of the possible evolutionary "function" of such variation. On one hand are those that see song dialects as a means by which populations are genetically structured. Marler and Tamura (1962) and Nottebohm (1969, 1970) suggested that behavioral responses to dialects may subdivide, and therefore genetically isolate, populations. If panmixia hinders adaptation to the local environment, behavioral responses to song dialects might isolate members of a population exposed to similar selective pressures (Nottebohm 1972). In this way, offspring are more likely to be genetically specialized to local conditions (Payne 1981). This model, as described by Baker and Cunningham (1985) and Shields (1985), requires an irrevocable commitment to the song heard before dispersal from the natal population. In this way, dialects provide information about deme membership and relatedness.

If the biotic or abiotic environments are subject to periodic fluctuations, a population that irreversibly commits itself to one genetic option may be at a selective disadvantage. Dialects may be a way to restrict gene flow and facilitate adaptation without an irrevocable commitment

to speciation (Nottebohm 1970). It can be argued that this scenario would require group-selection, and therefore cannot be resolved with our current understanding of natural selection.

Behavioral responses to dialect differences could limit gene flow between dialect populations in three ways (Baker and Mewaldt 1978). First, juveniles may constrain their dispersal with reference to dialect boundaries, settling within the region in which their natal dialect is sung. Secondly, both males and females may be more aggressive toward and (or) less cooperative with individuals from a distant population singing a foreign song. Young males might establish territories with less effort within the confines of their own dialect boundary. Finally, females might discriminate among potential mates, favoring males whose song matches her natal dialect. In this way, each female would be choosing mates whose genes are also adapted for the same local conditions under which she had been successfully raised (Wasserman 1979; Payne 1983b). Individual adaptation to specific regional conditions may be particularly valuable when a species is widely distributed over heterogeneous environments (Konishi 1965).

The paternal song may have a profound influence on the mate choice decisions of daughters (Møller 1982; Shields

1985). A female may be inclined to choose a mate whose song is like that of her father to ensure that the chosen mate is a local male similarly adapted to local conditions (Payne 1981), or to ensure genetic compatibility through the recognition of kin (Payne et al. 1987).

In their study of song and patterns of mating in the Great Tit (Parus major), McGregor and Krebs (1982) found results consistent with predictions of optimal outbreeding. A female apparently chooses mates whose songs display an intermediate degree of difference from her father, suggesting an optimal balance between inbreeding and outbreeding. Even so, the critical assumption that females learn the paternal song type was left untested (McGregor and Krebs 1982). The ability to recognize the paternal song type has been demonstrated in captive female Zebra Finches (Miller 1979). Having been raised by their parents for 35 days, females were subjected to the broadcast of two song types at 100 days of age. Females were more likely to approach a speaker broadcasting their fathers' songs than the songs of a different male, suggesting that females are able to discriminate among songs and recognize the paternal type, even after extended isolation from it (Miller 1979).

Within the framework of genetic structuring of populations, behavioral responses to song differences may serve to ensure outbreeding. In Saddlebacks, song types

are restricted to groups of two to eight males on contiguous territories (Jenkins 1977). A young male, attempting to establish a territory, will settle among unrelated individuals some distance from his father's territory, and adopt the local song pattern. Jenkins (1977) suggested that dialects may serve as a reference system, enabling Saddlebacks to avoid inbreeding.

Orejuela and Morton (1975), Avery and Oring (1977), Heinemann (1981), McGregor and Krebs (1982) and Balaban (1988) identified five conditions that must be satisfied if an individual is to be discriminated against because its song identifies it as having been born into a distant population: (1) there must be some reproductive advantage to discrimination between members of different populations when choosing between potential mates, either in genetic terms (above) or in terms of experience with local conditions; (2) there must have been sufficient time for discrimination to have evolved and become fixed in the population; (3) the female must learn her natal (generally her father's) song dialect, as does the male, and be able to distinguish it from other dialects; (4) most individuals must show fidelity to their population of origin; and (5) song differences must reliably reflect the singer's population of origin. Shields (1985) suggested that the final condition may not be an evolutionarily stable

strategy. If young males are frequently forced to disperse from their natal population, individuals that could defer song learning until after dispersal might be favored over those that cannot.

Song differences may also provide group structure in a non-genetic sense. In caciques, each song variant is unique to a breeding colony (Feeles 1977). The colony's song changes within and between seasons, and newcomers seem able to adopt the prevailing song. Feeles (1977) suggested that resident caciques may detect potential intruders by their foreign songs, and prevent their settlement. If song serves a "bonding" function in this species, then the colony-specific song may serve as a password, "helping to maintain a temporal community" (Feeles 1977).

In contrast to the view of dialects as a mechanism by which populations are genetically structured is the belief that dialects are an epiphenomenon (Andrew 1962; Jenkins 1977; Wiens 1982; Trainer 1983). From this perspective, individuals cannot attain greater fitness by interacting preferentially with those singing the local dialect. Song learning has evolved as a mechanism to ensure the transmission of species-specific song from one generation to the next, and dialects represent a functionless by-product of song learning, of no special consequence with regard to natural selection. Song learning may permit

sufficient variation in songs within a population to facilitate individual recognition, and this may be a selective benefit independent of population processes (Andrew 1962).

Baker and Cunningham (1985) argue that, under this scenario, population structure would be unstable, and that dialect integrity should eventually "dissolve" unless migration between dialect populations is restrained. Waser (1985) counters that the distribution of song types can be an unselected consequence of a limited sensitive period for song learning and aspects of population demographics, such as fidelity to the region of birth.

Milligan and Verner (1971) and Baptista and Morton (1982) warned that the investigator must demonstrate the ability of the subject to discriminate dialectal differences before attempting to evaluate the possible functional significance of those dialects. In order to demonstrate such an ability, one might quantify the responses given by birds in the wild to songs of different dialects. Milligan and Verner (1971) documented differential response of both male and female White-crowned Sparrows (Z. l. nuttalli) to the playback of their "native" and "non-native" dialects. For both genders, the response was weaker to the non-native dialect. For Starlings, recognition of whistled songs appears at two levels.

Individuals can recognize the conspecific song regardless of its dialect form, but are apparently also able to distinguish their own dialect from another (Adret-Hausberger 1982). Further, the ability to discriminate between dialects seems a reasonable assumption in light of a number of experiments (e.g., Brooks and Falls 1975a, b; Baker et al. 1981b; Baptista and Morton 1982) that have demonstrated the ability to discriminate among individuals within a dialect.

Also critical to an understanding of the possible function of song differences is the differentiation of the communicatory role of different song components (Pleszczynska 1980; Brenowitz 1985; Gottlieb 1985). It may be pointless to assign a function to dialect differences in a song component whose primary role is communication of individual identity (Brenowitz 1985). In trying to assign functions to various components of song, most studies have considered the responses of territorial males to song playback (Becker 1982). However, song also has an intersexual function, and surprisingly little is known about the features most important in pair formation (Becker 1982). An exception is the study of female Song and Swamp sparrows that treated subjects with estradiol and documented their postural responses to manipulated songs (Searcy et al. 1981).

Mate Selection and Song Dialects

Crow and Felsenstein (1968) and Burley (1983) define assortative mating in terms of mated pairs being more similar with regard to some phenotypic trait than if pairs had been selected at random from the population. Assortative mating results in greater genetic homozygosity, and greater population genetic variance (Johnston and Johnson 1989). Phenotypic similarity may be a direct consequence of genetic relatedness (i.e., members of a portion of a subdivided population share a common ancestry), or assortative mating may result from phenotypic similarity, in which case genetic relatedness is a consequence of similar phenotypes (Crow and Felsenstein 1968).

A classic example of assortative mating on the basis of a genetically-based phenotypic trait involves the Lesser Snow Goose (Chen caerulescens). This species has both blue and white color phases, and the trait is regulated by a single autosomal gene (Cooke et al. 1972). Individuals tend to mate with others of the same color phase, and parental color greatly influences mate choice by offspring (Cooke et al. 1972).

What then, is the meaning of the term assortative mating in regard to song, a learned characteristic? If

song type is a reliable indicator of the singer's genetic constitution, then song may serve as an easily-measured indicator of the genotype of many other traits. Konishi (1965) considered assortative mating from the perspective of song differences and mate choice by females. If the ability of a female to learn the dialectal nuances of song reflects an ability to discriminate between song dialects, and if this ability facilitates mating with males singing her natal dialect, then mating among members of the same dialect population may result. This could lead to appreciable inbreeding, facilitating adaptation to specific local conditions.

Given the potential genetic value of assortative mating, do members of species with song dialects choose mates on the basis of song type? Studies of species other than the White-crowned Sparrow provided limited positive evidence. The "gargle" call of Black-capped Chickadees is given throughout the breeding season in intra-pair interactions (Ficken et al. 1985). This call varies geographically, and playback experiments have demonstrated that males respond more to calls of their own dialect than to alien versions (Ficken et al. 1985). Since females also produce this call, and given the sexual nature of the call, Ficken et al. (1985) suggest that mating is unlikely among birds of different dialect groups.

Most male Corn Buntings in a population share a single song type (Hegelbach 1986). Males singing foreign dialects are able to establish territories, but are apparently unable to attract mates (Hegelbach 1986). Hegelbach (1986) suggested that females might maximize their reproductive success by avoiding foreign singers who would presumably be unfamiliar with local conditions.

The songs of male Zebra Finches of the allopatric Taeniopygia guttata guttata and T. g. castanotis show considerable subspecific difference (Clayton 1990). In captivity, members of these subspecies will hybridize, but mate assortatively if maintained as large captive colonies (Clayton 1990). When treated with estradiol, female Zebra Finches responded with more copulation-solicitation displays to the playback of songs of their own subspecies than to songs of either the other subspecies or a different species (Clayton and Pröve 1989; Clayton 1990).

Studies unable to demonstrate assortative mating on the basis of song type are more common. Payne (1973) found no clear evidence that captive female Paradise Whydahs were more attracted to playback of songs of their natal population than to other conspecific versions. Further, Payne (1983a) and Payne et al. (1987) found no evidence that the song dialects of Indigo Buntings correspond to deme membership, or that females mate assortatively by song

type or body size. In 38 of 42 cases, the songs of the father and the chosen mate of female buntings were dissimilar. Of the remaining four females, two were mated with their father (Payne et al. 1987). In their study of Medium Ground Finches (Geospiza fortis), Millington and Price (1985) found that females appear to choose mates at random with respect to song, avoiding neither extreme inbreeding nor extreme outbreeding. Fleischer and Rothstein (1988) studied two highly divergent subspecies of Brown-headed Cowbird (Molothrus ater obscura and M. a. artemisiae), each with a unique whistle given prior to copulation, a behavior that is likely to be important in mate choice. Members of these subspecies hybridize freely, in conflict with the suggestion that vocal differences lead to assortative mating (Fleischer and Rothstein 1988). In contrast to Hegelbach's (1986) findings, female Corn Buntings were not influenced by their father's song type when choosing between males of different song dialects (McGregor et al. 1988).

Studies of the impact of dialectal song variation on patterns of mating in White-crowned Sparrows have provided contradictory results. Studies by Baker and coworkers have observed behaviors consistent with assortative mating by song type. Baker captured nestling, fledgling, and adult female Z. l. oriantha (Baker 1982), and fledgling female Z.

l. nuttalli (Baker 1983), and tutored them with the local song type. After implanting them with estradiol, he documented their behavioral responses to the playback of local and foreign dialects. In both studies, the local dialect was a more potent stimulus in eliciting copulation-solicitation displays. Once implanted with testosterone, subjects captured as adults sang the local dialect rather than a song of some other population, suggesting that these subjects had learned the local song during an early critical period (Baker et al. 1981a). These studies suggest that early experience with a particular song type predisposes a young female White-crowned Sparrow to be sexually responsive to that song type as an adult (Baker et al. 1981a). They also suggest that a male singing an alien dialect would be at a disadvantage in attracting a mate (Baker et al. 1981a).

A number of studies have provided evidence contrary to that of Baker and coworkers; that is, that mating of White-crowned Sparrows is not assortative by song type. Baptista and Morton (1982) induced singing in female Z. l. oriantha, and found that their song type matched that of their mates in only two of ten cases. Petrinovich and Baptista (1984) compared the songs of male Z. l. nuttalli and their testosterone-treated mates, and found no evidence of assortative mating by song type. Further, the reproductive

success of those pairs whose songs were dissimilar was no lower than pairs whose songs were of the same type (Petrinovich and Baptista 1984). Petrinovich (1988b) considered 32 female White-crowned Sparrows for whom the songs of both father and mate were known, and found no tendency for individual females to choose a mate that sang the same song as her father. Male White-crowned Sparrows singing foreign songs in populations dominated by a single song type are apparently able to attract mates and breed successfully (Baptista 1985a).

If behavioral responses to dialect differences were to prevent mating between members of different dialect populations, then substantial genetic differentiation between populations might result (Baker 1981; Baker et al. 1982c). In an electrophoretic analysis of protein variation in White-crowned Sparrows, Baker et al. (1982c) concluded that "the observed genetic isolation is caused primarily by dialects, not geographic distance". However, Zink and Barrowclough (1984) reanalysed the data of Baker et al. (1982c) and found no greater genetic differentiation between populations that span dialect boundaries than between sites within dialects. Zink and Barrowclough (1984) felt it unlikely that restricted gene flow between dialects resulted in genetic differentiation among dialect populations in White-crowned Sparrows.

The data of Baker et al. (1982c) was also reconsidered by Hafner and Petersen (1985) who found that "genetic transition boundaries are not exactly coincident with dialect transition boundaries". If song dialects and genetic differentiation arise in allopatry, then coincident genetic and dialect boundaries might be viewed as artifacts of subsequent secondary contact, and not as a consequence of assortative mating (Hafner and Petersen 1985).

Summarizing the studies of allozyme frequencies and mate-choice behavior of White-crowned Sparrows available at the time, Baptista (1985a) concluded that the literature provided no clear-cut evidence that the song dialects of White-crowned Sparrows caused reduced gene flow between populations or that mating was assortative on the basis of song type.

General Biology of White-crowned Sparrows

The American Ornithologists' Union Check-list of North American birds, 5th edition (A.O.U. 1957) recognizes five subspecies of White-crowned Sparrow. These are differentiated on the basis of body size and color of the bill and plumage. These subspecies likely diverged in glacial refugia during the Pleistocene glaciation (Rand 1948). The breeding and non-breeding distributions of

these subspecies were described by Cortopassi and Mewaldt (1965).

A number of authors have provided detailed descriptions of the biology of one or more subspecies of White-crowned Sparrow. These include Taverner (1926; Z. l. gambelii), Clement (1968; leucophrys) and Blanchard DeWolfe (1968a, b, c, d; nuttalli, gambelii, oriantha, and pugetensis, respectively). Blanchard (1941) compared Z. l. pugetensis and Z. l. nuttalli in terms of breeding and wintering ranges, morphometrics, plumage, molt, sexual and nesting behaviors, and behavioral and environmental correlates of the gonadal cycle. DeWolfe and DeWolfe (1962) described the preferred breeding habitat and aspects of the breeding cycle of Z. l. oriantha in California. Banks (1964) described the geographic variation in morphometrics, plumage, and molt of each subspecies of White-crowned Sparrow. Morton (1992) described the premigratory behavior and natal dispersal of Z. l. oriantha. The following account is drawn from these sources.

The principal behavioral differences among subspecies of White-crowned Sparrow are the tendency to migrate and the timing of breeding. Z. l. nuttalli is non-migratory. Members of northern populations of Z. l. pugetensis are migratory, while those in the southern part of its range

are not. Members of non-migratory populations breed earlier in the year than migratory individuals. Members of all other subspecies are migratory.

By comparing localities in which Z. l. oriantha was known to breed with nearby localities in which it did not, DeWolfe and DeWolfe (1962) described five habitat features apparently essential to successful reproduction in this species: grass, bare ground, water, dense shrub or scrub conifers, and tall conifers. The specific nature of these features (e.g., species composition) varies with locality, but the arrangement of grass and other vegetation with respect to bare ground is apparently invariant (DeWolfe and DeWolfe 1962). White-crowned Sparrows are particularly common in habitats where the surface has been disturbed by fire or the activities of man.

Monogamy is the most common mating system in all subspecies. Mates are retained between breeding seasons in Z. l. nuttalli, while in other subspecies females choose anew from among available males each spring.

In migratory subspecies, males arrive in the breeding areas before females, and establish breeding territories that are defended against intrusion by conspecific males. The male chooses the specific site for its first breeding attempt shortly after arrival in the spring, and returns to breed on that site in successive years.

With infrequent exceptions, each male has a single song type which it repeats throughout the breeding season. The rate of song production is highest between 5:00 and 10:00, with a lesser evening peak. Individual sessions involve 15 to 20 minutes of uninterrupted singing at four to six songs per minute. The rate of song production decreases after mating, but increases again if the male loses its mate. While males sing less frequently late in the breeding season than they do before attracting a mate (Clement 1968; unpublished observations), they have been observed to sing in the vicinity of their nests after feeding nestlings (Cunningham and Baker 1983). This behavior may ensure transmission of songs between generations.

The territorial song of all subspecies of White-crowned Sparrow is about 2 s in duration, and between 2.6 and 7.2 kHz in pitch. Songs are composed of a series of pulsed whistles, trills, buzzes, and more complex syllables. Representative original audiospectrograms of male songs have been given by Marler and Tamura (1962, 1964; nuttalli), DeWolfe et al. (1974; gambelii) Orejuela and Morton (1975; orianta), Baptista (1977; pugetensis), Lein (1979; orianta), Baptista and King (1980; orianta), Pleszczynska (1980; leucophrys), Baker et al. (1981b; nuttalli), Baker and Thompson (1985; nuttalli), Lein and

Corbin (1990; oriantha and gambelii), and Austen and Handford (1991; gambelii). These audiospectrograms indicate the variation in song among individuals within subspecies and between subspecies.

Females build nests, incubate 3 to 5 eggs, brood young, and are responsible for the majority of feeding of the young for 2 to 3 days after hatching. Males contribute to feeding thereafter. Young leave the nest between 9 and 12 days after hatching. Broods are usually divided between the parents at this time. Family units may remain on the natal territory or may wander up to several kilometers from it. Young become independent of parental care at about 50 days.

Some members of the subspecies nuttalli and pugetensis are multi-brooded, while members of the other subspecies tend to be single-brooded.

Mean natal dispersal distances of White-crowned sparrows were reported as 555 m (male) and 614 m (female) (Z. l. nuttalli; Baker and Mewaldt 1978), and as 1172 m (male) and 1719 m (female) (Z. l. oriantha; Morton 1992).

SPECIFIC OBJECTIVES

My working model considers the song dialects of White-crowned Sparrows to be a consequence of song learning during an early sensitive period. Dialect boundaries are maintained by fidelity to the natal area, and by the ability of those yearling males who settle in a different dialect population to adopt the local song type. In a mixed-dialect population, experience with two song types during the sensitive period for song learning precludes an irrevocable commitment to one song type over another. In this scenario, song dialects have no special consequence for population processes.

This model generates two predictions regarding the behavior of adult female White-crowned Sparrows born into the mixed-dialect population. The first is that females choose from among potential mates on the basis of characteristics other than song type. From this it follows that:

Prediction 1. An individual female will not consistently choose mates singing the same song type in successive breeding seasons. The song type of her mate in a given year will match the song type of her mate in the previous year no more often than expected by chance.

Prediction 2. An individual female will show no special

tendency to choose mates with the same song type as her father. The songs of father and chosen mate will be of the same type no more often than expected by chance.

Prediction 3. When an individual female is induced to sing with exogenous testosterone, her song will be of the same type as her mate's no more often than expected by chance.

The second prediction generated by the model concerns the sexual posturing of captive females in response to the playback of conspecific male song of different types. This bioassay has been used extensively as it eliminates such confounding variables as territory quality and the rate and volume of singing (Catchpole 1987). Assuming that young females in the mixed-dialect population hear both song types when most sensitive to song learning, the model suggests that their early experience should preclude a subsequent sexual commitment to one song type over the other. It follows that:

Prediction 4A. The frequency and intensity of solicitation displays given by a female from the mixed-dialect population to the two local song types will be independent of her mate's song type. **4B.** The frequency and intensity of her responses will also be independent of her own song type. **4C.** As a group, females from this population will not solicit more to one of the common song types than to the other. Subjects will solicit less to an unfamiliar

song from a distant conspecific population.

Prediction 5. In contrast to subjects from the mixed-dialect population, females from a single-song population will solicit more to the familiar local song type than to unfamiliar song types.

MATERIALS AND METHODS

Study Areas and Populations

Fortress Mountain

Two subspecies of White-crowned Sparrow intergrade over an extensive zone in southwest Alberta (Rand 1948; Banks 1964). Birds with black lores, indicative of Z. l. oriantha, dominate populations in the southern-most portion of this intergrade zone, while gray-lored birds of the Z. l. gambelii subspecies dominate more northerly populations (Lein and Corbin 1990). The transition from one lore color to the other is gradual, occurring over a distance of greater than 400 km between the United States border and Banff National Park. In allopatry, males of these subspecies sing songs of different dialects. In contrast with the gradual change in lore color, populations in which both the oriantha and gambelii song types are common are found only in a 50 to 100 km region at the centre of the intergrade zone (Lein and Corbin 1990).

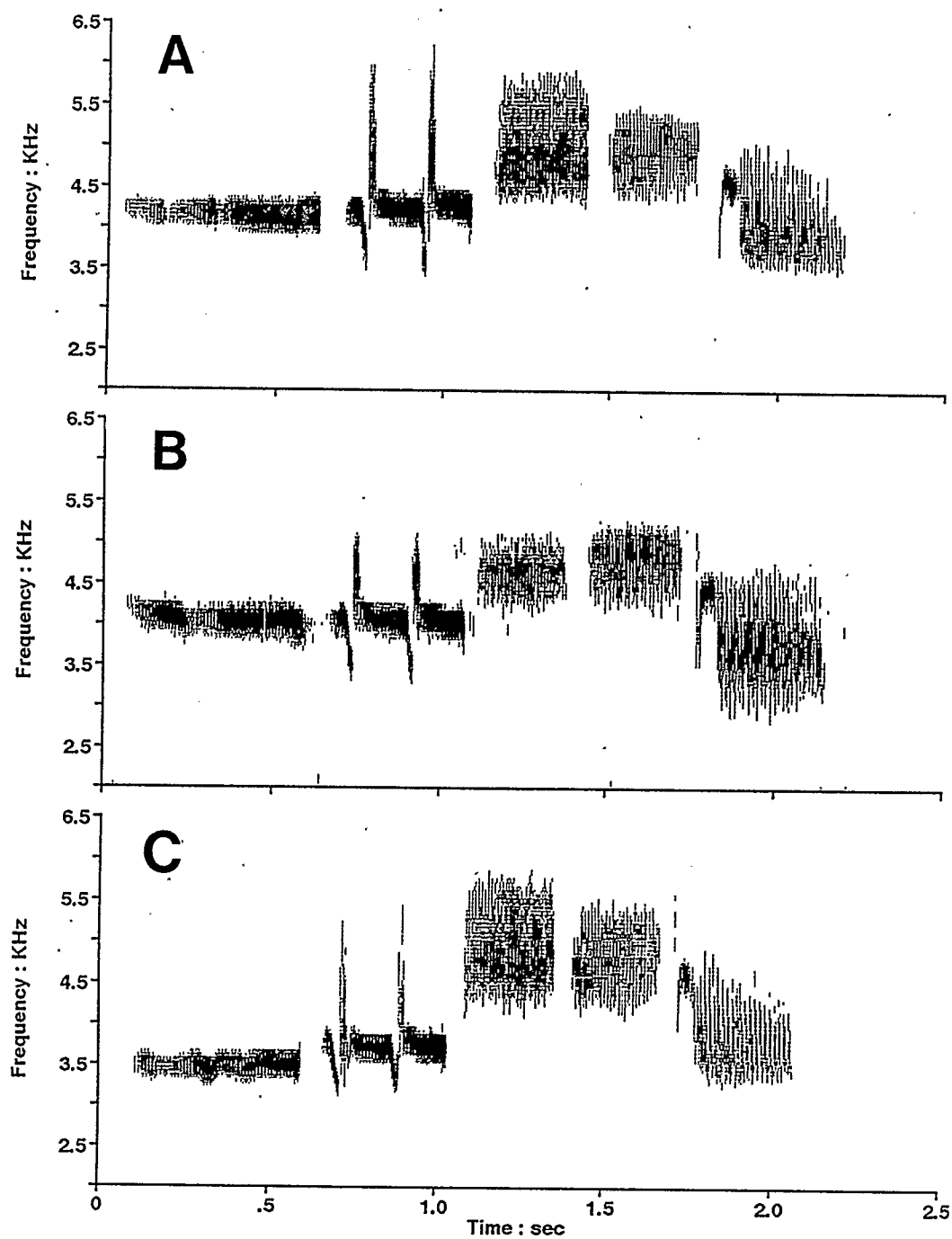
Fortress Mountain (50° 50'N, 104° 10'W) is near the midpoint of the zone of subspecific intergrade. Lein and Corbin (1990) found that 48.6% of White-crowned Sparrows at Fortress Mountain had black lores, 37.8% had predominantly

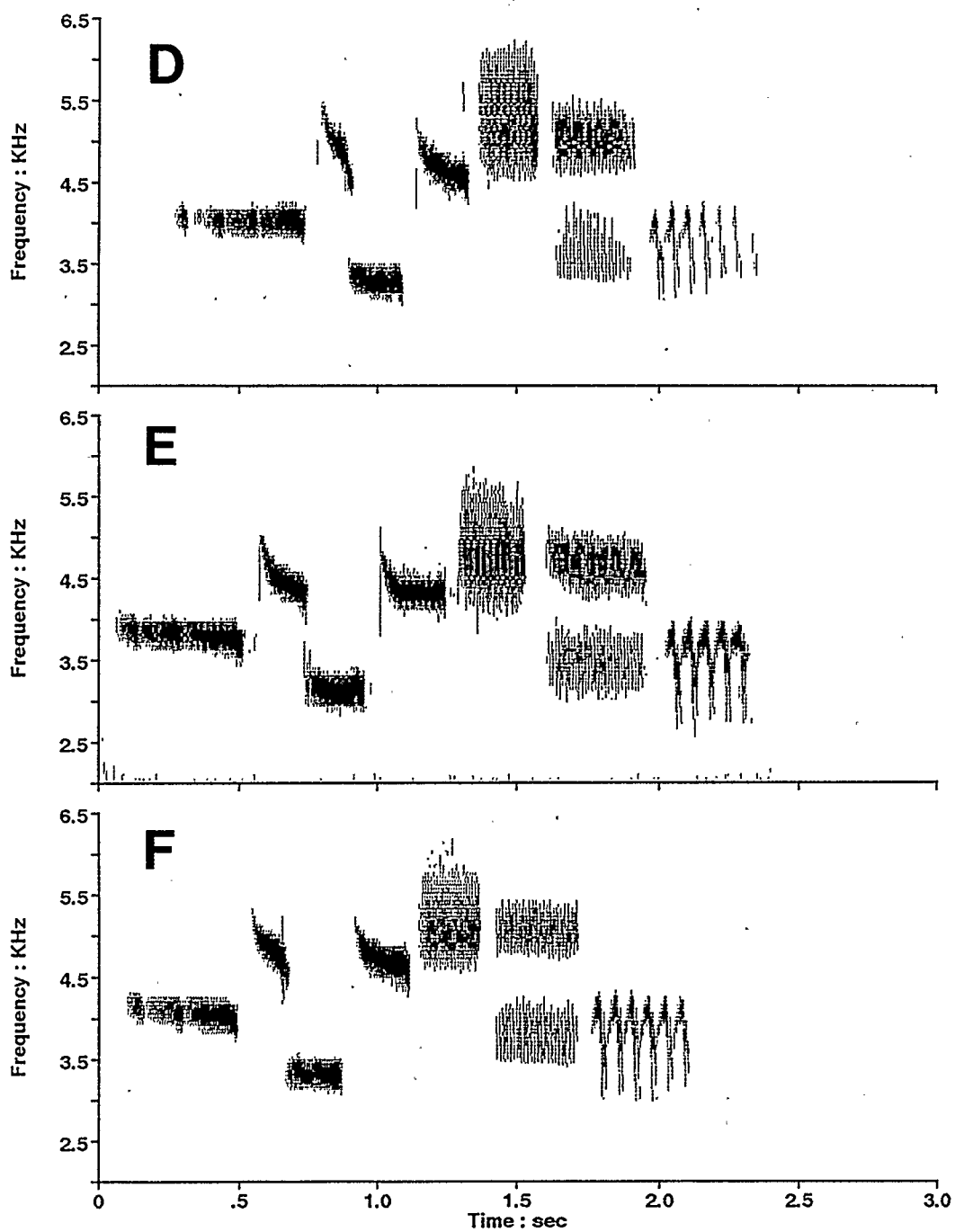
gray lores, while the remainder had lores of intermediate coloration.

Most male White-crowned Sparrows at Fortress Mountain sing one of two song types. Because these songs are identical to songs given by males in allopatric Z. l. oriantha and Z. l. gambelii populations adjacent to the contact zone, I hereafter refer to these song types as oriantha and gambelii (Fig. 1). Both song types begin with an introductory whistle, followed by a complex syllable, two buzzes, and a terminal trill. The complex syllable of the oriantha song is a high-low-high triplet of whistles, while a pulsed whistle at one frequency is characteristic of the gambelii song. The oriantha terminal trill is composed of a number of distinct hook-shaped notes, while the gambelii trill is composed of a very brief syllable, followed by a buzz. These song types also vary slightly in the form of the two buzzes, but not enough to be used as a reliable diagnostic feature. The differences between song types are much greater than the variation within a song type (Lein, unpublished data), and each male's song can be assigned to type by a human observer in the field without error.

The third most common song type at Fortress Mountain ends in a gambelii-type terminal trill, but is otherwise identical to the oriantha song type, and is referred to

Figure 1. Audiospectrograms of songs of male White-crowned Sparrows recorded at Fortress Mountain. A - C. Songs typical of Z. l. gambelii. D - F. Songs typical of Z. l. oriantha. An audiospectrogram is a graphic representation of an audio event, encoding frequency (Y-axis) and duration (X-axis).





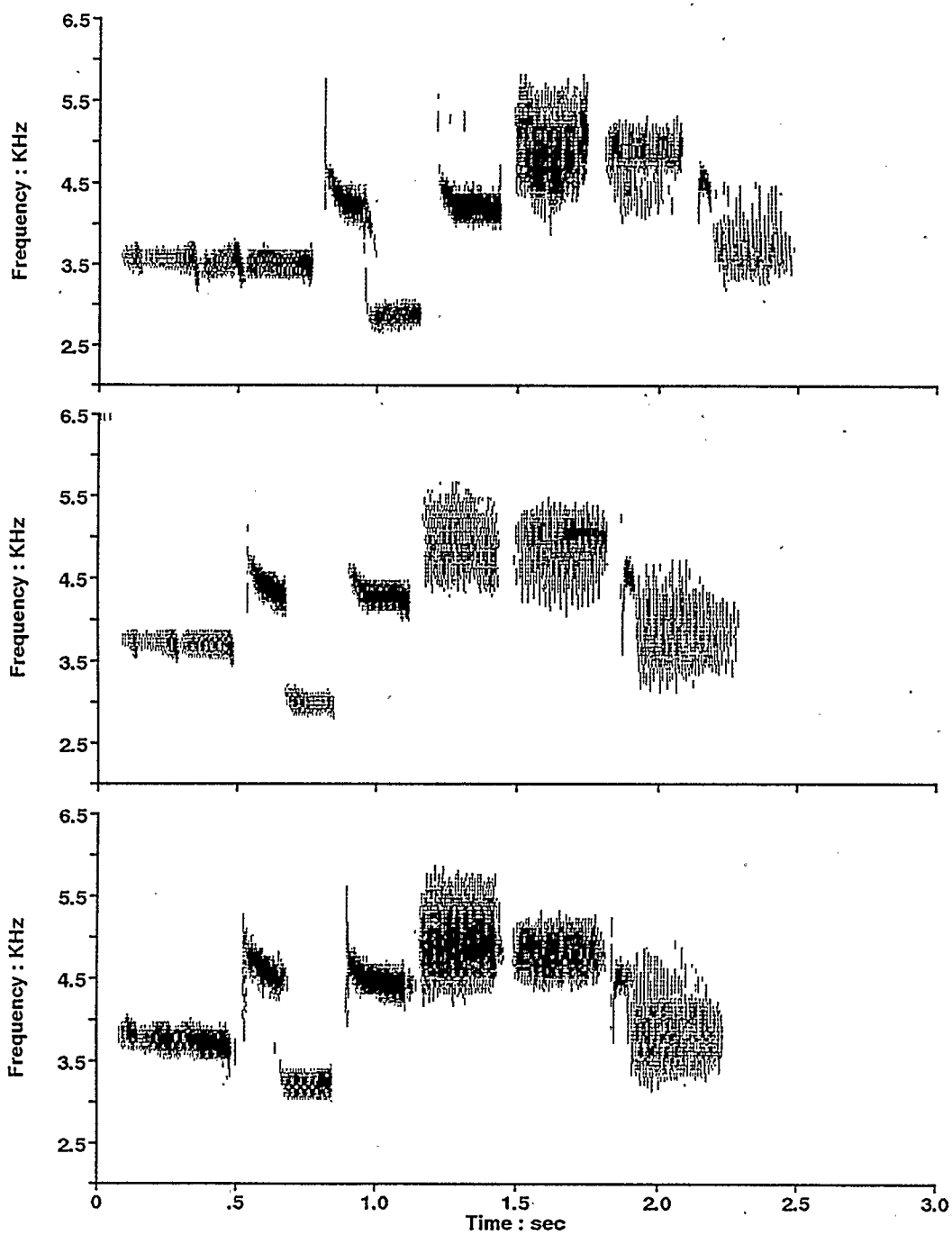
hereafter as the "hybrid" song (Fig. 2).

A few males at Fortress Mountain produced songs that did not fit into any of the preceding categories. Some males produced songs consistently lacking terminal trills, while other males sang more than one song type. One male sang a song characteristic of populations in Idaho and Oregon (L. F. Baptista personal communication).

The Fortress Mountain population of White-crowned Sparrows has been studied intensively by M. R. Lein and coworkers since 1984. I was involved in the study of this population through four breeding seasons, 1987 through 1990.

The study area includes ca. 275 ha of vegetated hillsides and valley bottoms at an elevation of 1900 to 2200 m. This area, formerly covered by mature coniferous forest, was burned by a major fire in 1936 (Fryer and Johnson 1988). Regrowth of forest is slow in this area, and the habitat is still relatively open, dominated by small scattered trees and shrub growth. Further removal of shrub and trees for a ski resort has accentuated the openness of the habitat. Drainage is poor, and standing water persists throughout the breeding season in all parts of the study site. These conditions provide all the features described by DeWolfe and DeWolfe (1962) as essential for breeding populations of White-crowned

Figure 2. Audiospectrograms of "hybrid" songs of male White-crowned Sparrows recorded at Fortress Mountain.



Sparrows.

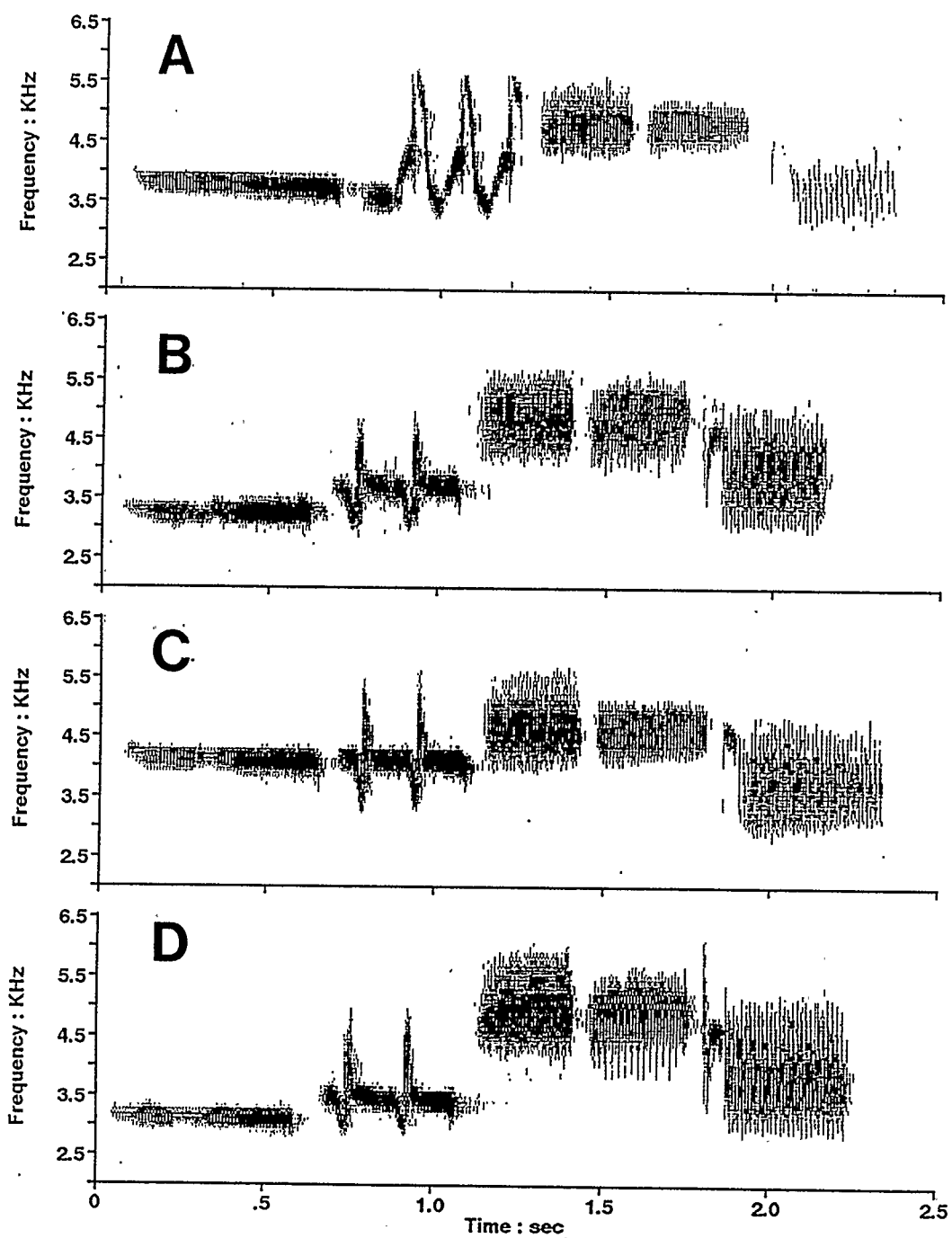
Clearwater River

I captured twelve female White-crowned Sparrows from an area around the Mile Seven Recreation Area in the Clearwater River Region of central Alberta ($52^{\circ} 00'N$, $115^{\circ} 22'W$) between 29 May and 9 June 1989. In contrast to the mixed-dialect population of White-crowned Sparrows at Fortress Mountain, all males of the Clearwater River region sang the same song type. In laboratory experiments, the responses of females from this single-song population served as a control for the responses of females from Fortress Mountain.

Of the forty or so males heard in 1989, most produced songs identical to the gambelii type heard at Fortress Mountain. The remainder produced a gambelii song with a variant complex syllable (Fig. 3) which is heard on occasion in other populations of Z. l. gambelii (M. R. Lein unpublished data; unpublished observations).

Females from the Clearwater River study site did not demand the same criteria for capture as females from Fortress Mountain (see below). Because male White-crowned Sparrows in this region were heard to sing only the gambelii song type, it was assumed that each female would

Figure 3. Audiospectrograms of songs of male White-crowned Sparrows recorded at Clearwater River. A. gambelii song with a variant complex syllable. B - D. Songs identical to the gambelii songs heard at Fortress Mountain.



be mated to a male singing that type, and so any female from this population was deemed suitable for this study. No effort was made to determine their position in the breeding sequence.

Field Techniques

Capture and Banding

Between 1984 and 1989, 327 male and 201 female adult White-crowned Sparrows were trapped and banded on the Fortress Mountain study site. Individuals were identified by one numbered aluminum leg band (U.S. Fish and Wildlife Service) and three colored plastic leg bands, in combinations unique to the individual. Most adults were trapped for banding in three-celled drop-door traps. The centre cell of these traps housed a captive male White-crowned Sparrow, while both lateral cells had a treadle-released door. Playback of recorded male songs or of vocalizations of interacting adult White-crowned Sparrows drew territorial males into the vicinity of the trap, while the presence of the decoy and seeds beneath the trap drew them into a drop-door cell. Many female White-crowned Sparrows were captured along with their mates in drop-door traps early in the breeding season. Those females that

were not trapped and banded before nesting were captured in mist nets late in the nesting sequence (see below).

To be deemed suitable for laboratory study, female White-crowned Sparrows from Fortress Mountain had to fulfill a number of criteria. All individuals were the product of a previous breeding season, had not been banded previously, and were paired at the time of capture. The song type of the mate of each female had been documented at the time of capture. An effort was made to procure an equal number of females whose mates sang oriantha and gambelii song types. In order to minimize the impact on ongoing research, females were captured from the periphery of the study site.

Some females were captured before nesting began, while the remainder were taken late in the nestling period. In the pre-nesting period, individuals were assumed to be mated to one another when they were observed in persistent social association. Males of many passerine species "guard" their mates against extra-pair copulation during the female's fertile period (Westneat et al. 1990). Females often joined their mates in responding to conspecific intruders in the pre-nesting period, and this behavior facilitated capture. As for capture for color banding (see above), females were taken in drop-door traps, having been lured into the vicinity by playback of songs

and interaction vocalizations.

During the nesting sequence, individuals were assumed to be mated to one another when both fed nestlings and "scolded" intruders at a nest. Though unbanded before capture, possible confusion with females on adjacent territories at the time of capture could be eliminated by noting individual differences in lore color.

Females were less likely to enter drop-door traps when feeding nestlings, and so were caught in mist nets. A net was erected adjacent to the nest, and the taped distress calls of nestlings were broadcast. Parents generally responded to playback by flying toward the nest, usually causing both male and female to become tangled in the fine netting.

The following numbers of females were taken captive: six between 25 June and 13 July 1985; five between 4 and 18 July 1986; ten between 2 and 15 July 1987; eleven between 11 June and 9 July 1988; and eight between 1 June and 20 July 1989. A few of these individuals died in captivity before testing. M. R. Lein directed the capture of females in 1985 and 1986.

All females from the Clearwater River region were captured with a drop-door trap, having been lured into the area with gambelii song playback. I took twelve females captive from this population between 29 May and 9 June

1989.

As part of the ongoing work by M. R. Lein, 335 active White-crowned Sparrow nests were located, and 777 nestlings were banded at Fortress Mountain between 1984 and 1988. Nestlings were banded six to ten days after hatching, receiving aluminum and colored plastic leg bands in combinations unique to the nest of origin. As a result, the parents of almost all banded nestlings that returned to breed on the study site were known.

Song Recording

The songs of virtually all territorial male White-crowned Sparrows on the study site since 1984 have been recorded on audio tape. Songs were recorded on Sony LNX, HF-S, HFX, and FeCr cassette tapes, using Sony TCM-5000, TCM-5000EV, TC-142, or TC-D5 cassette tape recorders, with Gibson EPM 650 parabolic microphones or Sony PBR 330 parabolic reflectors and AKG D190E and Sony ECM 33P microphones.

Laboratory Techniques

Housing of Captive Birds

Captive females were housed individually in wire mesh cages, 40 cm on each side, in the animal-holding facilities of the Kananaskis Centre for Environmental Research (1988 subjects) and the Faculty of Science (all other years).

In the studies of Baker and coworkers involving female songbirds treated with estradiol (see below), subjects were maintained on a short-day photoperiod, usually 8 L : 16 D for a period between six weeks (Baker 1982) and four months (Baker 1983), followed by a long day photoperiod, usually 16 L : 8 D.

In this study, female White-crowned Sparrows captured in 1985, 1986, and 1987 were taken from a photoperiod of 17 L : 7 D to one of 8 L : 16 D over a period of ten weeks, and held on these short days for two months. Subjects were then switched to 16 L : 8 D for one month before testing. At the time of testing, subjects were transferred from their home cages to smaller cages in acoustic isolation chambers (Industrial Acoustics Company Inc.)

Too few of the subjects captured between 1985 and 1987 responded to the playback of conspecific songs with copulation-solicitation displays (see below) for meaningful

interpretation. After consultation with J. C. Wingfield of the University of Washington, the lighting and housing protocols were altered for subjects captured in 1988 and 1989.

From the time of capture, these subjects were maintained on a photoperiod that approximated the natural state at the time of capture, that is 17 L : 7 D. Estradiol experiments began within one month of capture. Each subject was moved in its home cage from the communal holding facility to the testing room at least six hours before the test session to allow acclimatization.

For females captured between 1985 and 1987, testosterone experiments preceded estradiol experiments, while those captured in 1988 and 1989 were subjected to the estradiol experiments first.

Estradiol Experiments

A number of techniques have been employed in an effort to quantify the sexual potency of songs of different types. Among these are quantification of a variety of behaviors in response to the playback of song to subjects in the wild (Petrinovich and Patterson 1981), and the alteration of the captive subject's heart rate in response to the playback of song (Zimmer 1982). Care must be taken in drawing

conclusions from the results of these procedures; females in the wild do not respond to song playback as consistently as do males, and laboratory responses of this sort may not have a sexual component.

A more popular experimental approach used to address the relationship between sexual preference and song type involves a stereotyped copulation-solicitation display (see below) commonly given by females of many bird species at the time of copulation (Baker et al. 1981a). Captive females, treated with exogenous estradiol, respond to the playback of conspecific song with this display, even in the absence of other specific stimuli (Kern and King 1972; Searcy et al. 1981). The number and intensity of these displays has been used as a measure of the efficacy of different song types to stimulate females sexually (e.g., Baker 1982, 1983; Baker et al. 1981a, 1982b, 1986, 1987; Catchpole et al. 1984; Wasserman and Cigliano 1991).

In this study, β -estradiol (Sigma Chemical E-8875) was packed into implant housings made of 10 mm lengths of Dow Corning Silastic brand medical grade tubing (0.058 in. inside diameter, 0.077 in. outside diameter), sealed at both ends by Dow Corning Silastic brand medical adhesive silicone type A. A single implant was slipped under the skin of each subject through a small incision in the right or left lateral apterium (featherless tract) seven days

prior to the first playback trial. Implants were removed after the final playback trial.

Playback experiments used the two song types commonly heard at Fortress Mountain, plus a third type unique to a disjunct population of White-crowned Sparrows in the Cypress Hills of southeast Alberta (Lein 1979), employed as a control. Each song type was represented by a single song recorded from each of two different males. Both gambelii songs (Fig. 4) were recorded at Fortress Mountain; one on 2 July 1978, the other on 12 July 1979. Both oriantha songs (Fig. 5) were recorded at Fortress Mountain; one on 2 July 1978, the other on 12 July 1979. Both Cypress Hills songs (Fig. 6) were recorded at Reesor Lake, Cypress Hills Provincial Park, on 7 and 8 June 1978.

Original recordings were made on Scotch Brand AV177 1/4" audio tape at 7 1/2 inches per second with a Nagra 4.2 reel-to-reel tape recorder and a Gibson EPM parabolic microphone. Audio tape with each song pair was inserted into a 30-s endless loop of 1/4" tape and copied to a Realistic (43-402a) 30-s outgoing message tape from a Nagra 4.2 recorder through a high-pass filter (2000 Hz) to a Sony TCM-5000 cassette recorder.

During testing, these tapes were played through a Marantz PMD 220 cassette recorder and JVC S-A3 speaker. The signal strength of playback was 77 db (re:20uPa SPL @

Figure 4. Audiospectrograms of gambelii songs of male White-crowned Sparrows used in playback to estradiol-treated captive female White-crowned Sparrows.

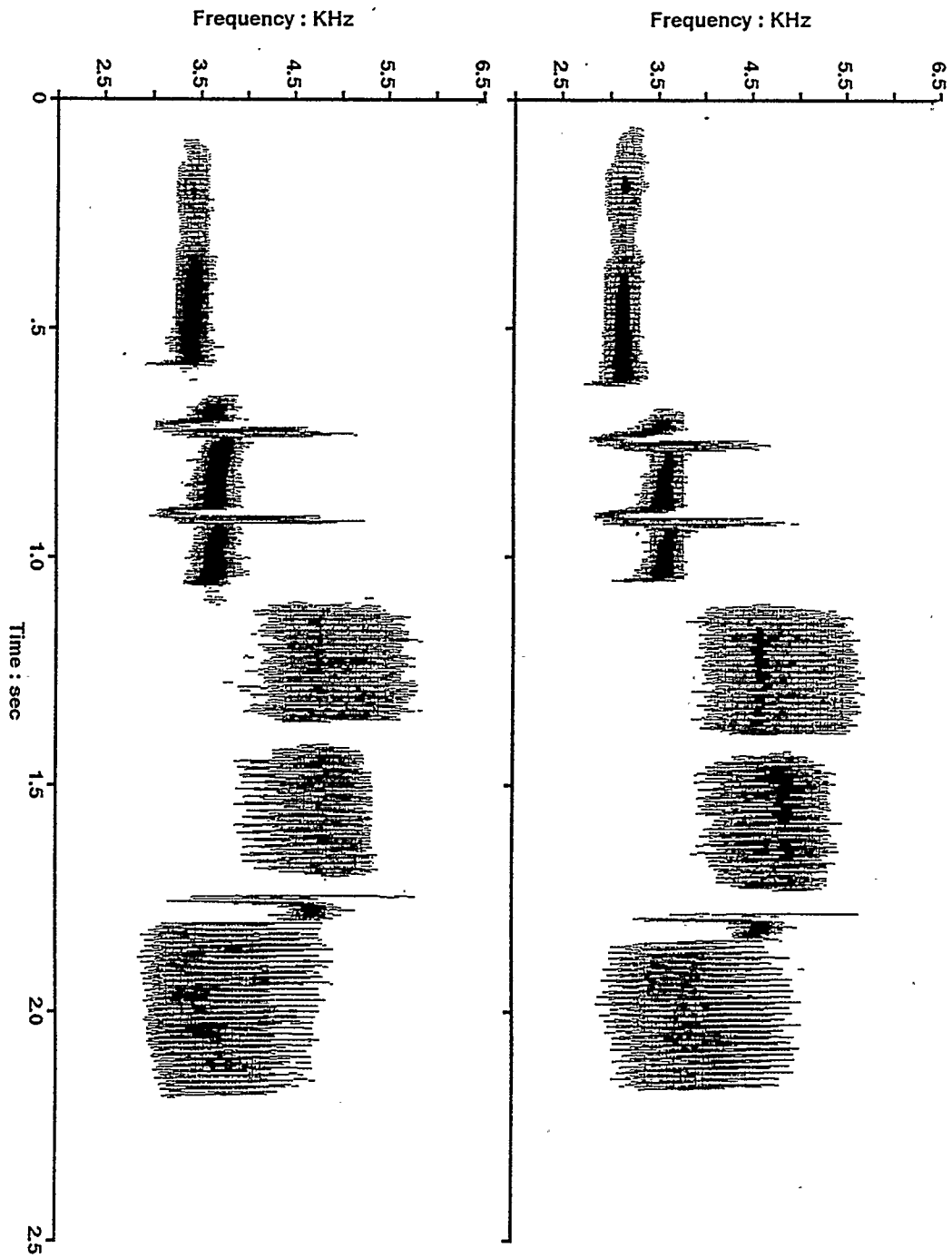


Figure 5. Audiospectrograms of oriantha songs of male White-crowned Sparrows used in playback to estradiol-treated captive female White-crowned Sparrows.

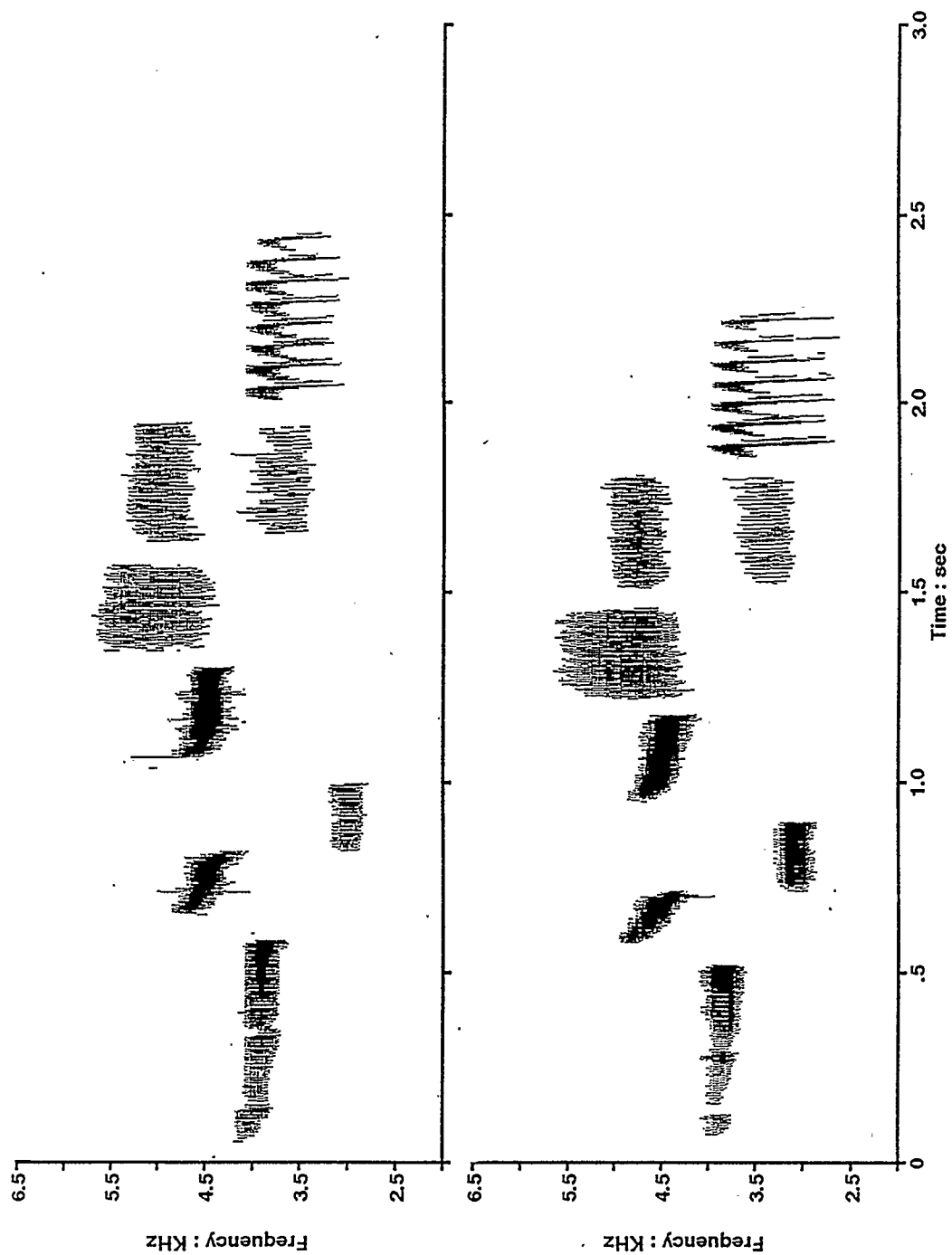
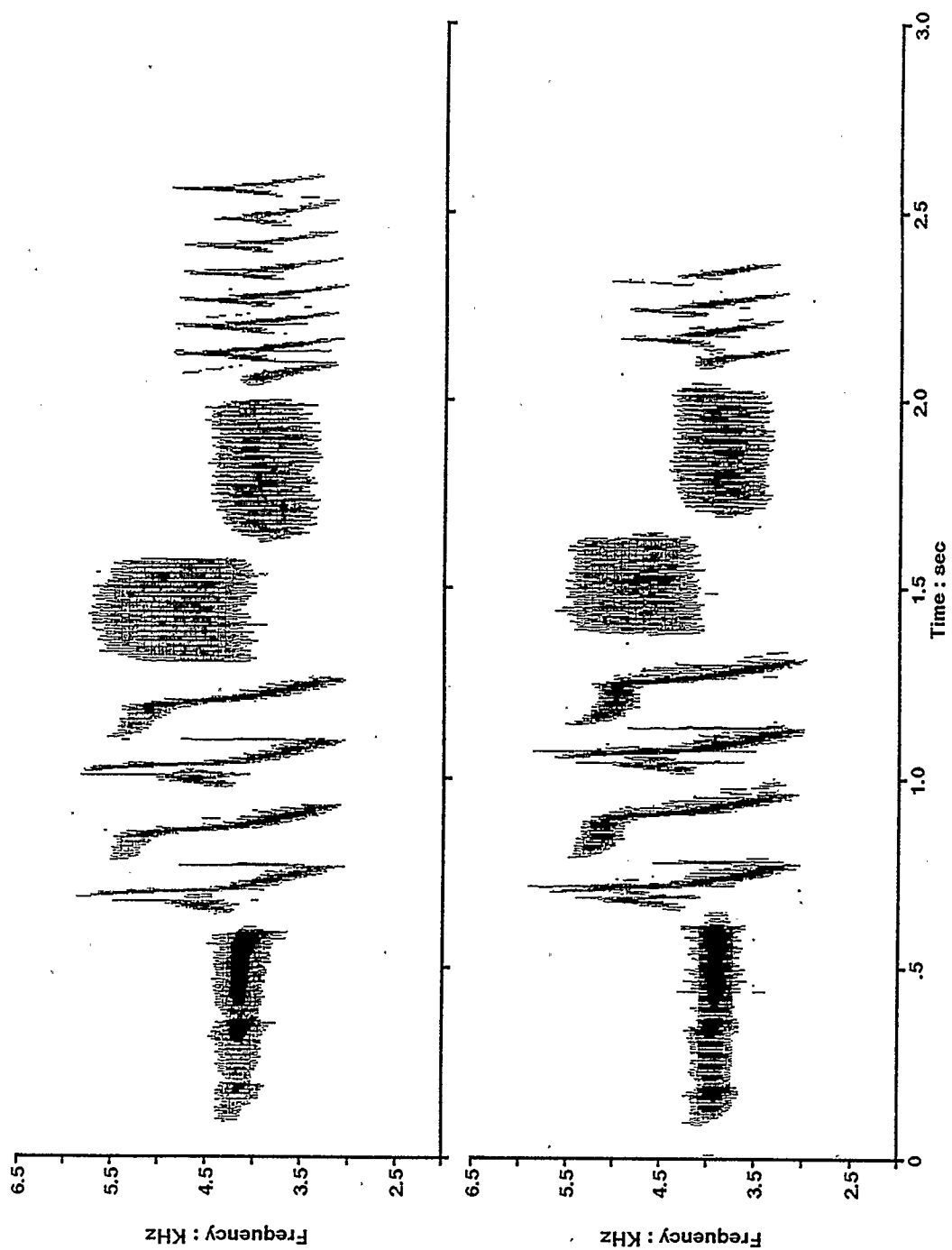


Figure 6. Audiospectrograms of songs of male White-crowned Sparrows from the Cypress Hills used in playback to estradiol-treated captive female White-crowned Sparrows.



10cm) as measured by a Realistic sound level meter (42-3019), at "A" weighting and slow response settings, set 23 cm from the speaker grill, against an ambient noise of less than 60 db (lower limit of the meter). Each subject was video- and audio-taped throughout each test session, using a Sony Betamax SL-2000 videocassette recorder, Sony HVC video camera, Sony KV-5300 monitor, and Tandberg TM6 microphone. Sony, TDK, and Kodak Betamax videotapes were utilized on B3 setting.

Each playback session consisted of three minutes of silence followed by three bouts of three minutes of song alternating with three minutes of silence. During song sequences, subjects heard 1 song every 15 seconds, for a total of 36 songs per session. This protocol is identical to that of Baker and coworkers (e.g., Baker et al. 1981a, 1982b, 1987; Baker 1982, 1983), facilitating the comparison of their results to those of the current study.

Each subject was tested in four sessions separated by not less than one day. An individual heard either the oriantha or gambelii song type in the first and fourth sessions, the other Fortress Mountain song in the second session, and the Cypress song type in the third session. This protocol was designed to permit testing for order of presentation effects, and to account for them should they exist.

Copulation-solicitation displays given in response to the playback of conspecific song vary in their intensity and duration. The following definitions were used to categorize each female's responses. A **full display** involved a slight crouch with tail cocked to vertical, with or without a slight quiver. Wings were held out slightly from the body, with or without a slight quiver. The bill was pointed upward. This display involved a noticeable pause. Parting of the feathers around the cloaca, as described by Baker (1983), was rarely seen because of the angle of the subject to the video camera. Full displays were given with or without a trilled vocalization which is characteristic of free-living female White-crowned Sparrows when soliciting copulations (Hill and Lein 1985). A **partial display** was one in which some component of a full display (crouch, tail to vertical, wings out, or bill upward) was absent, or when the display did not involve a noticeable pause. Partial displays were also given with or without trills. Trills were given very rarely in response to song playback without any apparent sexual posturing. Copulation-solicitation displays were never observed in subjects in the absence of song playback.

In order to account for differences in the intensity of copulation solicitation display, each display was weighted in the calculation of response scores. Full displays with

trills were weighted by a factor of three, partial displays with trills and full displays without trills were each weighted by a factor of two, while partial displays without trills were weighted by one. In this scheme, full displays with trills given in response to all 36 songs in a session would score the maximum of 108 points. Responses consisting of a trill without a postural component were not used in the scoring.

Testosterone Experiments

Song can be induced via treatment with exogenous testosterone in a number of species in which singing by females is a rare behavior (Mulligan and Erickson 1968; Kern and King 1972). The resulting songs given by females may be considered crude renditions when compared to a male's songs, but generally have most species-specific traits (Mulligan and Erickson 1968).

In the present study, testosterone (Sigma Chemical T-1500) was administered via subcutaneous implants, as in the estradiol experiments. Implants were 20 mm in length, but otherwise identical to those used in estradiol experiments.

Audio recording began five days after implantation. Most captives were recorded in acoustic attenuation chambers (Industrial Acoustics Company Inc.) on Sony LNX or

HF-S 90-minute cassette tapes using Sony TCM-5000EV voice-activated tape recorders with Realistic brand pressure zone microphones (PZM 33-1090). The photoperiod in each chamber was 17L:7D. A few subjects were recorded outside attenuation chambers with a Sony MTLF-96 dynamic microphone suspended above the cage, a TCM-5000EV recorder and LNX or HF-S cassette tapes. Implants were removed and subjects returned to the holding facility after five days of recording.

Song Analysis

An audiospectrogram, or sound spectrograph, is a graphic representation of an audio event, encoding frequency, amplitude, and duration. Audiospectrograms were made of the vocalizations of each subject. Tapes were played on either a Sony TCM-5000 or TCM-5000EV cassette recorder through either a Kay digital Sona-Graph 7800 Sound Analyzer and 7900 printer or Kay Sona-Graph 6061B Sound Spectrograph. When an individual gave only a few vocalizations, an audiospectrogram was made of each. When an individual gave many vocalizations, each was viewed on a Uniscan II audiospectrograph (Multigon Industries Inc.), and audiospectrograms were made of representative utterances.

Audiospectrogram figures in this thesis were generated using SIGNAL system software (Engineering Design, Belmont, MA) and a Hewlett Packard LaserJet Series III laser printer.

To avoid experimenter bias, audiospectrograms were categorized by five judges not familiar with the specific identity of the subjects. Each judge was given a figure with three complex syllables (Fig. 7); the gambelii, oriantha, and gambelii variant sometimes heard at the Clearwater River study site were labelled "A", "B", and "C" respectively. Each judge was asked to view each audiospectrogram in the file of each female, and decide if there was evidence of a complex syllable, and which of the three choices it most closely resembled. Audiospectrograms of female songs were judged similarly for the occurrence of oriantha and gambelii trill types (Fig. 8). If at least four of five judges categorized the complex syllables or trills of a female in the same way, they were considered to be in agreement.

The songs of twelve captive female White-crowned Sparrows from the Clearwater River, 36 captives from Fortress Mountain, and a single free-living female recorded at Fortress Mountain were judged in this way.

Figure 7. Audiospectrograms of complex syllables of male White-crowned Sparrows used in categorizing the songs of testosterone-treated female White-crowned Sparrows. A. syllable typical of gambelii songs. B. syllable typical of oriantha songs. C. gambelii syllable variant from Clearwater River.

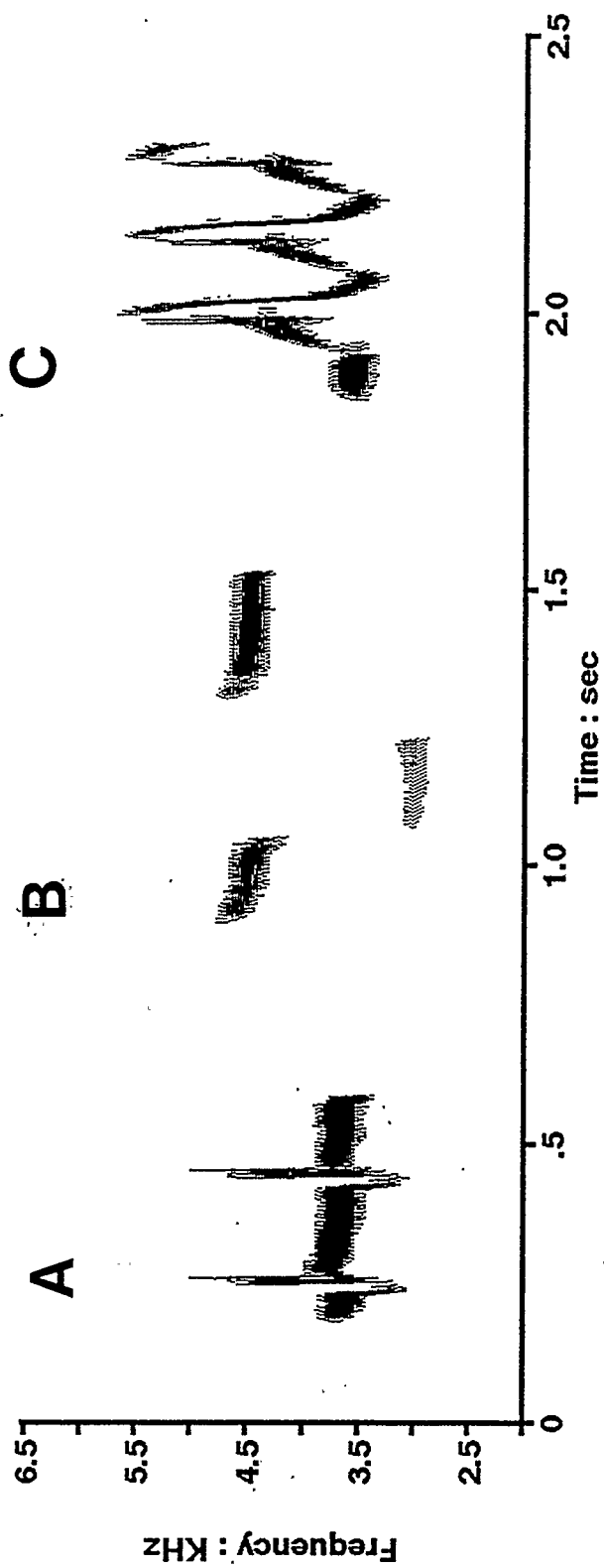
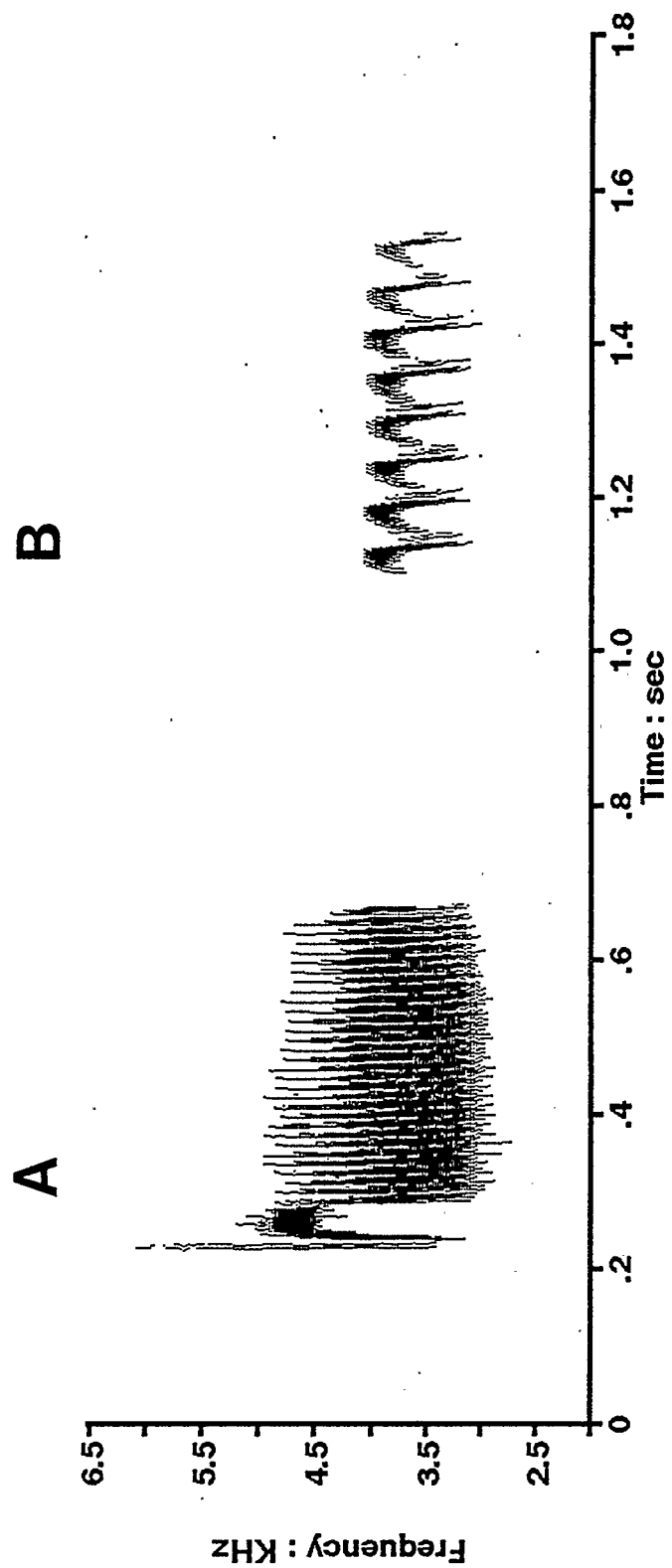


Figure 8. Audiospectrograms of trills of male White-crowned Sparrows used in categorizing the songs of testosterone-treated female White-crowned Sparrows. A. trill typical of gambelii songs. B. trill typical of oriantha songs.



Statistical Analysis

The prediction that the distribution of song types of the mates of females in one year was independent of the distribution of song types of their mates in the preceding year was tested using chi-square tests, with the Yates correction for continuity. When the identity of the mate of an individual female was known in more than two successive years, the choice of mate in each breeding year was treated as an independent event. On occasion, a female would mate with the same individual in two or more successive years; these cases were entered only once in the analysis.

The prediction that the distribution of song types of mates of females was independent of the distribution of song types of their fathers was tested using Fisher's exact test.

Differences in the distribution of responses of estradiol-treated females to the playback of songs of different types were examined using the Wilcoxon signed rank test, having ensured overall heterogeneity with Friedman's two-way non-parametric ANOVA for both Fortress Mountain and Clearwater River subjects. The responses of females from Fortress Mountain were considered in the following pairwise song-type comparisons: oriantha vs.

gambelii; oriantha vs. Cypress Hills dialect; gambelii vs. Cypress Hills; mate's song type vs. other Fortress Mountain song type; mate's song vs. Cypress Hills; other Fortress Mountain song type vs. Cypress Hills. Responses by females from the Clearwater River were considered in the first three pairwise comparisons listed above. This approach was also used to compare responses to the first and final presentation of the same song type to test for habituation. All tests were one-tailed except where the alternate hypothesis provided no a priori reason to expect responses to be greater to one treatment than the other. Responses given by females from Fortress Mountain and from the Clearwater River were not combined for any analyses.

The prediction that the frequency of song types among testosterone-treated females taken from Fortress Mountain was independent of the frequency of song types among free-living males at the same location was tested using chi-square tests, with the Yates correction for continuity. The prediction that the distribution of song types of testosterone-treated females was independent of the distribution of song types of their mates was tested using Fisher's exact test.

The prediction that the distribution of responses given by estradiol-treated females from Fortress Mountain to different song types was independent of the distribution of

their own song type was tested using Fisher's exact test.

RESULTS

Consistency of Mate Choice by Song Type

Between 1984 and 1989, 90 banded female White-crowned Sparrows were seen on the study site in more than one breeding season. Of these, 17 individuals are not considered further because observations did not provide information about their mates in at least two years. A further 14 individuals were never known to have mated with more than one male, and so were not considered. In a consideration of song type and patterns of mating, mating with the same male in successive years does not represent two independent mate choice decisions.

Of the remaining 59 females, two individuals were on the study site for six years, two for five years, six for four years, 14 for three years, and 35 for two years, for a total of 99 possible pair-wise comparisons of mate decisions in successive years. In six cases, the identity of a mate was not determined with certainty. In four cases, females were not observed on the study site in a particular breeding season, although they were known to be alive by their appearance in subsequent years. In three

cases, the mate's song type was not known. In one case, a female mated with two males in successive breeding attempts in a single year. In 12 cases, an individual was mated to the same male in subsequent years. Eliminating these cases, 73 pair-wise comparisons of the song type of different mates in successive years are possible (Table 1).

The null hypothesis states that mate choice should be random with respect to song type. That is, an individual female should not consistently choose mates singing the same song type in successive years. In light of this hypothesis, these data may be examined in a number of ways, all of which produce similar results. First, considering only cases in which successive mates sang either of the two common song types, gambelii or oriantha (the four cells in the upper left corner of Table 1), females were no more likely to choose mates of the same song type in successive years than expected by chance (Yates corrected $\chi^2 = 0.10$; $df = 1$; $P = 0.75$; $n = 52$). Second, if hybrid songs are combined with oriantha songs on the basis of the shared complex syllable, the song types of mates in successive breeding seasons are independent ($\chi^2 = 0.00$; $df = 1$; $P = 1.00$; $n = 66$). Third, if hybrid songs are combined with gambelii songs on the basis of the shared terminal trill, the song types of males in successive breeding seasons are, again, independent ($\chi^2 = 0.19$; $df = 1$; $P = 0.66$; $n = 66$).

Table 1. Comparison of song types of mates of female White-crowned Sparrows in successive breeding seasons. or. indicates oriantha; ga. indicates gambelii. Numbers in parentheses represent the comparison of song types of the first two mates of each female only.

Song type of mate in second year	Song type of mate in first year						
	<u>or.</u>	<u>ga.</u>	hybrid	<u>or.</u> no trill	<u>ga.</u> both trills	<u>ga.</u> odd trill	both songs
<u>oriantha</u>	12 (8)	7 (3)	3 (3)	1 (1)	0	1 (1)	0
<u>gambelii</u>	18 (15)	15 (12)	4 (4)	0	1 (1)	0	1 (1)
hybrid	2 (2)	4 (3)	1 (1)	0	0	0	0
<u>oriantha</u> , both trills	2 (2)	0	0	0	0	0	0
<u>gambelii</u> , <u>oriantha</u> trill	0	0	0	1 (1)	0	0	0

Finally, 72 of 73 cases may be considered if the terminal trill is discounted, classifying all songs as either oriantha or gambelii on the basis of complex syllables. Again, song types of mates of individual females in a breeding season are independent of the songs of their mates in the previous year ($X^2 = 0.15$; $df = 1$; $P = 0.70$).

Including mates of individual females in their third and subsequent breeding seasons has no effect on any of these analyses. If only the first two mates of each female are considered (numbers in parentheses in Table 1), song types of mates in successive breeding seasons are no more likely to be of the same type than expected by chance (Yates corrected X^2 ; all $P > 0.45$).

Comparison of Songs of Fathers and Mates

Twenty-five females that were banded as nestlings returned to breed on the study site between 1985 and 1989. Of these, 11 had fathers that sang the gambelii song type, eight had fathers that sang oriantha, while six had fathers that sang the hybrid song type. Three of these females were never known to have had a mate. Of the remainder, 15 females had one known mate each, six had different mates in two consecutive years, and one had different mates in three years, for a total of 30 possible pair-wise comparisons of

the song types of fathers and mates (Table 2).

The null hypothesis states that the song types of mates of an individual female are independent of the song type of her father. In light of this hypothesis, the data may, again, be examined in a number of ways. First, considering only the two most common song types, oriantha and gambelii (the four cells in the upper left corner of Table 2), the songs of the father and mate of each female are no more likely to be of the same song type than expected by chance (Fisher's exact test, $P = 1.00$; $n = 15$). Second, if hybrid songs are combined with oriantha songs on the basis of the shared complex syllable, the song types of fathers and mates are again no more likely to be of the same type than expected by chance ($P = 0.70$; $n = 28$). Third, if hybrid songs are combined with gambelii songs on the basis of the shared trill, the song types of fathers and mates are, again, no more likely to be of the same type than expected by chance ($P = 0.69$; $n = 28$). Finally, if the songs are categorized on the basis of complex syllable alone, ignoring the terminal trill, song types of fathers and mates are still no more likely to be of the same type than expected by chance ($P = 0.69$; $n = 30$).

Including mates of individual females in more than one year has no effect on any of these analyses. If only the mates of females in their first breeding season are

Table 2. Comparison of song types of fathers of individual female White-crowned Sparrows to those of their mates. Numbers in parentheses represent females in their first breeding season only.

Song type of mate	Song type of father		
	<u>oriantha</u>	<u>gambelii</u>	hybrid
<u>oriantha</u>	5 (5)	5 (4)	5 (4)
<u>gambelii</u>	2 (1)	3 (1)	4 (2)
hybrid	1 (0)	3 (3)	0
<u>gambelii</u> , odd trill	1 (1)	0	0
<u>oriantha</u> , no trill	0	1 (1)	0

considered (numbers in parentheses in Table 2), song types of fathers and mates are no more likely to be of the same type than expected by chance (Fisher's exact test; all $P > 0.35$).

Estradiol Experiments

Because of the weak and infrequent responses to playback by females captured in 1985, 1986, and 1987, and the modification of protocol for later tests (see Materials and Methods), only the responses given by females captured in 1988 and 1989 were considered in this analysis.

Nineteen female White-crowned Sparrows, taken from Fortress Mountain in 1988 and 1989, were treated with estradiol implants and subjected to the playback of the songs of male White-crowned Sparrows. Of these, 14 responded with copulation-solicitation displays. In order to test for the possible impact of exposure to song in early trials on the responses given in later trials, the responses given by each subject to the first and second presentations of the same song type were compared (Table 3). Females did not respond differently to the first or last presentation of the same song (Wilcoxon's signed rank test, $P = 0.40$). Consequently, an average of the weighted responses to the first and last presentation was used in

Table 3. Comparison of the number of copulation-solicitation displays, weighted for intensity of response, given by female White-crowned Sparrows from Fortress Mountain in response to the playback of the same conspecific song type in the first and fourth trials.

Individual	Playback song	Sum of weighted responses	
		First trial	Fourth trial
PR/K	<u>oriantha</u>	2	17
Pb/K	<u>gambelii</u>	1	1
PP/K	<u>gambelii</u>	67	88
O/PK	<u>gambelii</u>	1	0
P/KR	<u>gambelii</u>	27	86
P/KY	<u>oriantha</u>	2	11
P/KO	<u>gambelii</u>	13	2
Pg/K	<u>oriantha</u>	86	81
PO/K	<u>gambelii</u>	2	0
PW/K	<u>oriantha</u>	2	2
PP/R	<u>gambelii</u>	2	2
P/Kb	<u>oriantha</u>	3	3
W/PK	<u>gambelii</u>	9	5
P/KK	<u>oriantha</u>	26	8

subsequent analyses of response and song type (Table 4).

The following results consider responses in pairwise comparisons, that is, the number and intensity of solicitation displays given to the playback of one song type versus another. Except where noted, one-tailed probability is given for a Wilcoxon's signed rank test. Because multiple pair-wise comparisons increase the likelihood of Type I and Type II errors, the critical value of the test statistic is made more rigorous, i.e. $\alpha = 0.017$ ($\alpha_c = 1 - (1 - 0.05)^{1/3}$).

Subjects from Fortress Mountain were less responsive to playback of the Cypress Hills dialect than to playback of either the oriantha song ($P = 0.003$; significant) or the gambelii song ($P = 0.03$; approaching significance). Subjects did not respond significantly more to playback of either of the two songs commonly heard at Fortress Mountain (two-tailed $P = 0.20$).

Considering the responses of individual females in relation to the song types of their mates, subjects did not respond more strongly to their mate's song type than to the other song type commonly heard at Fortress Mountain ($P = 0.35$). Individuals responded less to playback of the Cypress Hills dialect than to either their mate's song type ($P = 0.0046$; significant) or the other Fortress Mountain song type ($P = 0.0009$; significant).

Table 4. The number of copulation-solicitation displays, weighted for intensity of response, given by captive female White-crowned Sparrows taken from Fortress Mountain in 1988 and 1989 in response to the playback of three conspecific male song types. The song type of the mate of each subject is also given.

Individual	Mate's song	weighted response to		
		<u>gambelii</u>	<u>oriantha</u>	Cypress Hills
PR/K	<u>oriantha</u>	1	9.5	0
Pb/K	<u>oriantha</u>	1	1	0
PP/K	<u>oriantha</u>	77.5	76	22
O/PK	<u>oriantha</u>	0.5	10	1
P/KR	<u>oriantha</u>	56.5	102	7
P/KY	<u>oriantha</u>	4	6.5	0
P/KO	<u>oriantha</u>	7.5	0	0
Pg/K	<u>gambelii</u>	105	83.5	1
PO/K	<u>gambelii</u>	1	3	1
PW/K	<u>gambelii</u>	0	2	4
PP/R	<u>gambelii</u>	2	2	0
P/Kb	<u>gambelii</u>	7	3	0
W/PK	<u>gambelii</u>	7	35	12
P/KK	<u>gambelii</u>	5	17	0

These data may be viewed from a different perspective. Of 14 females that responded to the playback of song with copulation-solicitation displays, two responded equally to orianta and gambelii songs. Of the four that gave greater response to gambelii songs, two had been mated to males that sang orianta songs, and two to males that sang gambelii songs. Of the eight that responded more to orianta songs, four had been mated to males that sang orianta songs, and four to males that sang gambelii songs.

In these estradiol experiments, a female White-crowned Sparrow from Fortress Mountain may be more responsive to one of the local song types than to the other, but this preferential response is no more likely to be reflected in the song type of her chosen mate than expected by chance.

Of 12 subjects taken from the Clearwater River region, where males sing only the gambelii song type, nine responded with copulation-solicitation displays (Table 5). These females solicited more strongly in response to playback of gambelii songs than to the playback of either the orianta song type ($P = 0.014$; significant) or the Cypress Hills song type ($P = 0.048$; approaching significance). The subjects did not respond differently to the orianta and Cypress Hills songs (two-tailed $P = 0.77$)

Table 5. The number of copulation-solicitation displays, weighted for intensity of response, given by captive female White-crowned Sparrows taken from Clearwater River in 1989 in response to the playback of three conspecific male songs. The song type of the mate of each female is known or assumed to be the gambelii type.

Individual	weighted response to		
	<u>gambelii</u>	<u>oriantha</u>	Cypress
PK/B	23	11	3
PG/K	75	1	32
PG/B	9	0	0
PB/G	12	0.5	0
PG/G	78.5	24	60
KP/G	94	85	89
GP/K	19	28	53
BP/K	6	4.5	0
GP/B	2.5	1	0

Testosterone Experiments

In this study 36 captive female White-crowned Sparrows, taken from Fortress Mountain between 1985 and 1989, were implanted with testosterone to induce singing behavior. Two produced no recognizable complex syllables or trills. Songs of the remaining 34 subjects are described in Table 6. Of these, 25 were judged as having oriantha type complex syllables, while six had gambelii type complex syllables (Fig. 9). Excluding PK/W (see below), twelve females were considered to have produced oriantha type trills, while three gave gambelii trills (Fig. 9). No individual female was judged as having produced more than one type of complex syllable or trill.

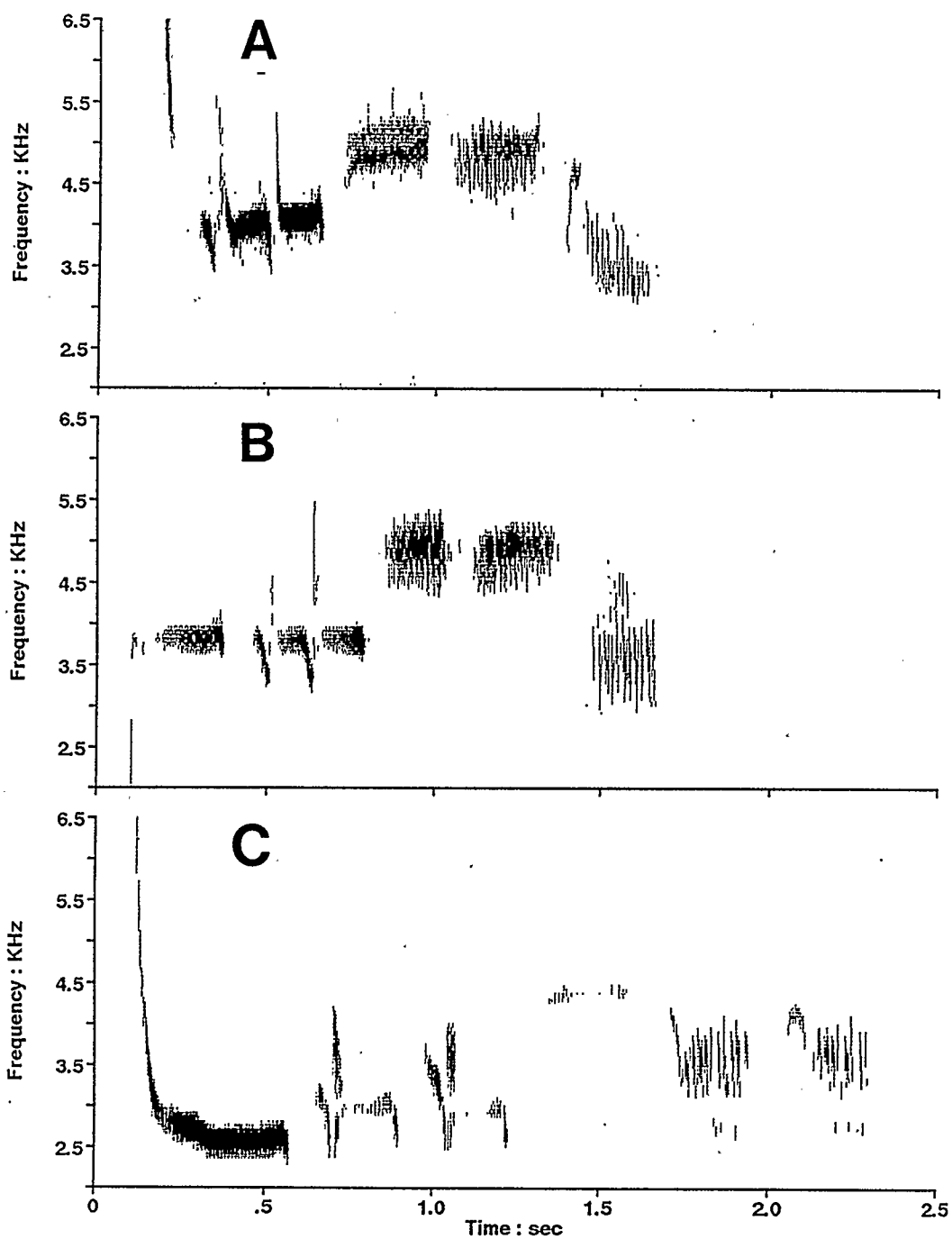
One female from Fortress Mountain (PK/W) sang a song unlike either of the two common forms (Fig. 10). This song is very similar to the songs of male White-crowned Sparrows recorded in Idaho and Oregon (Fig. 2 E and Fig. 6 A-D in Baptista and King 1980; Baptista personal communication), and it is described as "foreign oriantha" in Table 6. The songs of this female were not categorized by the naive judges. Neither her complex syllable nor trill were used in song-type comparisons of females and their mates.

Two captive female White-crowned Sparrows from Fortress Mountain received testosterone implants from M. R.

Table 6. Complex syllables and trills of captive female White-crowned Sparrows taken from Fortress Mountain between 1985 and 1989, treated with testosterone, and the song types of their mates. "?" indicates that complex syllable or trill was not judged without ambiguity. Two additional females were judged to have produced no complex syllable or trill.

Individual	Capture year	Complex syllable	Trill	Mate's song type
Pb/K	89	<u>orianta</u>	<u>orianta</u>	<u>orianta</u>
PP/K	89	<u>orianta</u>	<u>orianta</u>	<u>orianta</u>
P/Kg	88	<u>orianta</u>	<u>orianta</u>	<u>orianta</u>
P/KY	88	<u>orianta</u>	<u>orianta</u>	<u>orianta</u>
P/Pg	87	<u>orianta</u>	<u>orianta</u>	<u>orianta</u>
P/PY	86	<u>orianta</u>	<u>orianta</u>	<u>orianta</u>
PO/K	89	<u>orianta</u>	<u>orianta</u>	<u>gambelii</u>
PW/K	89	<u>orianta</u>	<u>orianta</u>	<u>gambelii</u>
R/PK	87	<u>orianta</u>	<u>orianta</u>	<u>gambelii</u>
g/PK	87	<u>orianta</u>	<u>orianta</u>	<u>gambelii</u>
P/PW	86	<u>orianta</u>	<u>orianta</u>	<u>gambelii</u>
PY/K	89	<u>orianta</u>	none	<u>orianta</u>
P/KR	88	<u>orianta</u>	none	<u>orianta</u>
P/PP	87	<u>orianta</u>	none	<u>orianta</u>
P/PK	87	<u>orianta</u>	none	<u>orianta</u>
P/PR	86	<u>orianta</u>	none	<u>orianta</u>
PK/R	85	<u>orianta</u>	none	<u>orianta</u>
PK/g	85	<u>orianta</u>	none	<u>orianta</u>
Pg/K	89	<u>orianta</u>	none	<u>gambelii</u>
W/PK	88	<u>orianta</u>	none	<u>gambelii</u>
P/KK	88	<u>orianta</u>	none	<u>gambelii</u>
O/PK	88	<u>orianta</u>	?	<u>orianta</u>
P/OK	87	<u>orianta</u>	?	<u>orianta</u>
P/PO	86	<u>orianta</u>	?	hybrid
Y/PK	87	<u>orianta</u>	?	<u>gambelii</u>
K/PK	88	<u>gambelii</u>	<u>gambelii</u>	<u>gambelii</u>
PK/K	87	<u>gambelii</u>	<u>gambelii</u>	<u>gambelii</u>
PK/Y	85	<u>gambelii</u>	<u>gambelii</u>	<u>gambelii</u>
P/Kb	88	<u>gambelii</u>	none	<u>gambelii</u>
P/KP	88	<u>gambelii</u>	none	<u>gambelii</u>
P/KO	88	<u>gambelii</u>	none	<u>orianta</u>
PR/K	89	?	<u>orianta</u>	<u>orianta</u>
PK/W	87	foreign <u>orianta</u>	<u>orianta</u>	<u>orianta</u>
PP/R	89	?	?	<u>gambelii</u>

Figure 9. Audiospectrograms of songs of six captive female White-crowned Sparrows, treated with testosterone. A - C. Complex syllables categorized as gambelii. D - F. Complex syllables and trills categorized as oriantha. The downward-sweeping note at the beginning of songs A and C are artifacts resulting from voice-activated recording.



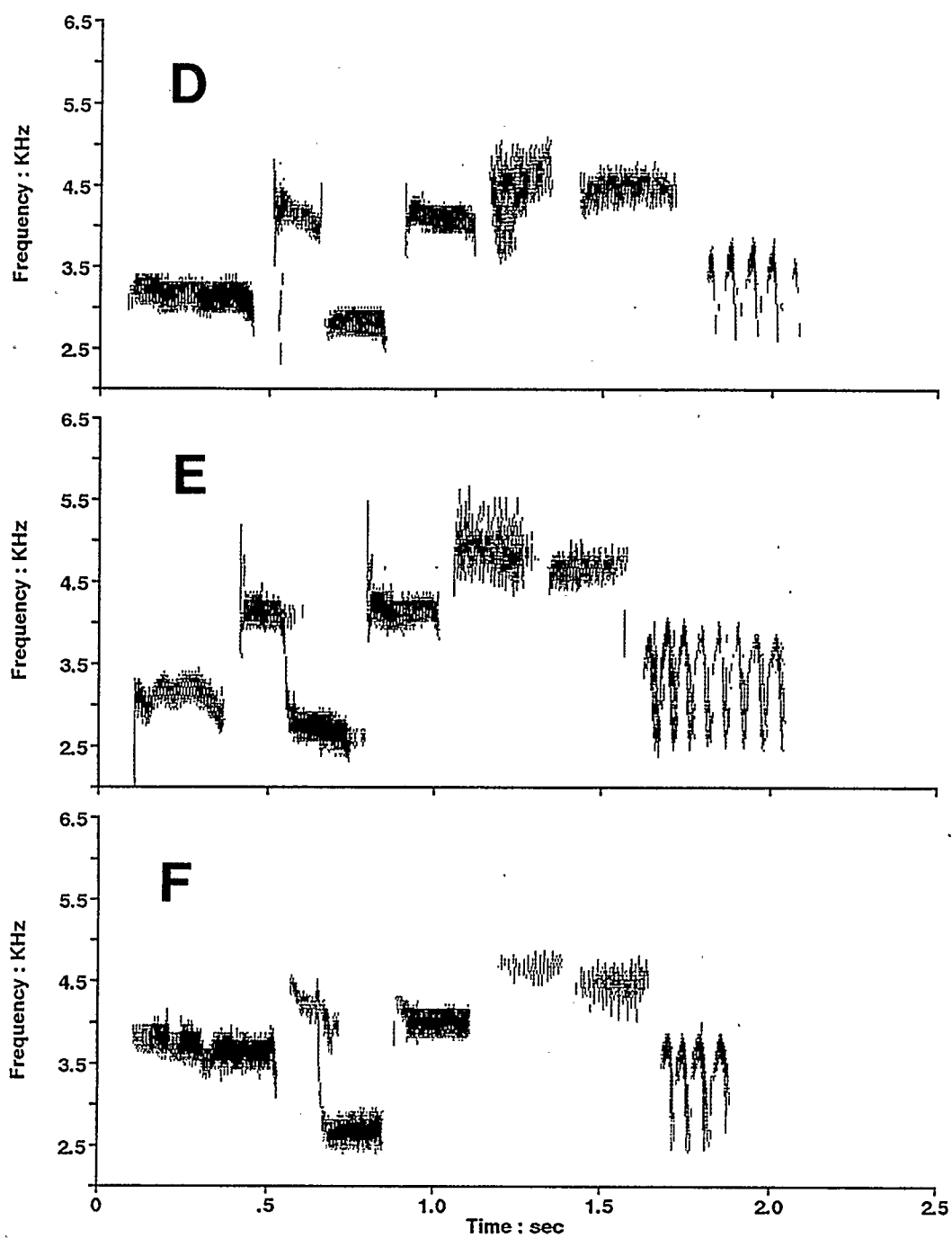
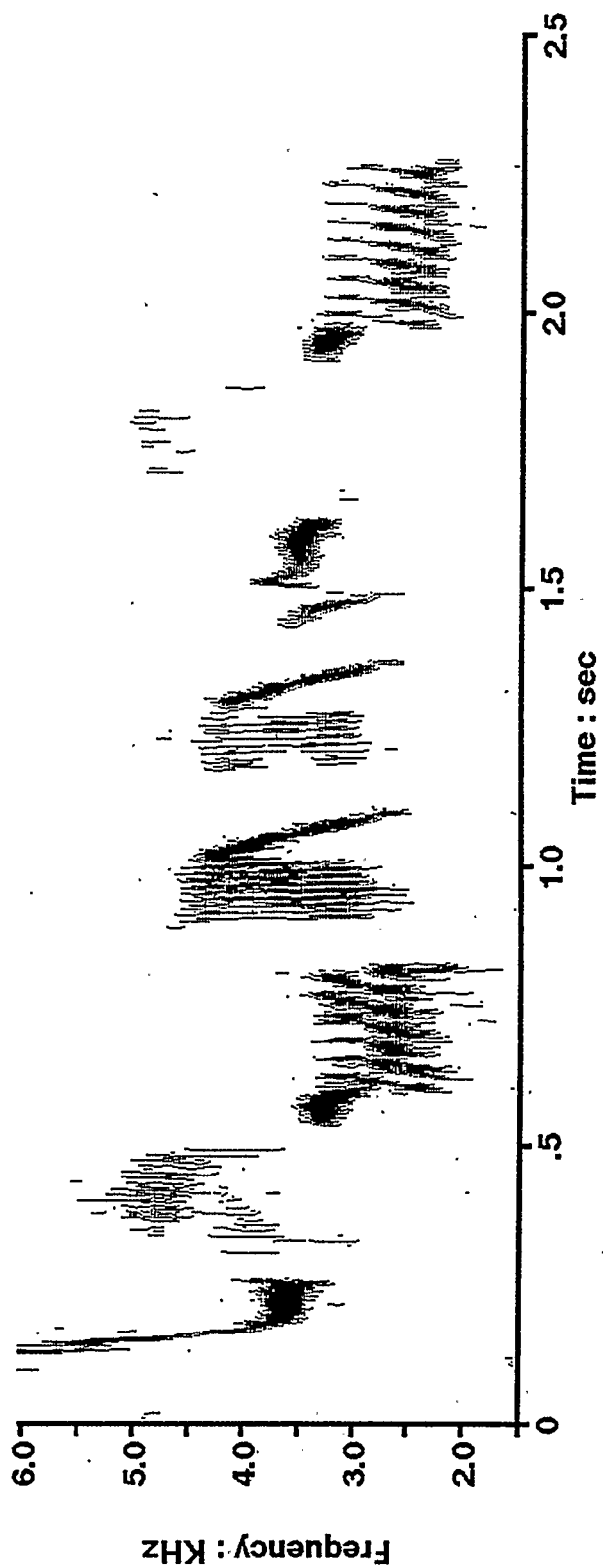


Figure 10. Audiospectrogram of song of captive female White-crowned Sparrow, banded PK/W. The downward-sweeping note at the beginning of the song is an artifact resulting from voice-activated recording.



Lein in 1985. One gave a single vocalization; a pulsed whistle and orianta-type complex syllable, not unlike the vocalization given when re-implanted in the present study. The second subject gave a single vocalization, judged to be unlike a component of either orianta or gambelii songs, and died in captivity before re-testing in the present study.

Between 1984 and 1989, only three White-crowned Sparrows known to be females were heard singing on the Fortress Mountain study site. The female banded GA/WW was heard to sing full orianta songs in 1986 and orianta songs without trills in 1987. WG/Ab was heard to sing orianta songs without terminal trills in 1987. Recordings were made of the hybrid songs and orianta songs without trills given by GG/Ab in 1987.

The songs of 295 color-banded male White-crowned Sparrows were documented at the Fortress Mountain study site between 1984 and 1988 (M. R. Lein, unpublished data). Of these males, 116 sang the orianta song type, 113 sang the gambelii song, 46 sang the hybrid song, while 20 sang some other version of the themes described above. When only the complex syllables of these males are considered, 162 sang the orianta form, while 115 sang the gambelii form. Considering only the terminal trills, 117 sang the orianta form, while 159 sang the gambelii form. Table 7

Table 7. Distribution of complex syllable and trill types of banded male White-crowned Sparrows at Fortress Mountain, 1984 to 1988, and of captive female White-crowned Sparrows taken from Fortress Mountain, 1985 to 1989.

	Complex syllable		Trill	
	<u>oriantha</u>	<u>gambelii</u>	<u>oriantha</u>	<u>gambelii</u>
Males	162	115	117	159
Females	25	6	12	3

summarizes the distribution of complex syllable and trill types of these free-living male and the captive female White-crowned Sparrows described above. Oriantha complex syllables and oriantha trills were significantly more common among the sample of females taken captive from Fortress Mountain than among free-living males in the same population (complex syllables: Yates corrected $X^2 = 4.85$; $df = 1$; $P = 0.028$; trills: $X^2 = 6.70$; $df = 1$; $P = 0.010$). If the three free-living female White-crowned Sparrows whose songs were heard at Fortress Mountain are included in this comparison, the data again suggest that females sing oriantha complex syllables and oriantha trills out of proportion to the incidence of these song components given by males (complex syllables: $X^2 = 6.29$; $df = 1$; $P = 0.012$; trills: $X^2 = 6.22$; $df = 1$; $P = 0.013$).

Songs of captive females were compared to the song types of their chosen mates (Table 8). The null hypothesis that the complex syllable of a female should match the complex syllable of her mate no more often than expected by chance is rejected (Fisher's exact test $P = 0.050$). Instead, the results support the alternate hypothesis that a female was more likely to be mated to a male whose complex syllable was of the same song type as hers. The null hypothesis that the trill of a female should match the trill of her mate no more often than expected by chance was

Table 8. Complex syllables and trills of female White-crowned Sparrows taken from Fortress Mountain between 1984 and 1989, and the song type of their mates.

Mate's song type	Female's song			
	Complex syllable		Trill	
	<u>oriantha</u>	<u>gambelii</u>	<u>oriantha</u>	<u>gambelii</u>
<u>oriantha</u>	15	1	7	0
<u>gambelii</u>	9	5	5	3
hybrid	1	0	0	0

not rejected (Fisher's exact test $P = 0.12$).

Of the 31 captive females that produced recognizable complex syllables, 12 were taken captive before egg-laying, while 19 were taken late in the nestling stage. Females taken late in the breeding effort (i.e., those mated the longest) were no more or less likely to match the complex syllable type of their mate than those taken before egg-laying (Table 9; Yates corrected $\chi^2 = 0.09$; $df = 1$; $P = 0.77$; Fisher's exact test, two-tailed $P = 0.70$). The probability that the complex syllable of a female and her mate will be of the same type does not appear to increase or decrease with the duration of the pair bond.

The twelve female White-crowned Sparrows from the Clearwater River region used as a control in estradiol/playback experiments were also treated with testosterone to induce singing. Table 10 summarizes the songs given by these subjects. Of those whose songs were classified without ambiguity, only one was judged to have produced a song with a component unlike the gambelii songs heard locally; this was an oriantha-type trill.

Table 9. Comparison of extent of matching of complex syllables of female White-crowned Sparrows taken captive before and after egg-laying with the complex syllables of their mates. The first two rows represent matching of complex syllables, while the last two rows represent pairs mismatched by complex syllable type.

Complex syllable		Female captured	
Female's	Male's	before laying	after laying
<u>oriantha</u>	<u>oriantha</u>	6	10
<u>gambelii</u>	<u>gambelii</u>	3	2
<u>oriantha</u>	<u>gambelii</u>	2	7
<u>gambelii</u>	<u>oriantha</u>	1	0

Table 10. Complex syllables and trills of songs of captive female White-crowned Sparrows taken from Clearwater River in 1989. Song type of their mates were known or assumed to be gambelii. CR-gambelii indicates a variant of the gambelii complex syllable common among male White-crowned Sparrows in the Clearwater River region. "?" indicates that the complex syllable or trill was not judged without ambiguity.

Individual	Complex syllable	Trill
PG/B	<u>gambelii</u>	<u>gambelii</u>
PB/G	CR- <u>gambelii</u>	<u>gambelii</u>
KP/G	CR- <u>gambelii</u>	<u>gambelii</u>
KP/B	CR- <u>gambelii</u>	<u>gambelii</u>
PB/B	<u>gambelii</u>	?
PB/K	<u>gambelii</u>	?
PG/G	<u>gambelii</u>	?
PK/B	<u>gambelii</u>	?
PG/K	CR- <u>gambelii</u>	?
GP/K	?	none
BP/K	?	none
GP/B	?	<u>oriantha</u>

Integration of Testosterone and Estradiol Experiments

Of the 14 captive female White-crowned Sparrows from Fortress Mountain that responded to the playback of song with copulation-solicitation displays, ten sang songs with oriantha complex syllables, two sang songs with gambelii complex syllables, and two gave songs with complex syllables that could not be classified without ambiguity (Table 11). The null hypothesis states that a female should solicit no more in response to the playback of songs in which the complex syllable matches her own than to the playback of the other song type. Of ten that sang oriantha complex syllables, seven responded more to the playback of oriantha songs than to the playback of gambelii songs, two responded more to gambelii than to oriantha, while one responded equally to these songs (Wilcoxon's signed rank test two-tailed; $P = 0.10$; one-tail $P = 0.049$). Both females that sang gambelii complex syllables responded more strongly to the playback of gambelii songs than to the playback of oriantha songs. In summary, of eleven females that produced songs with a recognizable complex syllable and responded preferentially to the playback of either oriantha or gambelii songs, nine responded more strongly to their own song type than to the other type (Fisher's exact test $P = 0.11$).

Table 11. Complex syllable types of songs of captive female White-crowned Sparrows taken from Fortress Mountain in 1988 and 1989, and the number of copulation-solicitation displays, weighted for intensity of response, given by those females in response to the playback of conspecific gambelii and oriantha male song. "?" indicates that the female's complex syllable was not judged without ambiguity.

Individual	Complex syllable	weighted response to	
		<u>gambelii</u>	<u>oriantha</u>
O/PK	<u>oriantha</u>	0.5	10
P/KR	<u>oriantha</u>	56.5	102
P/KY	<u>oriantha</u>	4	6.5
PO/K	<u>oriantha</u>	1	3
PW/K	<u>oriantha</u>	0	2
W/PK	<u>oriantha</u>	7	35
P/KK	<u>oriantha</u>	5	17
PP/K	<u>oriantha</u>	77.5	76
Pg/K	<u>oriantha</u>	105	83.5
Pb/K	<u>oriantha</u>	1	1
P/Kb	<u>gambelii</u>	7	3
P/KO	<u>gambelii</u>	7.5	0
PR/K	?	1	9.5
PP/R	?	2	2

DISCUSSION

Gene Flow Across Dialect Boundaries

Marler and Tamura (1962) and Nottebohm (1969, 1970) suggested that behavioral responses to dialectal differences in the songs of birds may subdivide, and therefore genetically isolate, their breeding populations. Baker et al. (1984) described locale-specific song features as "population markers" which might be used in male-male and male-female interactions. By promoting breeding among members of a genetically-restricted population exposed to similar selective pressures, the resulting offspring may be better genetically specialized to local conditions than they would be if the population were open to immigrants (Nottebohm 1972; Payne 1981; Beecher 1988). Adaptation to local conditions through assortative mating may be of particular value to bird species that are widely distributed across heterogeneous environments (Konishi 1965)

If song dialects are to provide reliable information about deme membership, the individual must be irrevocably committed to the song dialect heard during the early sensitive period for learning (Baker and Cunningham 1985; Shields 1985). For males, this commitment is, in part, one

of performance. As an adult, each male should sing the song dialect of his natal population. His song type should serve as a reliable indicator of his population of origin. For females, the commitment to song is one of discrimination, and is sexual in nature. Each adult female should settle to breed within the limits of her natal population, and, when choosing from among potential mates, should favor those males singing the dialect she heard as a youngster (Baker and Mewaldt 1978).

This view of song dialects and mate choice decisions suggests that males singing foreign songs should be less able to attract mates than are males singing the local dialect. If so, female mate choice will retard the flow of genes across boundaries between dialect populations (Baker et al. 1981a)

Female White-crowned Sparrows will be exposed to potential mates of more than one song type in two situations. First, individual males singing foreign songs occasionally occur in populations dominated by a single song type, far from borders with other dialect populations (Baptista and Morton 1982; Baptista 1985a). Presumably these males have dispersed from a distant dialect population. Even though adult females in such situations presumably have little or no experience with these foreign songs, these males are apparently able to attract mates and

breed successfully (Baptista 1985a). Further, Petrinovich and Baptista (1984) found that male White-crowned Sparrows (Z. l. nuttalli) that sang a different dialect than did their testosterone-treated mates fledged no fewer young than males whose songs were of the same dialect type as those of their mates. If these males with foreign songs breed far from their natal population, then their reproductive success represents a saltatory movement of genes.

Second, female White-crowned Sparrows routinely will encounter potential mates of two song types at boundaries between dialect populations. If behavioral responses to dialect differences are to restrict gene flow between dialect populations, discrimination must operate at these boundaries where dispersal of males from one dialect population to another is most frequent (Baker and Mewaldt 1978). However, in these situations, where one dialect replaces another, either abruptly or across a zone in which both songs are common, young birds will be exposed to both dialects when most sensitive to song learning, and may not form an irrevocable commitment to either dialect group as adults (Nottebohm 1972; Baker and Mewaldt 1978).

In some regards, female White-crowned Sparrows at Fortress Mountain face mate choice decisions similar to those of females at sharper dialect boundaries.

Individuals are exposed to two song types early in life, when they are presumably most sensitive to song learning, and again when choosing between potential mates as adults. How then does the early experience with two song types influence the subsequent mate choice decisions of adult female White-crowned Sparrows?

Consistency of Mate Choice by Song Type

Individual female White-crowned Sparrows at Fortress Mountain were as likely to choose mates of different song types in successive years as they were to choose different mates of the same song type (Table 1). Females born into this mixed-dialect population apparently did not form an irrevocable sexual commitment to one song type or the other, but rather, chose mates on the basis of criteria other than song type.

If this situation reflects the behavior of female White-crowned Sparrows at sharper dialect boundaries, in that young are exposed to two song types, then mate choice by females is probably not an effective block to gene flow between dialect populations. Males of a particular song type could presumably attract mates for some unspecified distance across the border separating dialect populations. This result does not preclude the possibility that a male

from a distant population, singing a song unfamiliar to local females, would be less able to attract a female and breed successfully.

My working model predicted that females in the mixed-dialect population would choose from among potential mates on the basis of characteristics other than song type. The alternate position would view each adult female with a sexual preference for one song type or another. Under the latter scenario, if unmated males of both song types were always available, and if the costs to the female of searching for mates was low, then females would always obtain mates singing the preferred song type. Individual females would rarely be observed to switch between males of different song types.

Successive mates were as likely to be of different song types as of the same song type. Either my working model is correct, or individual females did have a sexual preference for a particular song type, but then some constraint frequently prevented the individual from obtaining a mate of that song type. Constraints might be either temporal (e.g., brevity of the breeding season) or energetic (e.g., cost of traveling between the territories of bachelor males).

Comparison of Songs of Fathers and Mates

A previous study of male White-crowned Sparrows at Fortress Mountain (Lein, Chilton and Walker unpublished ms) has shown that the father's song type has a demonstrable effect on the learning of songs for performance by sons. Males were more likely to sing the song types of their fathers than the other commonly heard song type. This is probably not surprising given that males help their mates in the feeding of young, sing in the vicinity of the nest when delivering food, and often stay with their young through the early weeks of post-fledging life (Clement 1968; Baptista and Morton 1982; Cunningham and Baker 1983; M. R. Lein, unpublished data; unpublished observations).

In the absence of evidence to the contrary, it seems reasonable to assume that young females in this population would also learn, for performance, the song type of their fathers (Kroodsma et al. 1985; but see below). Several authors (e.g., Payne 1981; Cunningham and Baker 1983; Petrinovich 1985; Baptista and Petrinovich 1986; Payne et al. 1987) have extended this assumption to suggest that experience with the song type of the father should constrain the eventual mate choice decisions of his daughters. A female might be predisposed to choose as mates only those males singing her father's song type if

such behavior would increase the likelihood of choosing a male whose genotype was well suited for local conditions (Payne 1983b).

In a study similar to the current investigation, Petrinovich (1988b) examined the songs of fathers and mates of 32 female White-crowned Sparrows (Z. l. nuttalli). He found "no overall tendency for a female to mate with a male that sang the same songs as her father, or even songs with similar components" (Petrinovich 1988b). However, Petrinovich (1988b) considered the small differences in songs of individuals within a dialect population. In that population, the songs of males resembled the songs of their fathers no more than they resembled the songs of their neighbors (Petrinovich 1988b). Since the current study involves substantial song differences that are known to be transmitted from father to son (Lein, Chilton and Walker unpublished ms), a paternal influence over the mate choice decisions of daughters would be far more likely among members of the Fortress Mountain population.

Even so, female White-crowned Sparrows at Fortress Mountain, banded as nestlings, whose fathers' song types were known, did not consistently choose mates singing that song type. Individuals apparently chose mates independent of their song type, neither favoring nor avoiding males that sang the paternal song type (Table 2). The suggestion

that a father's song influences his daughter's choice of mates is not supported by results from the current study. Instead, early experience with two song types appears to preclude an irrevocable commitment to one song type or the other.

The apparent difference in the father's song's influence over his sons and daughters may be a matter of confusion between learning for performance and learning for discrimination. In this mixed-dialect population, a young male learns his father's song for eventual performance. In this same population, a young female apparently learns songs from the greater population for discrimination among potential mates as an adult. The mechanisms of learning for performance and for discrimination may differ profoundly (see Literature Review).

Again, the alternative interpretation of these results would view each adult female with a sexual preference for the song type of her father. In the absence of temporal and energetic constraints, and with an abundance of unmated males of both song types, a female would rarely be observed to mate with a male whose song type was not the song type of her father. This is not the case with female White-crowned Sparrows in this mixed-dialect population. If individual females did have a sexual preference for a particular song type, then some constraint(s) frequently

must have prevented the individual from obtaining a mate of that song type.

Estradiol Experiments

While the field component of this study demonstrates that female White-crowned Sparrows at Fortress Mountain do not consistently choose, as mates, males singing a particular song type, it is unable to demonstrate that they would not do so in the absence of other constraints. A female arriving on the breeding ground in the spring may find a limited choice of potential mates in the time and area allotted for mate search. While an individual female may have a preference for males of a particular song type, paternal or otherwise, other constraints may force her to accept a male with a less-preferred song type. Slagsvold and Dale (1991) have discussed costs involved in locating potential mates and assessing their quality.

It is "because it is seldom clear exactly what options a female has at the time of mate selection" (Baker 1983) that bioassays have been used extensively to predict the behavior of females in the wild in the absence of constraints. Among the advantages of these bioassays is the absence of confounding cues such as territory quality, male quality, and the rate and volume of his songs

(Catchpole 1987). The disadvantages include the artificial nature of the testing protocol, and the "inferential distance between the laboratory experiment and actual mate choice in the natural setting" (Baker 1983).

The current study used the most popular of these bioassays; conspecific songs were broadcast to captive female White-crowned Sparrows treated with exogenous estradiol. The number and intensity of copulation-solicitation displays given in response to playback of songs of different types were recorded.

The current study is most comparable to the studies of female White-crowned Sparrows by Baker and coworkers. Female Z. l. oriantha (Baker et al. 1981a; Baker 1982) and Z. l. nuttalli (Baker 1983) were captured as nestlings, fledglings, and adults, and were tutored in captivity with the taped songs of males from the local ("home" in Baker et al. 1981a; Baker 1982; "natal" in Baker et al. 1982b and Baker 1983) dialect. After photoperiod manipulation and treatment with exogenous estradiol, individuals were subjected to the broadcast of the local dialect and to one or more "alien" dialects.

Each of these studies found that subjects produced significantly more copulation-solicitations displays in response to the local dialects than to any of the alien dialects. Baker (1982) concluded that "females perceive a

difference between dialects and have a decided sexual preference for that representing their home dialect". Preference for a particular dialect was seen as "indicating preference for a sexual partner" (Baker et al. 1981a), and if faced with a choice in nature, a female White-crowned Sparrow would be more likely to mate with a male singing her home dialect than a male singing an alien dialect (Baker et al. 1981a; Baker 1983). Jenkins (1985) counters that preferential response to a tutored "home" dialect over a foreign one "can be equally well interpreted as a preference for a familiar song" over an unfamiliar one.

The subjects from Fortress Mountain used in the current study differ from those of Baker and coworkers in a number of important ways. Comparisons of the findings of the current study with the studies of Baker and coworkers must be viewed in light of these differences. First, all subjects from Fortress Mountain were captured as adults. Second, these birds were not tutored as captives, and presumably learned the songs of males in the wild. Third, the song type of the chosen mate of each female had been documented before capture. Finally, subjects were taken from a population in which two song types were frequently heard. The populations studied by Baker and coworkers were dominated by a single song type.

Baker et al. (1981a) suggested that the behavioral

responses of female White-crowned Sparrows to the songs of males make dialect populations "'viscous' with respect to gene flow". However, as suggested above, results of this study of the responses of females from a mixed-dialect population may be more indicative of behaviors at dialect boundaries than studies of females from single-song populations.

In the current study, females from the Clearwater River region, in which all males were heard to sing the gambelii song type, responded more strongly to playback of the familiar gambelii song than to either of the presumably unfamiliar song types (Table 5). These data provide no reason to question the interpretation of Baker and coworkers; in this region, males singing either oriantha or Cypress Hills songs may be less likely to attract mates than males singing the gambelii song type.

Subjects from Fortress Mountain were less responsive to the playback of the unfamiliar Cypress Hills dialect than to either of the familiar dialects; oriantha or gambelii (Table 4). This result is not unlike those of Baker and coworkers. The Cypress Hills dialect was apparently less stimulating sexually to these subjects, and a male singing this dialect might be less likely to attract mates than males singing either of the familiar local songs. Whether or not the Cypress Hills dialect would

absolutely preclude mate acquisition by its singer at Fortress Mountain is a matter of conjecture.

Of the 14 captive females from Fortress Mountain that responded to playback with copulation-solicitation displays, two were equally responsive to the playback of oriantha and gambelii songs; four were more responsive to gambelii songs, while eight were more responsive to oriantha songs (Table 4). This difference in response is not significant. This suggests that neither the oriantha nor the gambelii song type should leave its singer at a disadvantage in attracting mates when compared to males singing the other common song type.

By themselves, these data do not preclude the possibility that a male singing one of these song types might be at a disadvantage in attracting a particular female with a preference for the other song type. Females that solicited more strongly to the playback of oriantha, for instance, may be willing to mate only with males singing oriantha.

This study demonstrates that the strength of response to the playback of different song types by individual females is not a simple predictor of the song type of their chosen mates. Of the twelve females from Fortress Mountain that responded more strongly to the playback of either oriantha or gambelii songs, six had chosen mates that sang

the song type that elicited a lesser sexual response (Table 4). There are two explanations for this contradiction between bioassay response and mate selected. First, in those cases where a young female gains experience with two different song types, she may be more-or-less equally willing to choose as mates males singing those song types. In this case, differences in response to playback will be a poor predictor of actual mate choice behavior. This explanation is consistent with the working model of this thesis that considers mate choice decisions to be made independent of song type in this mixed-dialect population. Alternately, it is possible that an individual female would choose to mate with a male that sang the song type to which she was most responsive in laboratory testing, but she is often under some constraint that forces her into accepting a male with the less-favored song. Baker et al. (1981a) claimed that, because sex ratios are often skewed in favor of excess males, most or all females should have their choice of mates. Female Pied Flycatchers (Ficedula hypoleuca) visit the territories of as many as nine males before mating (Dale et al. 1990), and female White-crowned Sparrows presumably also reject some males before choosing a mate.

Testosterone Experiments

Female songbirds of some species sing, but do so less frequently than males, and only in specific circumstances. Female Song Sparrows sing most frequently when engaged in territorial interaction with other females (Arcese et al. 1988). These aggressive interactions likely result in high levels of plasma androgens, which in turn likely result in singing (Arcese et al. 1988).

This interpretation is consistent with the observation that treatment with exogenous testosterone often results in song from females of species for which singing is a rare behavior, including Canaries (Mulligan and Erickson 1968), White-crowned Sparrows (Konishi 1965, *Z. l. nuttalli*; Kern and King 1972, *Z. l. gambelii*; but see Baptista et al. in press), and Chaffinches (Kling and Stevenson-Hinde 1977). It is clear, however, that high levels of plasma testosterone are not required for song acquisition, but rather for song production (Marler et al. 1988).

The individual differences in songs given by female White-crowned Sparrows are much greater than individual differences in songs of males (e.g., Baptista et al. in press; this study Fig. 9). Even so, the songs of these females contain many of the dialectal nuances seen in male song (e.g., Figs. 1, 9; Konishi 1965). Behavioral

ecologists have used the dialectal variation in the induced songs of females in three contexts. First, dialectal variation facilitates study of transmission of song between generations (Baptista and Morton 1988). Second, variation has been used to determine whether or not individual females have settled to breed within their own dialect population (Konishi 1965; Baker et al. 1981a; but see Tomback and Baker 1984). Third, comparison of the songs of females and their mates has been used as the basis for studies of assortative mating.

In this third context, mating is assumed to be assortative if the songs of females are of the same type as their chosen mate more often than expected if males were chosen at random (Tomback and Baker 1984). To this end, Tomback and Baker (1984) recorded the songs of male White-crowned Sparrows (Z. l. nuttalli) at or near dialect boundaries, and then captured their mates and induced singing with testosterone. Twenty-four of 25 females had chosen mates whose song dialect matched their own, suggesting that they had mated assortatively (Tomback and Baker 1984).

Three other studies of the testosterone-induced songs of female White-crowned Sparrows found that males were not chosen as mates on the basis of their song type. Fourteen of 16 female Z. l. nuttalli taken from one dialect

population sang songs most like those of an adjacent population, and so their songs were unlike those of their chosen mates (Petrinovich et al. 1981). Baptista and Morton (1982) found that only two of ten captive female Z. l. oriantha (pooled data from two populations) sang the same dialect as did their mates. Of 15 female Z. l. nuttalli taken from a dialect boundary, only seven produced songs of the same dialect type as their chosen mate (Petrinovich and Baptista 1984).

Slater (1989) reviewed the evidence provided by singing female White-crowned Sparrows that suggested assortative mating (e.g., Tomback and Baker 1984) and contradicted assortative mating (e.g., Baptista and Morton 1982, 1988; Petrinovich and Baptista 1984) and found the latter evidence more compelling. Those females that sang songs more commonly heard in other populations "have clearly been elsewhere", while those singing the same song type as their mates "may have memorized their song types since pairing even if they did come from elsewhere" (Slater 1989).

Although an infrequent behavior, singing by female White-crowned Sparrows (Z. l. nuttalli) in nature is frequent enough for Baptista et al. (in press) to compare the naturally-produced songs of females to the songs of their chosen mates. On the basis of the song's second

phrase, either a whistle or a buzz, Baptista et al. (in press) "found no evidence that females consistently match their mate's song".

Of the 36 captive female White-crowned Sparrows from Fortress Mountain, 32 were judged to have produced complex syllables and/or trills which were similar to either the oriantha or gambelii songs of males (Table 6). This permits comparisons of songs of individual females to those of their mates, and of the frequencies of song types among males and females.

Between 1984 and 1988, 58.5% of male White-crowned Sparrows at the Fortress Mountain study site sang the oriantha complex syllable, while 41.5% sang the gambelii complex syllable (Table 7). The oriantha trill was given by 42.4% of males, while 57.6% sang the gambelii trill (Table 7). A significantly greater portion of female White-crowned Sparrows taken captive from Fortress Mountain between 1985 and 1989 and treated with testosterone sang oriantha complex syllables (81.6%) and oriantha trills (80.0%) than did their male counterparts. This high incidence of oriantha singers among captive females suggests that, unlike their brothers (Lein, Chilton and Walker unpublished ms), female White-crowned Sparrows at Fortress Mountain were not learning songs for performance from their fathers. This contradicts the general

assumption (e.g., Baker 1983) that learning of songs for performance by male and female White-crowned Sparrows is similar.

There are several possible explanations for the gender differences in frequency of song types. First, the high incidence of oriantha songs among captive females may be a function of small sample size. This explanation seems unlikely because oriantha singers outnumbered gambelii singers among female captives in all five years of study (Table 6). Second, the early sensitive period for song learning for performance by females may be longer than that for males. Females may learn their songs on migration or the wintering ground, as suggested for juvenile male Z. l. pugetensis (Heinemann 1981). Adult male White-crowned Sparrows are known to sing in both situations (Blanchard DeWolfe 1968a, 1968b, 1968d). Female Z. l. pugetensis are known to winter farther south than males (B. DeWolfe, unpublished observations). If male Z. l. oriantha winter farther south than male Z. l. gambelii, and if females born in the vicinity of Fortress Mountain winter farther south than males from that population, then wintering females may encounter mainly oriantha males, and consequently hear mainly oriantha songs and learn that song type rather than the gambelii equivalent. Third, oriantha complex syllables and trills may, in some way, be "easier" for females to

learn than their gambelii counterparts. The gambelii song was sung by all nine captive females from the Clearwater River that produced recognizable songs (Table 10), suggesting that most (or all) female White-crowned Sparrows are capable of learning that song type. Fourth, females at Fortress Mountain may have learned both common song types for performance, but are for some reason, better able or more motivated to sing oriantha song than gambelii songs. This explanation is difficult to falsify; performance of a single song type does not prove that an individual has not learned or is not capable of performing a second song type. Further, Baptista et al. (in press) have observed female White-crowned Sparrows singing more than one song "theme" in nature. Fifth, oriantha complex syllables are produced by more males than gambelii complex syllables. If females are learning songs for performance from unrelated males, and not from their fathers, then the more prevalent oriantha complex syllable may become the model for song learning by most females. This would not explain the gender difference in prevalence of trills, as gambelii trills are more common than oriantha trills among males. Sixth, it may be that females are predisposed to learn the songs of their fathers, but that the daughters of oriantha singers have a greater probability of surviving to breed than daughters of gambelii singers. This explanation is

not supported by the limited available data. Of the females that were banded as nestlings and returned to breed at Fortress Mountain, eight were fathered by males that sang orianta songs, six had fathers that sang hybrid songs, while eleven had fathers that sang gambelii songs. Seventh, in their first year as adults, many female White-crowned Sparrows may immigrate to Fortress Mountain from more southerly populations in which the orianta song type is more common. This suggestion is not supported by the published dispersal distances for female White-crowned Sparrows (Baker and Mewaldt 1978), or by the frequent return of banded female nestlings to Fortress Mountain. Female White-crowned Sparrows, like males, are likely philopatric, settling to breed within a kilometer or two of their place of birth.

It is of interest to note that the incidence of the orianta song has been increasing among male White-crowned Sparrows at Fortress Mountain since 1984 (M. R. Lein, unpublished data). It is possible that the high incidence of orianta singers among the female population and the increasing incidence of orianta singers among the male population at Fortress Mountain are somehow related.

Thirty-one of 36 female White-crowned Sparrows that were taken captive from Fortress Mountain between 1985 and 1989, and treated with testosterone, produced vocalizations

whose complex syllables were classified either as oriantha or gambelii (Table 6). However, only 15 of these subjects produced trills that could be classified as either oriantha or gambelii (Table 6). No female from Fortress Mountain was judged to have mixed oriantha complex syllables with gambelii trills, or gambelii complex syllables with oriantha trills. Therefore, the following discussion emphasizes the song type differences of females in terms of their complex syllables.

The working model for this thesis suggests that female White-crowned Sparrows in this mixed-dialect population do not favor males of one song type over the other when choosing between potential mates. From this it follows that the song type sung by the female after treatment with testosterone should be of the same type as that of her chosen mate no more often than expected by chance. However, the complex syllables of captive females from Fortress Mountain were of the same type as their chosen mate significantly more often than expected by chance (Table 8). Five of six females that sang gambelii complex syllables had chosen mates that sang gambelii songs, while 15 of 25 females that sang oriantha complex syllables had chosen mates that sang oriantha songs. There was a similar trend, though not significant, for the trills of females and their chosen mates to be of the same type (Table 8).

The frequent matching of complex syllables of females and their mates suggests that mating may be assortative by song type (i.e., as adults, individual female White-crowned Sparrows in the mixed-dialect population have a sexual preference for males singing their own song type). However, the tendency of the complex syllables of females to be of the same type as their mates conflicts with the observation of lack of consistency of mate choice by song type. If individual females preferred a particular song type, they would be expected to consistently choose mates of the same song type in consecutive breeding attempts. This is not the case (Table 1). The tendency of complex syllables of mated individuals to be of the same type also contradicts the lack of correlation between the individual's preferential response to playback of oriantha and gambelii songs and the song type of her chosen mate. If individual females preferred males singing a particular song type, they would be expected to solicit more strongly to the song type of their chosen mates. This is not the case (Table 4).

There are a number of possible explanations for these contradictions. First, mate choice decisions may be made independently of song type, and the similarity of songs of females and their mates may be a product of the small sample size, particularly with regard to females singing

gambelii songs. A larger sample size would help to verify or falsify this explanation.

The second possible explanation for the matching of complex syllables of females and their mates assumes that the song learned by a female for performance is also the song learned for discrimination between potential mates. In this scenario, each female learns a single song type, and will sing that song when treated with testosterone. The explanation does not specify her tutor, but assumes that her song is learned before her first mate is chosen. Males singing that song type will be preferred as mates over males singing the other familiar song types. In contrast with the explanations to follow, her song dictates, to a greater or lesser extent, her mate choice decisions; mating is assortative by song type.

If song matching was the single most important factor in mate choice decisions, and if unmated males of both song types were always available as potential mates, then the song type of each female would always be of the same type as her mate's. However, oriantha songs are produced by a greater portion of females than males (Table 7). Roughly 80% of females at Fortress Mountain would have sought males singing oriantha complex syllables. Since only 60% of males sang that complex syllable type, approximately 20% of all females would be oriantha singers forced to mate with

males singing gambelii complex syllables, mate polygynously with oriantha singers (this is not a common mating system in this or other populations of White-crowned Sparrow), or forgo breeding. If the energetic and temporal costs of searching for mates were insignificant, and if complex syllable types were the overriding factor influencing mate choice decisions, then all females that sang gambelii (20% of the female population) would be able to mate with males singing gambelii complex syllables. In this scenario, in a given year, 80% of all females would be mated assortatively by song type, while the remaining 20% would sing oriantha complex syllables if treated with testosterone, but be mated to males singing gambelii complex syllables.

This view of mate choice decisions is consistent with the frequent matching of complex syllables of females and their mates (Table 8). Anomalies, including the female P/KO that sang gambelii complex syllables but was mated to a male singing oriantha (Table 6), could be attributed to the potentially high temporal and energetic costs of searching for mates with the preferred song type. This view cannot, however, explain the lack of consistency of songs of mates in different years (Table 1). If most females were able to find unmated males of the preferred song type, then they should consistently obtain mates singing the same song type in successive years. This is

not the case. If the lack of consistency is attributed to the high costs of searching for mates, such that females are frequently forced to choose males that sing a less preferred song type, then the model no longer explains the matching of complex syllables of females and their mates.

This second explanation for this frequent matching of complex syllables, which views mating as being assortative by song type, cannot be resolved with other data which supports the position that mating is random with respect to song type.

This second explanation does not explain the gender difference in the incidence of oriantha and gambelii complex syllables. However, since the explanation does not specify the identity of the tutor, it is not falsified by the gender difference.

The third possible explanation for the frequent matching of complex syllables of females and their mates considers the mate choice decisions of individual female White-crowned Sparrows to be independent of song type in this mixed-dialect population. A female arriving on the mating ground in spring is not predisposed to reject males singing either of the most common song types, as a result of her early experience with both song types. However, having paired with a male, she is likely to adopt his song type for performance, regardless of any earlier experience.

Clearly, this behavior is not universal among female White-crowned Sparrows at Fortress Mountain (Table 8). Nine captive females sang oriantha complex syllables despite having been mated to males that sang gambelii songs, and one female mated to an oriantha singer sang gambelii complex syllables.

The suggestion that females adopt the song type of their mate for performance is not inconsistent with what is known of the behavior of male White-crowned Sparrows at Fortress Mountain. A number of males have been observed to sing two or more song types as they establish their first breeding territory. Within a day or two, most settle on a single song type, which they sing to the exclusion of all other song types thereafter (M. R. Lein, unpublished data; unpublished observations). The suggestion does, however, imply a gender difference in closure of the sensitive period for learning for performance. Most adult males sing only one song type and seem unable or unwilling to sing other types. If this third explanation is correct, adult females must be able to change their song type repeatedly to match those of different mates in different years. Jenkins (1985) has suggested that female White-crowned Sparrows may learn the songs of their mates after pairing, with no absolute closure of the sensitive period for learning, although in the scenario proposed here,

individual females would only have to adopt one of the song types with which they were already familiar. Tomback and Baker (1984) apparently did not consider the possibility that female White-crowned Sparrows learn the songs of their mates as an explanation for the frequent matching of song types (Jenkins 1985).

Evidence for or against this explanation for the tendency of the songs of mated individuals to be of the same type might be obtained from the following experiment. Adult females from the mixed-dialect population that had chosen mates singing either of the common song types would be taken captive and treated with testosterone to induce singing. Subjects would be released after documenting their songs. Of those that survived the non-breeding period and returned to breed the following year, some would presumably choose mates whose song type was different than that of the mate in the previous year. These females would be recaptured and treated with testosterone a second time. Those females that switched to perform the song types of their mates in both test years would provide support for the second explanation. The other three possible outcomes (first mate's song in both years; second mate's song in both years; first mate's song in second year, and second mate's song in first year) all contradict this third explanation of the matching of complex syllables of females

and their mates. Interpretation of this experiment would rely on the assumption that the testing protocol in the first year would not influence the outcome of the results obtained from tests in the second year.

This third explanation is consistent with the working model that claims that mate choice decisions are independent of song type. It is also consistent with the observations concerning the song types of mates in consecutive breeding attempts (Table 1), and the number and strength of copulation-solicitation displays given in response to playback of the mate's song type and the other common song type (Table 4). It is, however, unable to explain the ten captive females whose complex syllables did not match those of their mates (Table 8). Further, it cannot be reconciled easily with the results of earlier studies of testosterone-treated female White-crowned Sparrows (e.g., Baptista and Morton 1982, 1988) in which the songs of females and their mates were often dissimilar.

Like the third explanation, the fourth possible explanation for the frequent matching of complex syllables of females and their mates considers the mate choice decisions of individual female White-crowned Sparrows to be independent of song type in this mixed-dialect population.

Females are exposed to more than one song type in the natal area before migrating south, and possibly before

returning to breed the following spring. A male singing a common song type will be judged an appropriate mate by any female who has had experience with that song type. A mate is therefore chosen without regard for his song type.

While a female will have learned more than one song type for discrimination, her repeated exposure to the song type of the first chosen mate may override any previous experience with male song, including the song of her father, in terms of learning for performance. Her sensitive period for learning for performance closes sometime during her first breeding year. Thereafter, if the female sings, either in nature or in captivity, it will be the song type of her first mate, regardless of the song types of her subsequent mates.

An observation of the singing of adult female White-crowned Sparrows in nature by Baptista et al. (in press) may be relevant to the suggestion that females learn the songs of their mates. Early in the breeding cycle, female Z. l. nuttalli sometimes "countersing" with their mates, and when they do, often "match" the mate's song type. This observation "suggest that interaction with males may bring stored song types out of storage, but do not determine the 'typical' song of each female" (Baptista et al. in press). Perhaps the female White-crowned Sparrows at Fortress Mountain were more inclined to sing the song types of their

first mates, but the song was chosen from a variety of song types learned earlier in life. Marler (1990) has used the term "action-based learning" to describe the situation in which the impact of experience with a song type is closely associated in time with the production of that song type.

Nelson (1992) suggested that young male Field Sparrows (Spizella pusilla) acquire their song in a manner similar to the one suggested here for female White-crowned Sparrows. A young male Field Sparrow likely hears and learns a variety of song types early in life, and then select the song from his repertoire that most closely resembles his most actively singing neighbor when establishing his first breeding territory. For a female White-crowned Sparrow, the tutor likely heard most often in her first breeding attempt would be the chosen mate.

Since a female's experience with more than one song type likely precludes her rejection of males singing those song types, the likelihood of her first mate's song being of the same type as the song of any subsequent mate should be no greater than expected by chance.

The probability of an adult female White-crowned Sparrow at Fortress Mountain surviving to breed in the following year is about 50% (M. R. Lein, unpublished data). Therefore 50% of the adult female population should be composed of first time breeders. At the time of capture,

about 50% of the females subsequently treated with testosterone would have been mated for the first time. If females learn for performance the song of their first mate, then 50% of captives in this study might be expected to have produced the same song type as their mate because the mate was the specific tutor. Of the remaining captives, engaged in their second or subsequent breeding attempts, approximately one-half of these would have chosen mates whose song was of the same type as that of their first mate by chance. (Of those male White-crowned Sparrows banded between 1984 and 1988 that sang either oriantha or gambelii songs, 50.7% sang oriantha songs, and 49.3% sang gambelii songs). Therefore, about 75% of testosterone-treated females might have been expected to have sung their current mate's song. Of the 31 captive females that produced complex syllables, 21 (67.7%) sang the same complex syllable type as their chosen mate (Table 8).

This simple model is not meant as a test of the suggestion that females learn the song type of their first mate for performance. Rather, it is designed to show that the suggestion is not incompatible with the results observed. The obvious critical test would involve adult females that had been banded as nestlings. The proposed explanation suggests that the complex syllables of these females should be of the same type as their chosen mates,

but should match the complex syllables of all subsequent mates only by chance.

In this explanation, the father's song type has no special influence over the song(s) learned by his daughters, either for discrimination or performance. This lack of paternal influence over mate choice decisions is consistent with the behavior of females banded as nestlings (Table 2).

Further, this explanation for the frequent matching of complex syllables of females and their mates requires no gender differences in closure of the sensitive period for song learning for performance. The only gender difference is the identity of the tutor. The male usually learns, and performs, the song type of his father (Lein, Chilton and Walker unpublished ms), while the female learns, and is capable of performing, the song type of her first mate. Individuals of both genders perform those song types forever after.

When Petrinovich and Baptista (1984) found that the songs of male White-crowned Sparrows and their testosterone-treated mates were frequently of different dialect types, they suggested that the mismatching of songs might be the result of a gender difference in the inclination to copy the songs of neighboring males at the breeding site. Young males that modify their song to more

closely resemble other territory holders may be able to acquire a territory more easily (Petrinovich and Baptista 1984). Females that have dispersed away from their natal area may be under no pressure to change their song as they sing very little, and do not often interact with neighboring males (Petrinovich and Baptista 1984). Females may be more likely to sing the song of their natal population even if they disperse from it (Petrinovich and Baptista 1984). The view proposed in this thesis requires no gender difference in the propensity toward "action-based learning" of song at the time of first breeding. The only difference is the identity of the tutor; males interact with other territorial males, while females interact with their chosen mate.

This explanation sees mate choice decisions in a mixed-dialect population as being independent of the song types of potential suitors. Mates are chosen for something other than their song types. The first mate choice decision of a female dictates, to a greater or lesser extent, the song type she performs. Song type does not dictate mate choice decisions.

What neither the third nor the fourth explanation can resolve is the apparent gender difference in song type frequency. If females are performing the songs of their chosen mates, then females should sing oriantha and

gambelii song types with the same frequency as males in the population.

Integration of Results of Testosterone and Estradiol Experiments

Although a number of studies have treated female songbirds with exogenous testosterone to induce singing, and a number of other studies have tallied the copulation-solicitation displays given in response to the playback of song by female songbirds treated with exogenous estradiol (see Literature Review), only one previous study has subjected the same individuals to both experimental procedures. Having tallied the copulation-solicitation displays given by five female Z. l. oriantha, captured as adults, to the playback of their "home" dialect and an "alien" dialect, Baker et al. (1981a) obtained songs from three. The purpose was to demonstrate that these females had been breeding in their natal population. The subjects in the study by Baker et al. (1981a) were taken from a population in which males sang only one song type. The current study is the first to allow a comparison of a female's own song type to her responsiveness to the playback of male songs.

Of eleven female White-crowned Sparrows from Fortress

Mountain that produced a song with a recognizable complex syllable and responded preferentially to the playback of either oriantha or gambelii songs, nine responded more strongly to the song type with a complex syllable that matched their own (Table 11). This observation contradicts, though not statistically significant, the null hypothesis that an individual female should solicit no more strongly to her own song type than to the other common song type.

In the absence of all other male attributes, perhaps it should not be surprising that a female would solicit more strongly to her own song type. The individual has been exposed to that song type sufficiently often, and (or) in a sufficiently meaningful context, that she has chosen that song as a model for learning for performance.

It is important to note that while many females solicited more strongly to their own song type (Table 11), and many females sang the same song type as their chosen mate (Table 8), an individual female was not significantly more likely to be mated to a male whose song type elicited her strongest solicitation response (Table 4). The transition from results of this behavioral bioassay to the behavior of individuals in nature must be made with caution. The results of the current study agree with the contention of Baker et al. (1981a) that "early experience

with a song sensitizes the females to be more responsive at a later time", if the authors equate responsiveness with the strength of copulation-solicitation displays given by captives. The current study cannot support the contention that this response can be used as an indicator of preference for one potential mate over another (Baker et al. 1981a).

Significance of Findings

The behavior of White-crowned Sparrows has served as a model for our understanding of the significance of song variation in song birds. Specifically it has been suggested that song learning by White-crowned Sparrows allows the individual to acquire song features specific to the locale, and that these features can be used in male-male and male-female interactions to distinguish between individuals born into the local population and those born into a distant population (Baker et al. 1984). If, for instance, females mate selectively with males from their natal population, avoiding males from more distant populations, then gene flow between these populations will be reduced (Baker 1981; Tomback and Baker 1984). For the individual, the ultimate reason for assortative mating must be the attainment of greater fitness through some genetic

advantage in the offspring of the individual choosing from among potential mates (Warkentin et al. 1992). At a population level, discrimination against males singing foreign songs may facilitate rapid genetic adaptation to the local environment (Baker et al. 1981a).

Do the early experiences of a female White-crowned Sparrow cause her to discriminate against potential mates on the basis of their song type? Females born into a single-song population, far from boundaries with other dialect populations, will generally hear only a single song type during their sensitive period for song learning, and again when choosing among potential mates. If any male is to be at a disadvantage in attracting mates, it should be one that has dispersed far from his natal population, and sings a song unlike the type produced by most other males. However, the limited available data suggests that male White-crowned Sparrows singing "foreign" dialects are able to attract females and rear offspring. Whether or not these males suffer, on average, lesser fitness than males singing the local dialect remains to be demonstrated.

Females born at or near boundaries between dialect populations likely hear two songs during their early sensitive period for song learning. Is the individual entering the breeding population likely to choose mates singing only one song type or the other, or does her early

experience with both songs types preclude a bias against either? This study of the behavior of female White-crowned Sparrows at Fortress Mountain was designed to help answer this question. The results are not incontrovertible.

Sequential mates of banded adult females were just as likely to be of different song types than to be of the same song type. If individuals showed a strong preference for one song type over the other, they would always have been expected to choose mates singing one song type over the other. These observations support the working model of this thesis that mating is not assortative by song type.

In those cases where the father of a banded adult this female was known, the chosen mates were no more likely to sing the same song type as did her father than expected by chance. This contradicts the contention that a female ought to limit her range of potential mates to those singing her father's song type.

The behavioral responses of captive females to the playback of songs of different types have often been used to predict their choice of mates in nature. In this study, many female White-crowned Sparrows from Fortress Mountain were more responsive to one local song type or the other, but the "preferred" song type was no more likely to be the song type of her chosen mate than expected by chance. The responses of a captive female should not be used as a

simple predictor of her mate choice behavior in nature. Preference for one song type, as reported in previous studies, should not be interpreted as an unwillingness to mate with males singing other song types.

The working model of this thesis predicted that captive female White-crowned Sparrows from the mixed-dialect population should be no more likely to sing the song type of their chosen mates than expected by chance. However, 21 of 31 captives produced vocalizations whose complex syllables were of the same type as those of their chosen mates. One interpretation of this result sees individual females learning a single song type early in life, and then seeking to mate with males that sang that song type. This explanation is not easily reconciled with the lack of consistency in the songs of successive mates (see above). A more parsimonious explanation involves the identity of the female's song tutor, and the difference between song learning for discrimination and for performance. Because of its frequency and the context in which it is heard, the song of the first chosen mate of a female may serve as the model for song learning for performance in most cases. In a population in which 50% of females are first time breeders, more than half would sing the same song type as their mates. However, as a result of early experience with two song types, and ongoing song

learning for discrimination, a female in this mixed-dialect population should be willing to mate with males of either song type.

If the early experiences of female White-crowned Sparrows in the mixed-dialect population are similar to those of females at sharper boundaries between dialect populations, then the mate choice behaviors of individuals in these situations might be similar. This study suggests that individual female White-crowned Sparrows searching for mates on one side of a dialect boundary should accept, as mates, males singing the song type most commonly heard on the other side of the boundary. Males singing one song type should not be at a disadvantage in attracting mates for some distance across the border with another dialect population. A dialect boundary, and the behavioral responses of females to dialectal differences in male song, should not restrict gene flow between dialect populations of White-crowned Sparrows. A male's ability to attract mates may decline with increasing distance from the boundary with his natal dialect population.

A number of questions remain concerning the learning of songs by female White-crowned Sparrows and its influence over their mate choice behavior. Their answers are likely interdependent. What is responsible for the gender difference in frequency of song types in this mixed-dialect

population, and does a disparity exist in other intergrade zones? Are learning for discrimination and learning for performance discrete phenomena in terms of mate choice decisions? Is the first chosen mate the female's tutor when she is learning a song for performance? What key stimulus or stimuli are absent in the laboratory environment such that young captive female White-crowned Sparrows seem unable to learn a song for performance? In relative terms, how important are the complex syllable and trill components of the male song in the mate choice decisions of females? Is a rare but established song type, like the hybrid song at Fortress Mountain, as effective in attracting mates as a more common song type? When answers to these questions are available, they may support or contradict the position that the early experiences of a female White-crowned Sparrow in a mixed-dialect population, and perhaps at sharper dialect boundaries, prevent her from discriminating against potential mates of either song type.

LITERATURE CITED

- Adkisson, C. S. 1981. Geographic variation in vocalizations and evolution of North American Pine Grosbeaks. *Condor* 83:277-288.
- Adret-Hausberger, M. 1982. Social influences on the whistled songs of Starlings. *Behav. Ecol. Sociobiol.* 11:241-246.
- Anderson, M. E., and R. N. Conner. 1985. Northern Cardinal song in three forest habitats in eastern Texas. *Wilson Bull.* 97:436-449.
- Andrew, R. J. 1962. Evolution of intelligence and vocal mimicking. *Science* 137:585-589.
- American Ornithologists' Union. 1957. Check-list of North American birds. Fifth Edition. American Ornithologists' Union. Port City Press, Inc. Baltimore.
- Arcese, P., P. K. Stoddard, and S. M. Hiebert. 1988. The form and function of song in female Song Sparrows. *Condor* 90:44-50.
- Austen, M. J. W., and P. T. Handford. 1991. Variation in the songs of breeding Gambel's White-crowned Sparrows near Churchill, Manitoba. *Condor* 93:147-152.
- Avery, M., and L. W. Oring. 1977. Song dialects in the Bobolink (*Dolichonyx oryzivorus*). *Condor* 79:113-118.
- Bailey, E. D., and J. A. Baker. 1982. Recognition characteristics in covey dialects of Bobwhite Quail. *Condor* 80:317-320.
- Baker, A. J., and P. F. Jenkins. 1987. Founder effect and cultural evolution of songs in an isolated population of chaffinches, *Fringilla coelebs*, in the Chatham Islands. *Anim. Behav.* 35:1793-1803.
- Baker, M. C. 1981. Effective population size in a songbird: some possible implications. *Heredity* 46:209-218.
- Baker, M. C. 1982. Vocal dialect recognition and population genetic consequences. *Amer. Zool.* 22:561-569.

- Baker, M. C. 1983. The behavioral response of female Nuttall's White-crowned Sparrows to male song of natal and alien dialects. *Behav. Ecol. Sociobiol.* 12:309-315.
- Baker, M. C. 1987. Intergradation of song between two subspecies of White-crowned Sparrows on the west coast of North America. *Ornis. Scand.* 18:265-268.
- Baker, M. C., and M. A. Cunningham. 1985. The biology of bird-song dialects. *Behav. Brain Sci.* 8:85-133.
- Baker, M. C., and L. R. Mewaldt. 1978. Song dialects as barriers to dispersal in White-crowned Sparrows, Zonotrichia leucophrys nuttalli. *Evolution* 32:712-722.
- Baker, M. C., and D. B. Thompson. 1985. Song dialects of White-crowned Sparrows: historical processes inferred from patterns of geographic variation. *Condor* 87:127-141.
- Baker, M. C., K. J. Spitler-Nabors, and D. C. Bradley. 1981a. Early experience determines song dialect responsiveness of female sparrows. *Science* 214:819-821.
- Baker, M. C., D. B. Thompson, G. L. Sherman, and M. A. Cunningham. 1981b. The role of male vs male interactions in maintaining population dialect structure. *Behav. Ecol. Sociobiol.* 8:65-69.
- Baker, M. C., G. L. Sherman, T. C. Theimer, and D. C. Bradley. 1982a. Population biology of White-crowned Sparrows: residence time and local movements of juveniles. *Behav. Ecol. Sociobiol.* 11:133-137.
- Baker, M. C., K. J. Spitler-Nabors, and D. C. Bradley. 1982b. The response of female Mountain White-crowned Sparrows to songs from their natal dialect and an alien dialect. *Behav. Ecol. Sociobiol.* 10:175-179.
- Baker, M. C., D. B. Thompson, G. L. Sherman, M. A. Cunningham, and D. F. Tomback. 1982c. Allozyme frequencies in a linear series of song dialect populations. *Evolution* 36:1020-1029.
- Baker, M. C., D. F. Tomback, D. B. Thompson, T. C. Theimer, and D. C. Bradley. 1984. Behavioral consequences of song learning: discrimination of song types by male

- White-crowned Sparrows. Learn. Motiv. 15:428-440.
- Baker, M. C., T. K. Bjerke, H. Lampe, and Y. Espmark. 1986. Sexual response of female Great Tits to variation in size of males' song repertoires. Amer. Natur. 128:491-498.
- Baker, M. C., T. K. Bjerke, H. U. Lampe, and Y. O. Espmark. 1987. Sexual response of female Yellowhammers to differences in regional song dialects and repertoire sizes. Anim. Behav. 35:395-401.
- Balaban, E. 1988. Bird song syntax: learned intraspecific variation is meaningful. Proc. Natl. Acad. Sci. USA 85:3657-3660.
- Banks, R. C. 1964. Geographic variation in the White-crowned Sparrow Zonotrichia leucophrys. Univ. Calif. Publ. Zool. 70:1-123.
- Baptista, L. F. 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (Zonotrichia leucophrys nuttalli). Univ. Calif. Publ. Zool. 105:1-52.
- Baptista, L. F. 1977. Geographic variation in song and dialects of the Puget Sound White-crowned Sparrow. Condor 79:356-370.
- Baptista, L. F. 1982. Why birds sing. Pac. Disc. 35(4):1-9.
- Baptista, L. F. 1985a. The functional significance of song sharing in the White-crowned Sparrow. Can. J. Zool. 63:1741-1752.
- Baptista, L. F. 1985b. Bird song dialects: social adaptation or assortative mating? Behav. Brain Sci. 8:100-101.
- Baptista, L. F. 1990. Dialectal variation in the raincall of the Chaffinch (Fringilla coelebs). Die Vogelwarte 35: 249-256.
- Baptista, L. F., and J. R. King. 1980. Geographical variation in song and song dialects of montane White-crowned Sparrows. Condor 82:267-284.
- Baptista, L. F., and M. L. Morton. 1982. Song dialects and mate selection in montane White-crowned Sparrows.

Auk 99:537-547.

- Baptista, L. F., and M. L. Morton. 1988. Song learning in montane White-crowned Sparrows: from whom and when. Anim. Behav. 36:1753-1764.
- Baptista, L.F., and L. Petrinovich. 1984. Social interaction, sensitive phases and the song template hypothesis in the White-crowned Sparrow. Anim. Behav. 32:172-181.
- Baptista, L. F., and L. Petrinovich. 1986. Song development in the White-crowned Sparrow: social factors and sex differences. Anim. Behav. 34:1359-1371.
- Baptista, L. F., P. W. Trail, B. B. DeWolfe, and M. L. Morton. in press. Singing and the functions thereof in female White-crowned Sparrows. Anim. Behav.
- Barrington, D. 1773. Experiments and observations of the singing of birds. Phil. Trans. R. Soc. London 63:249-291.
- Becker, P. H. 1982. The coding of species-specific characteristics in bird sounds. In Acoustic communication in birds, Vol. 1. Edited by D. Kroodsma, E. H. Miller, and H. Ouellet. Academic Press, New York. pp 213 - 153.
- Beecher, M. D. 1988. Kin recognition in birds. Behav. Genet. 18:465-482.
- Blanchard, B. D. 1941. The White-crowned Sparrow (Zonotrichia leucophrys) of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publ. Zool. 46:1-178.
- Blanchard DeWolfe, B. 1968a. Zonotrichia leucophrys nuttalli Ridgway, Nuttall's White-crowned Sparrow. In Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part three. Edited by O. L. Austin. Dover Publications, New York. pp. 1292-1324
- Blanchard DeWolfe, B. 1968b. Zonotrichia leucophrys gambelli (Nuttall), Gambel's White-crowned Sparrow. In Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part three. Edited by O. L. Austin. Dover

- Publications, New York. pp. 1324-1338.
- Blanchard DeWolfe, B. 1968c. Zonotrichia leucophrys oriantha Oberholser, Mountain White-crowned Sparrow. In Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part three. Edited by O. L. Austin. Dover Publications, New York. pp. 1338-1344.
- Blanchard DeWolfe, B. 1968d. Zonotrichia leucophrys pugetensis Grinnell, Puget Sound White-crowned Sparrow. In Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part three. Edited by O. L. Austin. Dover Publications, New York. pp. 1344-1352.
- Borrer, D. J. 1956. Variation in Carolina Wren songs. Auk 73:211-229.
- Bowman, R. I. 1979. Adaptive morphology of song dialects in Darwin's Finches. J. Ornithol. 120:353-389.
- Brenowitz, E. A. 1985. Bird-song dialects: filling in the gaps. Behav. Brain Sci. 8:101-102.
- Brooks, R. J., and J. B. Falls. 1975a. Individual recognition by song in White-throated Sparrows. I. Discrimination of songs of neighbors and strangers. Can. J. Zool. 53:879-888.
- Brooks, R. J., and J. B. Falls. 1975b. Individual recognition by song in White-throated Sparrows. III. Song features used in individual recognition. Can. J. Zool. 53:1749-1761.
- Burley, N. 1983. The meaning of assortative mating. Ethol. Sociobiol. 4:191-203.
- Capranica, R. R., L. S. Frishkopf, and E. Nevo. 1973. Encoding of geographic dialects in the auditory system of the cricket frog. Science 182:1272-1275.
- 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. 1983. Variation in the song of the Great Reed Warbler Acrocephalus arundinaceus in relation to mate attraction and territorial defence. Anim. Behav. 31:1217-1225.

- Catchpole, C. K. 1987. Bird song, sexual selection and female choice. *Trends Ecol. Evol.* 2:94-97.
- Catchpole, C. K., J. Dittami, and B. Leisler. 1984. Differential responses to male song repertoires in female songbirds implanted with oestradiol. *Nature* 312:563-564.
- Clayton, N. S. 1990. Assortative mating in Zebra Finch subspecies, Taeniopygia guttata guttata and T. g. castanotis. *Phil. Trans. R. Soc. London B* 330:351-370.
- Clayton, N. S., and E. Pröve. 1989. Song discrimination in female Zebra Finches and Bengalese Finches. *Anim. Behav.* 38:352-354.
- Clement, R. C. 1968. Zonotrichia leucophrys leucophrys (Forster), Eastern White-crowned Sparrow. In *Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies*. Part three. Edited by O. L. Austin. Dover Publications, New York. pp. 1273-1291.
- Cooke, F., P. J. Mirsky, and M. B. Seiger. 1972. Color preferences in the Lesser Snow Goose and their possible role in mate selection. *Can. J. Zool.* 50:529-536.
- Cortopassi, A. J., and L. R. Mewaldt. 1965. The circumannual distribution of White-crowned Sparrows. *Bird-Banding* 36:141-169
- Crow, J. F., and J. Felsenstein. 1968. The effect of assortative mating on the genetic composition of a population. *Eugen. Quart.* 15:85-97.
- Cunningham, M. A., and M. C. Baker. 1983. Vocal learning in White-crowned Sparrows: sensitive phase and song dialects. *Behav. Ecol. Sociobiol.* 13:259-269.
- Cunningham, M. A., M. C. Baker, and T. J. Boardman. 1987. Microgeographic song variation in the Nuttall's White-crowned Sparrow. *Condor* 89:261-275.
- Dale, S., T. Amundsen, J. T. Lifjeld, and T. Slagsvold. 1990. Mate sampling behaviour of female Pied Flycatchers: evidence for active mate choice. *Behav. Ecol. Sociobiol.* 27:87-91.

- DeWolfe, B. B., and R. H. DeWolfe. 1962. Mountain White-crowned Sparrows in California. *Condor* 64:378-389.
- DeWolfe, B. B., D. D. Kaska, and L. J. Peyton. 1974. Prominent variations in the songs of Gambel's White-crowned Sparrows. *Bird-Banding* 45:224-252.
- DeWolfe, B. B., L. F. Baptista, and L. Petrinovich. 1989. Song development and territory establishment in Nuttall's White-crowned Sparrows. *Condor* 91:397-407.
- Dietrich, V. K. 1980. Vorbildwahl in der Gesangsentwicklung beim Japanischen Mövchen (Lonchura striata var. domestica, Estrildidae). *Z. Tierpsychol.* 52:57-76.
- Dittus, W. P. J., and R. E. Lemon. 1969. Effects of song tutoring and acoustic isolation on the song repertoires of Cardinals. *Anim. Behav.* 17:523-533.
- Dooling, R., and M. Searcy. 1980. Early perceptual selectivity in the Swamp Sparrow. *Develop. Psychobiol.* 13:499-506.
- Eales, L. A. 1989. The influences of visual and vocal interaction on song learning in Zebra Finches. *Anim. Behav.* 37:507-520.
- Eberhardt, C., and L. F. Baptista. 1977. Intraspecific and interspecific song mimesis in California Song Sparrows. *Bird-Banding* 48:193-205.
- Emlen, S. T. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* 41:130-171.
- Eriksson, D., and L. Wallin. 1986. Male bird song attracts females - a field experiment. *Behav. Ecol. Sociobiol.* 19:297-299.
- Feekes, F. 1977. Colony-specific song in Cacicus cela (Icteridae, Aves): the pass-word hypothesis. *Ardea* 65:197-202.
- Ficken, M. S., R. W. Ficken, and K. M. Apel. 1985. Dialects in a call associated with pair interactions in the Black-capped Chickadee. *Auk* 102:145-151.
- Fleischer, R. C., and S. I. Rothstein. 1988. Known

- secondary contact and rapid gene flow among subspecies and dialects in the Brown-headed Cowbird. *Evolution* 42:1146-1158.
- Fryer, G. I., and E. A. Johnson. 1988. Reconstructing fire behaviour and effects in a subalpine forest. *J. Appl. Ecol.* 25:1063-1072.
- Goodfellow, D. J., and P. J. B. Slater. 1986. A model of bird song dialects. *Anim. Behav.* 34:1579-1580.
- Gottlieb, G. 1985. The need to map auditory perception onto vocal production in bird song. *Behav. Brain Sci.* 8:104-105.
- Gould, J. L. 1982. Why do honey bees have dialects? *Behav. Ecol. Sociobiol.* 10:53-56.
- Grimes, L. G. 1974. Dialects and geographical variation in the song of the Splendid Sunbird Nectarinia coccinigaster. *Ibis* 116:314-329.
- Hafner, D. J., and K. E. Petersen. 1985. Song dialects and gene flow in the White-crowned Sparrow, Zonotrichia leucophrys nuttalli. *Evolution* 39:687-694.
- Handford, P. 1981. Vegetational correlates of variation in the song of Zonotrichia capensis. *Behav. Ecol. Sociobiol.* 8:203-206.
- Handford, P. 1988. Trill rate dialects in the Rufous-collared Sparrow, Zonotrichia capensis, in northwestern Argentina. *Can. J. Zool.* 66:2658-2670.
- Handford, P., and S. C. Loughheed. 1991. Variation in duration and frequency characters in the song of the Rufous-collared Sparrow, Zonotrichia capensis, with respect to habitat, trill dialects and body size. *Condor* 93:644-658.
- Hansen, P. 1979. Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Anim. Behav.* 27:1270-1271.
- Hartl, D. L. 1981. A primer of population genetics. Sinauer Associates, Inc. Sunderland, MA. 191 pp.
- Hegelbach, J. 1986. Gesangsdialekt und

fortpflanzungserfolg bei Graumammer-männchen Emberiza calandra. Orn. Beob. 83:253-256.

Heinemann, D. 1981. Song dialects, migration, and population structure of Puget Sound White-crowned Sparrows. Auk 98:512-521.

Hill, B. G., and M. R. Lein. 1985. The non-song vocal repertoire of the White-crowned Sparrow. Condor 87:327-335.

Hultsch, H., and M.-L. Kopp. 1989. Early auditory learning and song improvisation in Nightingales, Luscinia megarhynchos. Anim. Behav. 37:510-512.

James, R. D. 1976. Unusual songs with comments on song learning among vireos. Can. J. Zool. 54:1223-1226.

Jenkins, P. F. 1977. Cultural transmission of song patterns and dialect development in a free-living bird population. Anim. Behav. 26:50-78.

Jenkins, P. F. 1985. Song learning, competition, and dialects. Behav. Brain Sci. 8:108.

Johnston, R. F., and S. G. Johnson. 1989. Nonrandom mating in feral pigeons. Condor 91:23-29.

Kern, M. D., and J. R. King. 1972. Testosterone-induced singing in female White-crowned Sparrows. Condor 74:204-209.

Kling, J. W., and J. Stevenson-Hinde. 1977. Development of song and reinforcing effects of song in female Chaffinches. Anim. Behav. 25:215-220.

Konishi, M. 1965. The role of auditory feedback in the control of vocalization in the White-crowned Sparrow. Z. Tierpsychol. 22:770-783.

Konishi, M. 1978. Auditory environment and vocal development in birds. In Perception and experience. Edited by R. D. Walk and H. L. Pick. Plenum Press, New York. pp. 105-118.

Konishi, M. 1985. Birdsong: from behavior to neuron. Ann. Rev. Neurosci. 8:125-170.

Kroodsma, D. E. 1972. Variations in songs of Vesper Sparrows in Oregon. Wilson Bull. 84:173-178.

- Kroodsma, D. E., and R. Pickert. 1980. Environmentally dependent sensitive periods for avian vocal learning. *Nature* 288:477-479.
- Kroodsma, D. E., M. C. Baker, L. F. Baptista, and L. Petrinovich. 1985. Vocal "dialects" in Nuttall's White-crowned Sparrow. *Curr. Ornithol.* 2:103-133.
- Le Boeuf, B. J., and L. F. Petrinovich. 1974. Dialects of northern elephant seals, Mirounga angustirostris: origin and reliability. *Anim. Behav.* 22:656-663.
- Lein, M. R. 1979. Song pattern of the Cypress Hills population of White-crowned Sparrows. *Can. Field-Natur.* 93:272-275.
- Lein, M. R., and K. W. Corbin. 1990. Song and plumage phenotypes in a contact zone between subspecies of the White-crowned Sparrow (Zonotrichia leucophrys). *Can. J. Zool.* 68:2625-2629.
- Lemon, R. E. 1971. Differentiation of song dialects in Cardinals. *Ibis* 113:373-377.
- Lougheed, S. C., A. J. Lougheed, M. Rae, and P. Handford. 1989. Analysis of a dialect boundary in chaco vegetation in the Rufous-collared Sparrow. *Condor* 91:1002-1005.
- Marler, P. 1952. Variation in the song of the Chaffinch. *Ibis* 94:458-472.
- Marler, P. 1970a. A comparative approach to vocal learning: song development in White-crowned Sparrows. *J. Comp. Physiol. Psych.* 71:1-25.
- Marler, P. 1970b. Birdsong and speech development: could there be parallels? *Amer. Sci.* 58:669-673.
- Marler, P. 1990. Song learning: the interface between behaviour and neuroethology. *Phil. Trans. R. Soc. Lond. B* 329:109-114.
- Marler, P., and S. Peters. 1977. Selective vocal learning in a sparrow. *Science* 198:519-522.
- Marler, P., and S. Peters. 1982. Long-term storage of learned birdsongs prior to production. *Anim. Behav.* 30:479-482.

- Marler, P., and S. Peters. 1987. A sensitive period for song acquisition in the Song Sparrow, Melospiza melodia: a case of age-limited learning. *Ethology* 76:89-100.
- Marler, P., and S. Peters. 1988a. Sensitive periods for song acquisition from tape recordings and live tutors in the Swamp Sparrow, Melospiza georgiana. *Ethology* 77:76-84.
- Marler, P., and S. Peters. 1988b. The role of song phonology and syntax in vocal learning preferences in the Song Sparrow, Melospiza melodia. *Ethology* 77:125-149.
- Marler, P., and M. Tamura. 1962. Song "dialects" in three populations of White-crowned Sparrows. *Condor* 64:368-377.
- Marler, P., and M. Tamura. 1964. Culturally transmitted patterns of vocal behavior in sparrows. *Science* 146:1483-1486.
- Marler, P., S. Peters, G. F. Ball, A. M. Dufty, and J. C. Wingfield. 1988. The role of sex steroids in the acquisition and production of birdsong. *Nature* 336:770-772.
- McGregor, P. K. 1980. Song dialects in the Corn Bunting (Emberiza calandra). *Z. Tierpsychol.* 54:285-297.
- McGregor, P. K., and M. I. Avery. 1986. The unsung songs of Great Tits (Parus major): learning neighbours' songs for discrimination. *Behav. Ecol. Sociobiol.* 18:311-316.
- McGregor, P. K., and J. R. Krebs. 1982. Mating and song types in the Great Tit. *Nature* 297:60-61.
- McGregor, P. K., V. R. Walford, and D. G. C. Harper. 1988. Song inheritance and mating in a songbird with local dialects. *Bioacoustics* 1:107-129.
- Miller, D. B. 1979. Long-term recognition of father's song by female Zebra Finches. *Nature* 280:389-391.
- Milligan, M. M., and J. Verner. 1971. Inter-population song dialect discrimination in the White-crowned Sparrow. *Condor* 73:208-213.

- Millington, S. J., and T. D. Price. 1985. Song inheritance and mating patterns in Darwin's finches. *Auk* 102:342-346.
- Møller, A. P. 1982. Song dialects in a population of Yellowhammers Emberiza citrinella in Denmark. *Ornis Scand.* 13:239-246.
- Morton, M. L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the Mountain White-crowned Sparrow. *Condor* 94:117-133.
- Morton, M. L., M. E. Pereyra, and L. F. Baptista. 1985. Photoperiodically induced ovarian growth in the White-crowned Sparrow (Zonotrichia leucophrys gambelii) and its augmentation by song. *Comp. Biochem. Physiol.* 80A:93-97.
- Mulligan, J., and R. Erickson. 1968. Instrumental analysis of hormone induced singing in female canaries. *Amer. Zool.* 8:743-744.
- Mundinger, P. C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In *Acoustic communication in birds*. Vol. 2. Edited by D. E. Kroodsma, E. H. Miller, and H. Ouellet. Academic Press, New York. pp. 147-208.
- Nelson, D. A. 1992. Song overproduction and selective attrition lead to song sharing in the Field Sparrow (Spizella pusilla). *Behav. Ecol. Sociobiol.* 30:415-424.
- Nottebohm, F. 1969. The song of the Chingolo, Zonotrichia capensis, in Argentina: description and evaluation of a system of dialects. *Condor* 71:299-315.
- Nottebohm, F. 1970. Ontogeny of bird song. *Science* 167:950-956.
- Nottebohm, F. 1972. The origins of vocal learning. *Amer. Natur.* 106:116-140.
- Nottebohm, F. 1975. Vocal behavior in birds. *Avian Biol.* 5:287-332.
- Orejuela, J. E., and M. L. Morton. 1975. Song dialects in

- several populations of mountain White-crowned Sparrows (Zonotrichia leucophrys oriantha) in the Sierra Nevada. Condor 77:145-153.
- Payne, R. B. 1973. Vocal mimicry of the Paradise Whydahs (Vidua) and response of female Whydahs to the songs of their hosts (Pytilia) and their mimics. Anim. Behav. 21:762-771.
- Payne, R. B. 1981. Population structure and social behavior: models for testing the ecological significance of song dialects in birds. In Natural selection and social behavior: recent research and new theory. Edited by R. D. Alexander and D. W. Tinkle. Chiron Press, New York. pp. 108-120.
- Payne, R. B. 1983a. The social context of song mimicry: song-matching dialects in Indigo Buntings (Passerina cyanea). Anim. Behav. 31:788-805.
- Payne, R. B. 1983b. Bird songs, sexual selection, and female mating strategies. In Social behavior of female vertebrates. Edited by K. Wasser. Academic Press, New York. pp. 55-90.
- Payne, R. B. 1985. Behavioral continuity and change in local song populations of Village Indigobirds Vidua chalybeata. Z. Tierpsychol. 70:1-44.
- Payne, R. B. 1986. Bird songs and avian systematics. Curr. Ornithol. 3:87-126.
- Payne, R. B., L. L. Payne, and S. M. Doehlert. 1987. Song, mate choice and the question of kin recognition in a migratory songbird. Anim. Behav. 35:35-47.
- Pellerin, M. 1982. The role of silences and elements in the recognition of a dialect in the Corn Bunting. Behaviour 81:287-295.
- Petrinovich, L. 1985. Factors influencing song development in the White-crowned Sparrow (Zonotrichia leucophrys). J. Comp. Psych. 99:15-29.
- Petrinovich, L. 1988a. The role of social factors in White-crowned Sparrow song development. In Social learning: psychological and biological perspectives. Edited by T. R. Zentall and B. G. Galef, Jr. Lawrence Erlbaum Associates, Hillsdale. pp. 255-278.

- Petrinovich, L. 1988b. Individual stability, local variability and the cultural transmission of song in White-crowned Sparrows (Zonotrichia leucophrys nuttalli). Behaviour 107:208-240.
- Petrinovich, L., and L. F. Baptista. 1984. Song dialects, mate selection, and breeding success in White-crowned Sparrows. Anim. Behav. 32:1078-1088.
- Petrinovich, L., and T. L. Patterson. 1981. The responses of White-crowned Sparrows to songs of different dialects and subspecies. Z. Tierpsychol. 57:1-14.
- Petrinovich, L., T. Patterson, and L. F. Baptista. 1981. Song dialects as barriers to dispersal: a re-evaluation. Evolution 35:180-188.
- Pleszczynska, W. 1980. Interspecific and intraspecific song discrimination by Zonotrichia albicollis and Z. leucophrys. Can. J. Zool. 58:1433-1438.
- Rand, A. L. 1948. Glaciation, an isolating factor in speciation. Evolution 2:314-321.
- Searcy, W. A., P. Marler, and S. S. Peters. 1981. Species song discrimination in adult female Song and Swamp sparrows. Anim. Behav. 29:997-1003.
- Shields, W. M. 1985. Avian song dialects: genetic adaptation and deceptive mimicry? Behav. Brain Sci. 8:114-115.
- Slagsvold, T., and S. Dale. 1991. Mate choice models: can cost of searching and cost of courtship explain mating patterns of female Pied Flycatchers? Ornis Scand. 22:319-326.
- Slater, P. J. B. 1986. The cultural transmission of bird song. Trends Ecol. Evol. 1:94-97.
- Slater, P. J. B. 1989. Bird song learning: causes and consequences. Ethol. Ecol. Evol. 1:19-46.
- Slater, P. J. B., L. A. Eales, and N. S. Clayton. 1988. Song learning in Zebra Finches (Taeniopygia guttata): progress and prospects. Adv. Study Behav. 18:1-34.
- Slobodchikoff, C. N., and R. Coast. 1980. Dialects in the alarm calls of prairie dogs. Behav. Ecol. Sociobiol. 7:49-53.

- Taverner, P. A. 1926. Birds of Western Canada. Victoria Memorial Museum, Museum Bulletin No. 41. Ottawa. 380 pp.
- Temrin, H. 1986. Singing behaviour in relation to polyterritorial polygyny in the Wood Warbler (Phylloscopus sibilatrix). Anim. Behav. 34:146-152.
- Thielcke, G. 1969. Geographic variation in bird vocalizations. In Bird vocalizations. Edited by R. A. Hinde. Cambridge University Press, Cambridge. pp. 311-339.
- Thielcke, G. 1992. Stabilität und Änderungen von Dialekten und Dialektgrenzen beim Gartenbaumläufer (Certhia brachydactyla). J. Ornithol. 133:43-59.
- Thielcke, G., and K. Wüstenberg. 1985. Experiments on the origin of dialects in the Short-toed Tree Creeper (Certhia brachydactyla). Behav. Ecol. Sociobiol. 16:195-201.
- Tombback, D. F., and M. C. Baker. 1984. Assortative mating by White-crowned Sparrows at song dialect boundaries. Anim. Behav. 32:465-469.
- Trainer, J. M. 1980. Comments on a kin association model of bird song dialects. Anim. Behav. 28: 310-314.
- Trainer, J. M. 1983. Changes in song dialect distributions and microgeographic variation in song of White-crowned Sparrows (Zonotrichia leucophrys nuttalli). Auk 100:568-582.
- Trainer, J. M. 1989. Cultural evolution in song dialects of Yellow-rumped Caciques in Panama. Ethology 80:190-204.
- Treisman, M. 1978. Bird song dialects, repertoire size, and kin association. Anim. Behav. 26:814-817.
- Van Tyne, J., and A. J. Berger. 1971. Fundamentals of Ornithology. John Wiley and Sons. New York.
- Warkentin, I. G., P. C. James, and L. W. Oliphant. 1992. Assortative mating in urban-breeding Merlins. Condor, 94:418-426.
- Waser, P. M. 1985. Are dialects epiphenomena? Behav.

Brain Sci. 8:117.

Wasserman, F. E. 1977. Mate attraction function of song in the White-throated Sparrow. Condor 79:125-127.

Wasserman, F. E. 1979. The relationship between habitat and song in the White-throated Sparrow. Condor 81:424-426.

Wasserman, F. E., and J. A. Cigliano. 1991. Song output and stimulation of the female in White-throated Sparrows. Behav. Ecol. Sociobiol. 29:55-59.

Westneat, D. F., P. W. Sherman, and M. L. Morton. 1990. The ecology and evolution of extra-pair copulations in birds. Curr. Ornithol. 7:331-369.

Whitney, C. L. 1989. Geographical variation in Wood Thrush song: a comparison of samples recorded in New York and South Carolina. Behaviour 111:49-60.

Wiens, J. A. 1982. Song pattern variation in the Sage Sparrow (Amphispiza belli): dialects or epiphenomena? Auk 99:208-229.

Wilson, E. O., and W. H. Bossert. 1971. A primer of population biology. Sinauer Associates, Inc. Stamford, CT. 192 pp.

Winn, H. E., and L. K. Winn. 1978. The song of the humpback whale Megaptera novaeangliae in the West Indies. Marine Biol. 47:97-114.

Zimmer, U. E. 1982. Birds react to playback of recorded songs by heart rate alteration. Z. Tierpsychol. 58:25-30.

Zink, R. M., and G. F. Barrowclough. 1984. Allozymes and song dialects: a reassessment. Evolution 38:444-448.