Symmetry, Quality, and Sexual Success
in Male Red-winged Blackbirds

by

Kevin William Dufour

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy

Department of Biology

Carleton University
Ottawa, Ontario
October 1996
© 1996, Kevin W. Dufour

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 0-612-19398-5

Name Kevin W. Dufour

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.

0000

0000

U-M-I

SUBJECT TERM

SUBJECT CODE

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
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 0329
Language and Literature 0521
Mathematics 0280
Music 0522
Philosophy of 0598
Physical 0523

Psychology 0525
Reading 0535
Religious 0527
Sciences 0714
Secondary 0533
Social Sciences 0534
Sociology of 0340
Special 0520
Teacher Training 0530
Technology 0710
Tests and Measurements 0288
Vocational 0747

LANGUAGE, LITERATURE AND LINGUISTICS

Language 0670
General 0670
Ancient 0289
Linguistics 0290
Modern 0291
Literature 0401
General 0294
Classical 0295
Comparative 0295
Medieval 0297
Modern 0299
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 0318
General 0321
Biblical Studies 0319
Clergy 0320
History of 0322
Philosophy of 0469
Theology 0323
American Studies 0324
Anthropology 0326
Archaeology 0327
Cultural 0310
Physical 0272
Business Administration 0454
Accounting 0338
Banking 0385
Management 0501
Marketing 0503
Canadian Studies 0505
Economics 0508
General 0509
Agricultural 0510
Commerce-Business 0511
Finance 0358
History 0366
Labor 0351
Theory 0578
Folklore 0366
Geography 0351
Gerontology 0578
History 0578

SOCIAL SCIENCES

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

Ancient 0570
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 0615
General 0617
International Law and Relations 0616
Public Administration 0814
Recreation 0452
Social Work 0626
Sociology 0938
General 0631
Criminology and Penology 0628
Demography 0629
Ethnic and Racial Studies 0630
Individual and Family Studies 0700
Industrial and Labor Relations 0344
Public and Social Welfare 0709
Social Structure and Development 0999
Theory and Methods 0453
Transportation 0453
Urban and Regional Planning 0453
Women's Studies 0453

THE SCIENCES AND ENGINEERING

BIOLOGICAL SCIENCES

Agriculture 0473
General 0285
Agronomy 0475
Animal Culture and Nutrition 0476
Animal Pathology 0359
Food Science and Technology 0478
Forestry and Wildlife 0479
Plant Culture 0480
Plant Pathology 0817
Plant Physiology 0277
Range Management 0746
Wood Technology 0306
Biology 0306
General 0287
Anatomy 0308
Biostatistics 0309
Botany 0379
Cell 0329
Ecology 0353
Entomology 0369
Genetics 0793
Limnology 0410
Microbiology 0307
Molecular 0317
Neuroscience 0416
Oceanography 0433
Physiology 0821
Radiation 0778
Veterinary Science 0472
Zoology 0786
General 0760
Medical 0425
Biophysics 0996
Earth Sciences 0425
Biogeochemistry 0996
Geochemistry 0996

Geodesy 0370
Geology 0372
Geophysics 0373
Hydrology 0388
Mineralogy 0411
Paleontology 0425
Paleobotany 0426
Paleozoology 0418
Paleogeography 0985
Physical Geography 0368
Physical Oceanography 0415

HEALTH AND ENVIRONMENTAL SCIENCES

Environmental Sciences 0768
Health Sciences 0566
General 0300
Audiology 0992
Chemotherapy 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 0485
Chemistry 0749
General 0486
Agricultural 0487
Analytical 0488
Biochemistry 0738
Inorganic 0490
Nuclear 0491
Organic 0494
Pharmaceutical 0495
Physical 0754
Polymer 0405
Radiation 0605
Mathematics 0986
Physics 0606
General 0608
Acoustics 0748
Astronomy and Astrophysics 0607
Atmospheric Science 0798
Atomic 0759
Electronics and Electricity 0609
Elementary Particles and High Energy 0610
Fluid and Plasma 0752
Molecular 0756
Nuclear 0611
Optics 0463
Radiation 0346
Solid State 0984
Statistics 0984
Applied Sciences 0984
Applied Mechanics 0984
Computer Science 0984

Engineering 0537
General 0538
Aerospace 0539
Automotive 0540
Biomedical 0541
Chemical 0542
Civil 0543
Electronics and Electrical 0544
Heat and Thermodynamics 0545
Hydraulic 0546
Industrial 0547
Marine 0794
Materials Science 0548
Mechanical 0743
Metallurgy 0551
Mining 0552
Nuclear 0549
Packaging 0745
Petroleum 0554
Sanitary and Municipal 0790
System Science 0428
Technology 0796
Operations Research 0795
Plastics Technology 0673
Textile Technology 0621

PSYCHOLOGY

General 0621
Behavioral 0384
Clinical 0622
Developmental 0620
Experimental 0613
Industrial 0624
Personality 0625
Physiological 0989
Psychobiology 0349
Psychometrics 0632
Social 0451

The undersigned hereby recommend to
the Faculty of Graduate Studies and Research
acceptance of the thesis

Symmetry, Quality, and Sexual Success
in Male Red-winged Blackbirds

submitted by
Kevin William Dufour

in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

Chair, Department of Biology

Thesis Supervisor

External Examiner

Abstract

There has been much recent interest in subtle departures from perfect symmetry in bilaterally-paired morphological characters, the extent to which such departures reflect individual quality, and the significance of such asymmetry to female mate selection and male reproductive success. I investigated asymmetry variation and its relation to mate quality and male success using data from a field study of red-winged blackbirds (*Agelaius phoeniceus*) breeding in eastern Ontario.

An important assumption of many previous studies of asymmetry and male mating success is that asymmetry measures made on individual characters provide reasonable indices of overall developmental competence. In the present study, analysis of the external and skeletal morphology of individual males revealed significant concordance among asymmetries in a variety of paired structures, consistent with there being "organism-wide" developmental competence in this species. However, concordance was sufficiently weak that individual character asymmetries were poor predictors of asymmetry overall, affirming the importance of using a multiple-character approach when quantifying asymmetry at the individual level.

Character asymmetries, whether considered alone or in combination, were generally unrelated to measures of male health, viability, or parental effort. I found no evidence of an association between asymmetry and nutritional condition, nor were asymmetrical individuals more likely to suffer reduced survivorship or be infected with avian haematzoa. Composite

asymmetry was related to infestation by two classes of ectoparasites, but these relationships were weak and in the direction opposite to that predicted. Finally, I found no association between asymmetry and male nest defence effort, the primary form of paternal care in my study population.

Male removal experiments and breeding data, combined with DNA-based analysis of parentage, generally failed to support the prediction that males characterized by low levels of asymmetry realize a reproductive advantage. Territorial males were no more symmetrical than their non-territorial (non-breeding) counterparts, males defending territories in high quality habitat were no more symmetrical than those found in marginal habitat, and in high quality habitat, male symmetry was unrelated to recruitment of social mates, within-pair paternity, or extra-pair mating success. These results suggest that the fitness consequences of subtle, developmental inconsistencies may be less significant and/or less ubiquitous than initially suggested.

Acknowledgements

As many of the people that I am about to name will attest, this whole endeavour has been a formidable challenge for me. I sincerely hope, however, that these same people recognize how tremendously helpful they have been, and how appreciative I am of their support, encouragement, and friendship.

Pat Weatherhead, my thesis supervisor, deserves special credit for running a vibrant lab, for providing an enjoyable working environment, and for continually putting the concerns of his graduate students above his many other commitments. In my own case, Pat has provided immeasurable advice and support, not only during this particular project but throughout my academic career. Above all else, however, I thank Pat for his patience and understanding. I believe he knows what I mean by this.

Along more personal lines, I care not to imagine what the past few years would have been like without the extraordinary support and encouragement that I have received from Jennifer Magwood. Jennifer continues to believe in my capabilities more than I do myself, and not once has she wavered in her determination to see me through whatever difficulty I might face. In addition to providing outstanding moral and logistic support, Jennifer helped score DNA fingerprints and proof-read most of the thesis, much of it one paragraph at a time. For these and other contributions far too numerous and diverse to mention here, I am deeply indebted and eternally grateful.

Perhaps not surprisingly, some of the most significant help that I have had has come from my lab mates, both former and present. Stephen Yezerinac

in particular has been a constant source of advice and encouragement, and it is to him that I owe much of what I know about DNA fingerprinting. As post-doctoral fellows, Mark Forbes and Kev Teather provided considerable advice and entertainment during the early stages of my degree program, and both have continued to indulge my requests for assistance. Greg Brown, Chris Parent, Kent Prior, and Rick Lanctot have been very supportive confederates, and each has had an impact on the development of this thesis in one way or another. I extend special thanks to Greg, Mark, Kev, and Stephen for reviewing drafts of various chapters, and to Kent for bolstering my confidence during moments of self doubt. Many of these people also pitched in when I needed an extra hand in the field.

I consider myself fortunate to have had at my disposal the skills of a veteran redwing researcher, Kit Muma, for help with work in the field. Kit has been an outstanding field assistant and solid friend throughout. Field work was also made easier by the efforts of Raleigh Robertson and Frank Phelan, who run the excellent Queen's University Biological Station. Molecular work was conducted at Queen's University under the responsible supervision of Dr. Peter Boag and Denise Michaud-Freeman. Bob Montgomerie was a gracious host during my stay at Queen's, and Steve and Anne Loughheed deserve special thanks for accommodation, encouragement, and friendship. Steve was also instrumental in preparing specimens for skeletal analysis.

Drs. David Currie and Hans Damman have been enthusiastic and insightful advisors, and I am thankful to have had their input. I have also benefited from many discussions and arguments with Brian Leung. Dr. Gordon

Bennett and his associates scored blood parasite smears, and Dr. H.H.J. Nesbitt kindly identified ectoparasites. Funding was provided by the Natural Sciences and Engineering Research Council of Canada, through operating grants to Pat Weatherhead and through a personal post-graduate scholarship.

None of this would have been possible without the unquestioning support that I continue to receive from my parents, Larry and Shirley Dufour, and from Stan and Kathleen Magwood. I sincerely hope that someday I might have more opportunity to repay their kindness, generosity, and faith. Finally, special credit goes to Patrick Magwood-Dufour for helping to put it all in perspective and for taking it all in stride. Patrick has been remarkably understanding, particularly given that he was only three years old when I began work on this degree. If one is permitted to dedicate this sort of thing, I dedicate this thesis to Jennifer and Patrick, for everything I've mentioned and a great deal more.

Table of Contents

	Page
Abstract	iii
Acknowledgements	v
Table of Contents	viii
List of Tables	x
List of Figures	xiii
List of Appendices	xiv
General Introduction	1
 Chapter 1. Estimation of organism-wide asymmetry in red-winged blackbirds and its relation to studies of mate selection	
Introduction	11
Methods	19
Results	25
Discussion	41
 Chapter 2. Bilateral symmetry as an indicator of male quality in red-winged blackbirds: associations with measures of health, viability, and parental effort	
Introduction	46
Methods	54
Results	65
Discussion	86

Table of Contents
(continued)

Chapter 3. Reproductive consequences of bilateral asymmetry for individual male red-winged blackbirds	
Introduction	93
Methods	101
Results	116
Discussion	143
Summary and Conclusions	152
Literature Cited	156
Appendices	177

List of Tables

Table	Page
1-1 Bilaterally-paired morphological characters used in the present study	32
1-2 Within- and among-individual components of variance, percent measurement error, and repeatability estimates for asymmetry measures made on four external and five skeletal paired morphological characters	33
1-3 Statistics describing the distribution of asymmetry levels exhibited at four external and five skeletal paired morphological characters	34
1-4 Size and absolute asymmetry measures computed for four external and five skeletal paired morphological characters.....	35
1-5 Analysis of covariance evaluating effects of male age and character size on the level of asymmetry exhibited at four external and five skeletal paired morphological characters.....	37
1-6 Product-moment correlations and associated probability values among asymmetry levels exhibited at four external and five skeletal paired morphological characters.....	38
1-7 Component loadings and percentage of the total variance explained by each of the first three principal axes obtained from a correlation-based principal components analysis of asymmetry levels exhibited at four external and five skeletal paired morphological characters	39
2-1 Analysis of covariance evaluating effects of character asymmetry and age on the condition of individual male red-winged blackbirds	76
2-2 Prevalence and intensity of various parasitic infections among 34 SY and 33 ASY male red-winged blackbirds.....	77

List of Tables
(continued)

Table	Page
2-3 Analysis of covariance evaluating effects of character asymmetry and age on the intensity of ectoparasitic louse infestation among individual males	78
2-4 Analysis of covariance evaluating effects of character asymmetry and age on the intensity of ectoparasitic mite infestation among individual males	80
2-5 Levels of character asymmetry exhibited by males infected and those uninfected with haematozoa	82
2-6 Levels of character asymmetry exhibited by males that bred in a given year and either survived or did not survive to the subsequent breeding season	83
2-7 Simple linear regression models describing the relationship between intensity of male nest defence and asymmetry levels exhibited at each of five bilaterally-paired characters	85
3-1 Comparison of resident (territorial) and replacement (floater) male red-winged blackbirds with respect to asymmetry levels exhibited at each of five bilaterally-paired morphological characters	132
3-2 Levels of character asymmetry exhibited by males defending territories in high quality marsh habitat and those defending territories in relatively marginal upland field habitat	133
3-3 Multiple linear regression models evaluating effects of character asymmetry and age on the number of social mates recruited by individual males	135
3-4 Multiple linear regression models evaluating effects of character asymmetry and male size on the number of fledglings raised per female on the territory of a given male	137

List of Tables
(continued)

Table	Page
3-5 Levels of character asymmetry exhibited by males that secured full within-pair paternity and those that suffered reduced paternity as a result of extra-pair mating	139
3-6 Levels of character asymmetry exhibited by males that were known to have sired extra-pair young and those that were apparently unsuccessful in this regard	140
3-7 Multiple linear regression models evaluating effects of character asymmetry and age on the annual reproductive success of individual males	142

List of Figures

Figure	Page
1-1 Relationship between mean character size and mean character asymmetry, computed at the individual level as the average size of the left and right elements and as the absolute value of the difference between the left and right sides, respectively	40
2-1 Relationship between intensity of ectoparasitic louse infestation and a composite asymmetry index based on measurements made on four external and five skeletal paired morphological characters	79
2-2 Relationship between intensity of ectoparasitic mite infestation and a composite asymmetry index based on measurements made on four external and five skeletal paired morphological characters	81
3-1 Relationship between the number of social mates (harem size) and prior breeding experience among individual males in each of two years of study	134
3-2 Number of fledglings raised per female on the territory of a given male (i.e., average female reproductive success) in relation to overall male size	136
3-3 Proportion of multi-locus DNA fingerprint bands shared by nestlings and their putative parents, shown in relation to the number of novel bands detected in nestling fingerprints.....	138
3-4 Relationship between annual reproductive success and prior breeding experience among individual males.....	141

List of Appendices

Appendix	Page
1 Distribution of individual male red-winged blackbirds relative to asymmetry levels exhibited at four external and five skeletal paired morphological characters	177
2 Simple linear regression models describing the dependence of (a) character size and (b) character asymmetry on date of capture for males sampled from upland habitat	183
3 Analysis of covariance evaluating the dependence of (a) character size and (b) character asymmetry on both date and year of capture for males sampled from marsh habitat	184

General Introduction

Behavioural and evolutionary ecologists have long recognized the value of identifying phenotypic correlates of individual reproductive success. Reproductive success is a basic component of individual fitness, and a knowledge of the attributes that confer high reproductive fitness is central to the study of selection in progress and to understanding the adaptive significance of particular traits (Clutton-Brock 1988; Grafen 1988). Moreover, insofar as variation in reproductive fitness arises as a consequence of individual differences in mating success, the study of reproductive success can provide important insights regarding the extent to which sexual selection (*sensu* Darwin 1871) has shaped the morphology and behaviour of organisms. Perhaps not surprisingly, then, the evolutionary and ecological literature is rich with studies of associations between individual attributes and measures of reproductive performance, male mating success in particular (see, for instance, Andersson 1994, Table 6.A).

Traditionally, studies of phenotypic influences on reproductive success have focussed on the absolute magnitude of trait development. Thus, for instance, the size of sexual ornaments (e.g., the elaborate plumes of certain birds), the development of male weaponry (e.g., ungulate horns and antlers), and overall body size (in sexually dimorphic species) have all received substantial empirical attention in this regard (see Andersson 1994 for a review). More recently, however, it has become apparent that precision of trait development might also influence reproductive fitness. Specifically, there has

been much recent interest in the possibility that subtle departures from perfect symmetry in bilaterally-paired morphological characters might play a significant role in determining patterns of female choice of mates, and hence, male reproductive success. For the vast majority of paired characters, perfect symmetry represents the ideal developmental outcome (Palmer and Strobeck 1986). Thus, departures from perfect symmetry are thought to reflect the inability of individuals to develop normally in the face of contingencies imposed by the environment (e.g., Palmer and Strobeck 1986; Parsons 1990, 1992). Building on these and other observations, Møller (1990a) proposed that symmetry might provide conspecifics with a reliable indication of overall phenotypic and/or genotypic quality, and that members of the discriminating sex (in most cases, females) should use symmetry as a criterion for mate selection. Since it was initially put forward, Møller's hypothesis has become the focus of much debate and has engendered considerable skepticism (e.g., Balmford and Thomas 1992; Borgia and Wilkinson 1992; Jennions and Oakes 1994; see also Palmer 1996 and references therein). While there is now convincing evidence that symmetry is, in at least some sexual systems, associated with male mating success (see below), several of the assumptions underlying existing interpretations of these data remain largely untested, and several authors have recently questioned the generality of the phenomenon (e.g., Eggert and Sakaluk 1994; Jennions and Oakes 1994). The present thesis attempts to address both these issues using data assembled from a three-year study of free-living red-winged blackbirds (*Agelaius phoeniceus*). Below I provide a brief overview of the development of recent interest in symmetry as

a measure of individual "quality" and as a potential correlate of reproductive fitness. My intention here is not to furnish an exhaustive review of the literature (for this, I refer the reader to Polak 1996), but rather to provide background information specifically relevant to the present investigation, and to highlight limitations of existing data.

Biologists recognize three forms of bilateral asymmetry, distinguishable based on the frequency distribution of individuals with respect to the difference between the size of the left and right elements of the character in question (Van Valen 1962; see also Palmer and Strobeck 1992, Fig. 2). "Directional asymmetry" refers to the condition in which there exists a significant tendency towards greater development on one particular side of the body. Structures exhibiting this form of asymmetry are characterized by a mean left-minus-right value that differs appreciably from zero, a pattern evident in avian testes, for example (Lake 1981). For structures exhibiting "antisymmetry", symmetry is also uncommon, but departures from perfect symmetry are directionally random, such that the larger of the two elements occurs with equal frequency on the left and right sides of the body. In a sample of individuals, antisymmetry is characterized by a platykurtic or bimodal distribution of left-minus-right values centred on a mean of zero. The signalling claws of male fiddler crabs (*Uca* spp.) provide a classic example (e.g., Yamaguchi 1977). A key distinction here is that both directional asymmetry and antisymmetry presumably result from genetic predispositions towards asymmetrical development (Palmer and Strobeck 1992). In contrast, for the majority of paired characters, perfect symmetry is the norm (i.e., left-minus-right values are normally distributed

about a mean of zero), and departures from symmetry in such characters are thus thought to reflect developmental imprecision. Significantly, this form of asymmetry (termed "fluctuating asymmetry") has been shown to increase in response to various forms of environmental stress encountered during development (reviewed by Parsons 1990, 1992), and there is much evidence that individuals show heritable variation in their ability to cope with such stress (see Chapter 1 and references therein). It is primarily for this reason that symmetry is widely equated with "developmental stability", that is, the capacity to maintain normal development in the face of contingencies imposed by the environment (Mather 1953; see also Palmer and Strobeck 1992; Zakharov 1992).

The use of symmetry as a measure of developmental stability is not new, although until recently, the concept has most often been applied at the population level (Palmer 1996). Thus, for instance, symmetry has been used extensively to explore the developmental consequences of "genetic stress" (e.g., reduced genetic variation due to inbreeding; see Leary and Allendorf 1989), as well as putative relationships between developmental stability and heterozygosity in general (Mitton and Grant 1984; Mitton 1993). Likewise, symmetry has been used as a summary measure of overall population health (e.g., Zakharov et al. 1991) and there has been much discussion regarding the potential value of symmetry as a biomonitor of environmental degradation (e.g., Leary and Allendorf 1989; Parsons 1990, 1992). Interest in symmetry as an indicator of individual quality and as a source of adult fitness variation, however, is a comparatively recent development. Nevertheless, evidence

consistent with Møller's original proposal has been mounting. Most notably, inverse associations between asymmetry and male mating success have now been identified in a wide variety of taxa, including drosophilid flies (*Drosophila pseudoobscura*; Markow and Ricker 1992), scorpionflies (*Panorpa japonica*; Thornhill 1992a,b), damselflies (*Coenagrion puella*; Harvey and Walsh 1993), dung flies (*Scatophaga stercoraria*; Liggett et al. 1993), earwigs (*Forficula auricularia*; Radesater and Halldorsdottir 1993), chironomid midges (*Chironomus plumosus*; McLachlan and Cant 1995), crickets (*Gryllus campestris*; Simmons 1995), domestic flies (*Musca domestica*; Møller 1996), barn swallows (*Hirundo rustica*; Møller 1992a, 1993a, 1994), and zebra finches (*Taeniopygia guttata*; Swaddle and Cuthill 1994a). In most cases, however, the mechanisms responsible for these associations remain largely a matter of conjecture.

While many of the authors cited above interpreted their results as indicating female preferences for high quality (i.e., symmetrical) mates (e.g., Møller 1992a, 1993a, 1996; Swaddle and Cuthill 1994a; Simmons 1995), others have emphasized alternative explanations (e.g., Harvey and Walsh 1993; Liggett et al. 1993; McLachlan and Cant 1995). Because deviations from perfect symmetry are typically subtle, interpretations that invoke female choice based on symmetry *per se* appear most likely to apply to cases in which individual differences are large and asymmetries particularly conspicuous. Noteworthy in this regard is the observation that secondary sexual characters (e.g., plumage ornaments) often exhibit elevated levels of asymmetry relative to "ordinary" morphological characters (e.g., Møller and Hoglund 1991; Møller 1992b; although see Balmford et al. 1993; Evans et al. 1995; Tomkins and

Simmons 1995), and studies of sexual ornaments have indeed provided some of the most convincing evidence of female mate selection based on this aspect of morphology (Møller 1992a, 1993a; Swaddle and Cuthill 1994a). As several authors have noted, however, female preferences for symmetry do not necessarily imply adaptive female choice, and might instead reflect pre-existing perceptual biases toward symmetry in general (Enquist and Arak 1994; Johnstone 1994; Ryan et al. 1995). Furthermore, to the extent that departures from perfect symmetry might directly influence the mechanical functioning of certain traits (e.g., those associated with flight performance), the impact of asymmetry on male mating success might be mediated, not by female choice, but rather via effects on the ability of males to compete effectively for mating opportunities (Balmford and Thomas 1992; Palmer 1994). Finally, relationships between asymmetry and male mating success might arise as incidental by-products of associations between asymmetry and other male characteristics that confer high reproductive fitness. At present, there appears to be little consensus regarding the relative importance of these various mechanisms in accounting for observed associations between asymmetry and male reproductive success (Markow 1995; Polak 1996).

Alternative mechanisms notwithstanding, several authors have questioned existing empirical support for the male quality/female choice hypothesis on more fundamental grounds (e.g., Eggert and Sakaluk 1994; Palmer 1994; Ryan et al. 1995). Of particular concern is the fact that most previous studies of asymmetry in relation to mate quality and/or male reproductive success have been based on asymmetry measures made on a

rather limited number of traits, often a single (more or less arbitrarily chosen) bilaterally-paired character. At the same time, however, there is some uncertainty regarding the reliability of single character asymmetries as indices of overall developmental competence. For instance, previous studies have often failed to detect significant concordance (i.e., agreement) among asymmetry measures made on different characters in the same individual, contrary to what one might expect if single character asymmetries are adequate measures of developmental stability (see Chapter 1 and references therein). Despite recent emphasis on the importance of using multiple characters when quantifying asymmetry at the individual level (Palmer 1994; Watson and Thornhill 1994; Ryan et al. 1995), data on multi-character asymmetry and male reproductive performance are currently scant.

In sum, while growing evidence suggests that developmental stability and bilateral symmetry can have fitness consequences at the individual level, there is currently much debate regarding the mechanisms responsible and the extent to which simple measures of asymmetry can be used to predict individual quality and male reproductive success. Furthermore, it seems clear that additional data are needed before these issues are likely to be resolved. The general aim of the present study was to assess the significance of bilateral symmetry as a potential indicator of phenotypic (perhaps genotypic) quality in red-winged blackbirds, and in particular, to evaluate the reproductive consequences of asymmetry (and, by inference, developmental stability) for individual males. To this end, I have assembled morphological and breeding data from a series of field investigations that I conducted in eastern Ontario over three breeding

seasons between 1993 and 1995. In meeting the central aims of the study, I have endeavoured to employ a broader and more comprehensive approach than has been typical of studies of this nature, by evaluating correlates of asymmetry measures made on a variety of paired characters, both singly and in combination. Specific objectives of the study are outlined below.

Overview of the thesis

In the first chapter, I examine naturally occurring patterns of asymmetry variation in several external and skeletal paired morphological characters, based on a point sample of individuals collected from a communal roosting population. The purpose of this particular analysis is three-fold. First, by addressing a number of technical problems associated with quantifying asymmetry at the individual level (e.g., the impact of measurement error, directional biases, and size-scaling effects), I attempt to establish appropriate measures of asymmetry for each character, for use in all subsequent analyses. Second, based on this same sample of individuals, I assess a fundamental assumption of many previous studies of asymmetry and male mating success, namely, that individual males vary with respect to their levels of overall developmental competence. To this end, I test the specific prediction that individual character asymmetries covary at the individual level. Finally, having established the existence of an "organism-wide" asymmetry property in red-winged blackbirds, I explore the extent to which this property might be estimated from measurements made on individual characters.

In Chapter 2, I focus on the specific hypothesis that asymmetry

constitutes a morphological correlate (i.e., reliable indicator) of overall male phenotypic or genotypic quality. In the context of the present investigation, male quality is most appropriately defined in terms of fitness benefits that might accrue to discriminating females, either directly (through the production of more offspring) or indirectly (through the production of offspring with higher survival prospects). Thus, in this chapter, I examine associations between asymmetry and measures of overall male health (nutritional condition and parasitic infection), viability (between-year survival), and parental effort (in the form of active nest defence). The ultimate aim of this analysis is to determine the extent to which asymmetry conveys information that might be of value to females choosing among potential mates, and hence, whether there might be potential for adaptive female choice based on this particular aspect of morphology.

In Chapter 3, I take a broader and more direct approach to the question of whether asymmetry has fitness consequences for individual males. Here I make no assumptions regarding the relative importance of the various mechanisms that have been proposed, but rather, I simply evaluate each of several components of male reproductive success in relation to asymmetry measures made on a variety of paired characters. Components of male reproductive success in this territorial, polygynous species include territory acquisition, large-scale differences in territory quality, harem size, average success of females within the harem, within-pair paternity, and extra-pair mating success. Each of these components is considered in turn (based on breeding data and DNA-based analysis of parentage) and evaluated in relation

-10-

to the levels of asymmetry exhibited by individual males. I reasoned that this approach would provide insight into the mechanisms underlying any observed effects of asymmetry on male reproductive success overall.

CHAPTER 1

Estimation of organism-wide asymmetry in red-winged blackbirds and its relation to studies of mate selection

Introduction

Motile animals are almost invariably characterized by a bilaterally symmetrical body plan. Thus, under ideal conditions, individuals of most species are expected to develop identical morphologies on the left and right sides of the body. It is apparent, however, that not all individuals are able to achieve this ideal state; in a given population, many individuals will show slight but measurable differences between the size of the left and right elements of a particular paired character (Palmer and Strobeck 1986). Where there is no tendency toward greater development on one side or the other (i.e., no directional asymmetry or antisymmetry), these deviations are thought to reflect the cumulative effects of minor, environmentally induced perturbations of the developmental process (i.e., "developmental noise"; Waddington 1957). However, individuals apparently vary in their ability to resist or correct such perturbations, and several studies have shown that this variation can have a heritable basis (e.g., Mather 1953; Maynard Smith and Sordhi 1960; Hagen 1973; Thornhill and Sauer 1992; although see Eggert and Sakaluk 1994 and references therein). These observations have led to the widespread assumption that symmetry at adulthood provides a measure of developmental stability,

that is, an individual's intrinsic ability to develop normally in the face of environmental stress (see reviews by Palmer and Strobeck 1986; Parsons 1990, 1992).

Recent evidence suggests that developmental stability and bilateral symmetry may play a significant and previously unrecognized role in determining patterns of female mating preferences and male reproductive performance. In particular, numerous correlational studies involving a variety of insect species have reported inverse associations between asymmetry in certain characters (e.g., wing length) and male pairing success (Markow and Ricker 1992; Thornhill 1992a; Harvey and Walsh 1993; Liggett et al. 1993; McLachlan and Cant 1995; Simmons 1995). Similarly, experimental manipulations of the ornamental feathers of certain birds, involving both natural populations (Møller 1992a, 1993a) and captive flocks (Swaddle and Cuthill 1994a), have provided direct evidence that females of at least some species actively discriminate against asymmetrically ornamented males when making mate choice decisions. Thus, in a variety of taxa and under a variety of conditions, symmetrical males appear to be at a mating advantage.

A number of hypothesis have been proposed to explain the apparent relationship between asymmetry and male reproductive performance (see General Introduction for an overview), and it is entirely plausible that no single mechanism can account for all of the observed associations (Ryan et al. 1995). One hypothesis in particular, however, has received the bulk of recent attention. Møller (1990a) suggested that asymmetry in bilaterally-paired characters (sexual ornaments in particular) might provide females with a reliable indication

of overall male quality, where quality in this instance refers the possession of viability-enhancing genes. Thus, he proposed that female barn swallows (*Hirundo rustica*) preferentially mate with males exhibiting low levels of tail feather asymmetry to enhance the genetic quality, and the hence the viability, of their offspring (Møller 1992a, 1993a; see also Møller and Pomiankowski 1993). Thornhill (1992b) offered a similar explanation for his results on Japanese scorpionflies (*Panorpa japonica*), but noted that the primary benefit accrued to discriminating females might instead be material resources (e.g., high quality nuptial food items; see also Thornhill 1992a; Thornhill and Sauer 1992). In either case, the suggestion is that asymmetry reliably reveals male phenotypic or genotypic quality, and that females discriminate against asymmetrical males in order to obtain high quality mates.

The interpretation outlined above (hereafter called the male quality hypothesis) has met with considerable skepticism. While some authors have argued that alternative, more parsimonious explanations are equally viable (e.g., Balmford and Thomas 1992; Borgia and Wilkinson 1992; Swaddle and Cuthill 1994a; Ryan et al. 1995), others have emphasized that basic premises of the hypothesis have not yet been verified (Eggert and Sakaluk 1994; Ryan et al. 1995). Perhaps the most fundamental premise of the male quality hypothesis is that individuals vary with respect to their levels of overall developmental competence. This implies the existence of an "organism-wide" capacity for buffering against developmental perturbations (Van Valen 1962), which in turn suggests that asymmetries exhibited at different characters should be correlated (Evans et al. 1995). This assumption is in fact critical to

the interpretation of existing data on asymmetry and male mating success, because many of the relevant studies have been based on measurements made on a single or perhaps a few traits (e.g., Thornhill 1992a,b; Thornhill and Sauer 1992; Harvey and Walsh 1993; Liggett et al. 1993; Simmons 1995). Unless it can be reasonably assumed that asymmetry in any given character is an adequate measure of overall developmental competence, the applicability of the male quality hypothesis to these data will remain open to question (Ryan et al. 1995).

At present, there is little empirical basis for the assumption that the effects of developmental stability are organism-wide. While a number of studies have found significant correlations among character asymmetries at the population level (Soule 1967; Soule and Baker 1968; Vrijenhoek and Lerman 1982; Leamy 1984), and while concordance at the individual level has occasionally been detected among developmentally related traits (e.g., Bader 1965; Leamy 1993), the majority of individual-level studies conducted have failed to provide positive support (e.g., Van Valen 1962; Soule and Baker 1968; Fox 1975; Vrijenhoek and Lerman 1982; Evans et al. 1995; Ryan et al. 1995; see also Palmer and Strobeck 1986 and references therein). Thus, the existence of an organism-wide asymmetry property (*sensu* Soule 1967) remains largely a matter of conjecture. Here I present results of an analysis aimed primarily at determining whether such a property exists among red-winged blackbirds (*Agelaius phoeniceus*). Specifically, using asymmetry data assembled on several external and skeletal bilaterally-paired characters, I test the prediction that character asymmetries covary at the individual level.

Several authors have suggested that the general failure to detect individual-level concordance among characters might be attributable in large part to technical difficulties associated with quantifying asymmetry (Palmer and Strobeck 1986; Leamy 1993). Specifically, these authors have emphasized that the use of inappropriate asymmetry indices and the complicating influences of measurement error, directional asymmetry, and antisymmetry (see below), all contribute to reduce the discriminatory power of statistical tests.

Measurement error is a particularly important consideration in studies of bilateral variation, because bilateral asymmetries are typically subtle (Palmer and Strobeck 1986; Møller and Pomiankowski 1993) and because random measurement error and developmental instability can yield similar patterns of between-sides variation (i.e., differences between sides normally distributed with a mean of zero; see Palmer 1994). Thus, my first specific objective was to assess the level of imprecision associated with asymmetry scores and, in particular, to verify that observed differences between the left and right elements of the characters under study could not have arisen solely as the result of random measurement error. This was achieved through use of repeated measurements made on all individuals included in the analysis (Yezerinac et al. 1992; Palmer 1994).

A second important technical consideration is whether the characters under study exhibit evidence of genetic tendencies toward greater development on one side or the other (i.e., directional asymmetry and antisymmetry, see General Introduction). Palmer and Strobeck (1986, 1992) have repeatedly emphasized that such tendencies can seriously compromise the use of bilateral

variation as a measure of developmental stability. These authors suggested that, if possible, analyses should be restricted to those characters exhibiting "ideal fluctuating asymmetry" (ideal FA), in which differences between the left and right character values are normally distributed about a mean of zero (Palmer and Strobeck 1992). Although this view has recently been challenged (Graham et al. 1993; McKenzie and O'Farrell 1993), it nevertheless seems prudent to assess characters for departure from ideal FA. At the very least, directional biases will have implications for the development of asymmetry indices to be used in subsequent analysis (Palmer 1994). Thus, my second objective was to determine whether the paired characters used in the present study exhibit either directional asymmetry or evidence of antisymmetry.

A final technical consideration concerns the relationship between the degree of asymmetry and overall size of the trait. For purely allometric reasons, asymmetry might be expected to increase with increasing character size (Palmer and Strobeck 1986), and such a relationship has indeed been reported in a number of investigations (e.g., Markow and Ricker 1992; McLachlan and Cant 1995). More commonly, however, the relationship has been found to be curvilinear, with individuals at both ends of the size continuum showing elevated levels of asymmetry (e.g., Soule and Cuzin-Roudy 1982; Møller 1992b; Thornhill 1992a,c; Evans et al. 1995). Such a relationship is expected if phenotypically extreme individuals suffer reduced developmental stability, as has been suggested for traits subject to stabilizing selection (Soule and Cuzin-Roudy 1982; Møller and Pomiankowski 1993). Finally, it has been suggested that for certain bilateral traits (i.e., sexual ornaments), both the magnitude and

precision of development should vary in relation to individual quality, such that high quality individuals develop traits that are both large and at the same time symmetrical (Møller 1990a; Møller and Hoglund 1991). Under such a scenario, an inverse association between size and asymmetry is expected (see Møller and Pomiankowski 1993 for a detailed treatment of this argument). Regardless of the shape or direction of the relationship, however, any such size-dependence will usually necessitate some form of statistical control (Palmer and Strobeck 1986; Palmer 1994). Thus, my third objective was to evaluate the relationship between size and asymmetry in each of the characters measured. Finally, having established appropriate measures of asymmetry for each trait, I determined the extent to which these asymmetries demonstrated a concordant pattern of variation.

In addition to permitting a test of the central hypothesis outlined above, the analysis of asymmetry variation at a number of different characters provided an opportunity to assess one other prediction relevant to current debate. Møller and Pomiankowski (1993) have argued that asymmetry in bilaterally-paired secondary sexual characters should be particularly revealing of underlying individual quality, because such characters are likely to be subject to strong directional selection, and because strong directional selection is thought to favour weakened developmental control (see also Watson and Thornhill 1994). A prediction of this hypothesis is that sexual ornaments should exhibit elevated levels of asymmetry relative to "ordinary" morphological characters, i.e., those presumed to be under the influence of stabilizing selection (Møller and Pomiankowski 1993). While some empirical investigations have

supported this prediction (Møller and Hoglund 1991; Møller 1992b), others have not (Balmford et al. 1993; Evans et al. 1995; Tomkins and Simmons 1995), and thus, additional data on this issue would be of value. Male red-winged blackbirds are characterized by highly conspicuous epaulets, i.e., patches of brilliant red upper wing coverts that occur at the wrist of each wing. This bilaterally-paired display character is used extensively in both inter- and intra-sexual interactions (Orians and Christman 1968), and there is ample evidence to suggest that epaulets have evolved in response to sexual selection (see Searcy and Yasukawa 1995 for a review). Thus, a final objective of the present analysis was to determine whether this particular sexual ornament is characterized by high levels of asymmetry relative to non-ornamental traits.

Methods

Collection and processing of specimens

All analyses presented here are based on a point sample of red-winged blackbirds collected during the spring of 1993 at a communal, mixed-species roost. The roost was situated in a small (approx 2 ha) cattail marsh (*Typha* sp.) located approximately 40 km north of Kingston, Ontario (44°34'N; 76°20'W). Individuals were captured passively by mist net as they entered the roost at dusk. To avoid potential seasonal effects, netting was restricted to a one-week period beginning 23 April. Three evenings of netting yielded a total sample of 98 individuals. The sample was initially comprised of 67 males and 31 females. However, because red-winged blackbirds exhibit pronounced sexual size dimorphism (thus requiring that all analyses be conducted separately by sex), and because the sample of females was limited, only results for males are presented here.

Male red-winged blackbirds in their second calendar year (SY males) are readily distinguished from older individuals (ASY males) based on plumage (Searcy and Yasukawa 1995). Thus, upon capture each individual was classified according to age and weighed to the nearest 0.5 g using a hand-held Pesola spring scale (body mass data will be used in a subsequent chapter). The bird was then killed by exposure to chloroform and the carcass immediately frozen. Once all individuals had been collected, carcasses were thawed and external characters measured (see below). Carcasses were then skinned and sent to the Royal Ontario Museum (Toronto, Ontario), where the skeletons were cleared of soft tissue using dermestid beetles.

I chose four external and five skeletal bilaterally-paired characters for analysis of asymmetry variation (Table 1-1). Characters were chosen solely on the basis of ease of measurement (e.g., from among those having clearly defined landmarks; see Yezerinac et al. 1992), though an attempt was made to choose representative characters from various regions of the body. To avoid inter-observer variation, all characters were measured personally. I measured both the left and right elements of all characters except wing and tail (see Table 1-1) to the nearest 0.1 mm using callipers. The left and right elements of wing and tail were measured to the nearest 1 mm using flat rulers designed specifically for these purposes. All measurements were made twice to permit assessment of measurement error and to reduce its effects in analysis (see below). Skeletal characters were measured several weeks after external measurements had been completed, hence measurements for these two sets of characters were made without reference to each other. Within each character set, I obtained one complete set of measurements for an individual before that individual was remeasured. All feathers were inspected for evidence of either breakage or wear, and any showing such damage were excluded from consideration. Similarly, I made no attempt to measure skeletal elements that had been broken during specimen preparation. Consequently, sample sizes vary slightly among analyses.

Data analysis

All analyses were conducted using JMP® (version 3.1) statistical software (SAS Institute Inc. 1994). Asymmetry for each character was initially taken as the

signed difference between the size of the left and right elements (i.e., with information on the direction of departure from perfect symmetry retained). This index was used in the assessment of measurement error and conformity to ideal FA (see below). For subsequent analysis, I used the absolute value of the difference between the two sides, because in these instances the important parameter was the magnitude of departure from perfect symmetry, irrespective of direction (Palmer and Strobeck 1986; Palmer 1994). For convenience, this measure is hereafter referred to as "absolute asymmetry". Overall character size was taken as the mean value of the left and right elements (i.e., $[\text{right} + \text{left}] / 2$).

To assess the level of measurement error associated with asymmetry scores, I first computed replicate left-minus-right values for each individual (at each character), using the first set of measurements for one value and the second set for the other. These values were entered in a one-way, Model II analysis of variance (ANOVA; individuals as treatment levels) to partition total variability into within- and among-individual components ($\text{VAR}_{\text{within}}$ and $\text{VAR}_{\text{among}}$, respectively; see Yezerinac et al. 1992 for details). Estimates of these components were then used to compute percent measurement error (%ME) according to the equation:

$$\%ME = [\text{VAR}_{\text{within}} / (\text{VAR}_{\text{within}} + \text{VAR}_{\text{among}})] \times 100.$$

For comparison with other studies, I also computed repeatability (r_i) for each character as:

$$r_1 = [\text{VAR}_{\text{among}} / (\text{VAR}_{\text{within}} + \text{VAR}_{\text{among}})]$$

(Lessells and Boag 1987). It is important to recognize that this method assesses measurement error relative to all other forms of bilateral variation, including variance components due to directional asymmetry and antisymmetry (Merila and Bjorklund 1995; see Palmer 1994 for an alternative approach). The critical issue in any such analysis, however, is whether observed among-individual variability is greater than expected, given the magnitude of within-individual variability (i.e., measurement error). In the one-way ANOVA approach employed here, this is readily determined by evaluating the significance of the model (Sokal and Rohlf 1981). Finally, to minimize effects of measurement error in subsequent analysis, I computed the average of the two replicate measures for each individual at each character, and used these average values as the basis for all subsequent calculations (Yezerinac et al. 1992). Estimates of overall character size were derived in a similar manner.

To assess the extent to which character asymmetries conformed to "ideal FA" (Palmer and Strobeck 1992), I determined for each trait whether the mean left-minus-right value showed significant departure from zero (as expected if directional biases are present) and examined the corresponding frequency distribution for gross departures from normality. Of potential concern are characters that exhibit extreme antisymmetry (bimodality), which may suggest a genetic predisposition toward asymmetrical development (Palmer and Strobeck 1992). As subtler forms of antisymmetry are suggested by platykurtic (broad-peaked) distributions (Palmer and Strobeck 1992), I

further evaluated kurtosis statistically using methods outlined by Sokal and Rohlf (1981). Finally, to complete the statistical description of departures from normality, I determined the extent to which each of the left-minus-right distributions was skewed (Sokal and Rohlf 1981).

To determine the linear dependence of asymmetry on overall character size, and to evaluate simultaneously asymmetry differences between the two recognizable age classes, I conducted analysis of covariance (ANCOVA), specifying asymmetry as the response variable and treating character size and male age as continuous and categorical predictors, respectively. ANCOVA models were developed separately for each character and initially included an age*size interaction term. If the interaction was not significant ($P > 0.1$), it was removed and a reduced (i.e., main effects) model was developed. Significance of each predictor was evaluated based on Type III sums of squares (i.e., tests were independent of the ordering of effects in the model; SAS Institute Inc. 1985). To assess potential nonlinear relationships between character size and asymmetry, I used a combination of visual inspection of scatterplots and second-order polynomial regression. Regression models were developed both separately by age and with the age classes pooled.

I assessed the level of concordance among character asymmetries in three ways. First, I evaluated all possible pairwise product-moment correlations, controlling experimentwise Type I error rate using sequential Bonferroni adjustment (Rice 1989). Second, I computed and evaluated the significance of Kendall's coefficient of concordance (W), a nonparametric measure of association for ≥ 2 variables (Sokal and Rohlf 1981). Kendall's W

ranges from 0 (indicating complete lack of concordance) to 1 (perfect agreement among ranks; see also Zar 1984). Finally, I explored the pattern of covariation among character asymmetries using principal components analysis (PCA). The existence of a principal component describing positive covariation among most or all of the original asymmetry measures (and accounting for an appreciable amount of the total original variance) would provide further evidence of general concordance of asymmetry among the characters studied (see Rayment et al. 1984 for a general discussion of the application of PCA to morphometric data).

Results

Analysis of within- and among-individual components of variability revealed measurable departures from perfect symmetry at each of the nine characters studied: all character asymmetries exhibited highly significant among-individual variation (Table 1-2). Nevertheless, measurement error varied considerably among characters, and for some characters comprised a substantial proportion of the total original variance (range: 0.9 - 20.8%; Table 1-2). Interestingly, there was no obvious association between %ME in asymmetry scores and the level of difficulty, as perceived by the investigator, associated with measuring traits. For instance, skeletal elements were comparatively rigid and had clearly defined landmarks, characteristics that are generally thought to increase precision of measurement (Lougheed et al. 1991; Yezerinac et al. 1992). However, levels of measurement error associated with skeletal character asymmetries were among the highest observed (Table 1-2). In contrast, epaulet length was perceived as a difficult character to measure, yet measurement error in epaulet asymmetry was conspicuously low (<2%; Table 1-2). Inspection of the actual variance components, however, revealed that this last result was largely attributable to pronounced variability *among* the individuals sampled (Table 1-2). This in itself suggests high average levels of epaulet asymmetry, because as the mean individual departure from perfect bilateral symmetry increases, so too does the sample variance of left-minus-right character values (see Palmer and Strobeck 1986). I consider this issue in greater detail in a subsequent section.

Statistics describing the distribution of signed asymmetry values are

given in Table 1-3. The actual distributions are presented in Appendix 1. All distributions were in qualitative agreement with the criteria for ideal FA (i.e., approximately normal and centred near zero; Appendix 1). Nevertheless, statistical departures from ideal FA were evident. Specifically, two of the nine characters measured showed slight but significant ($P < 0.05$) departures from a mean of zero; a third departure was marginally significant at $P = 0.07$ (Table 1-3). Moreover, seven of the nine mean deviations occurred in the same direction (binomial test, $P = 0.09$; Table 1-3), suggesting that directional biases may not have been character-specific. Expressed as a percentage of the maximum deviation from perfect bilateral symmetry, departures of the mean from zero ranged from 0.0 to 13.3. The corresponding average value computed across characters was just 5.9%. None of the characters examined showed evidence of antisymmetry (i.e., bimodality or negative kurtosis), though some distributions were leptokurtic and/or slightly skewed (Table 1-3). Again, inspection of the actual frequency distributions indicated that departures from normality were moderate (Appendix 1).

Because none of the characters measured exhibited serious departure from ideal FA, all were retained for subsequent analysis. To eliminate the biasing effects of the directional tendencies described above, individual signed asymmetry values were adjusted to a mean of zero (Palmer 1994). Thus, for each individual (at each character), absolute asymmetry was computed according to the equation:

$$\text{Asymmetry} = |d_i - \bar{d}|$$

where d_i is the signed left-minus-right character value for individual i , and $\bar{d}$ is the corresponding mean value computed across all individuals sampled. In other words, asymmetry is hereafter defined as individual departure from the sample mean, which for most characters was not significantly different from zero (Table 1-3).

A consequence of the use of absolute values in the computation of individual asymmetry scores was that the resulting distributions were distinctly non-normal (i.e., positively skewed). As this had potential to violate assumptions of parametric statistical procedures (Swaddle et al. 1994), I sought to determine an appropriate transformation before proceeding with further analysis. Employing the series of power transformations described by Sokal and Rohlf (1981:425), and using visual inspection of normal probability plots to assess normality (SAS Institute Inc. 1994), I determined that the most generally useful transformation for these data was $Y' = \sqrt{Y}$. For five of the characters, transformation to square roots all but eliminated departure from normality, and for the remaining four characters the square root transformation was clearly superior to the others examined. All distributions showed obvious improvement as determined by normal probability plots. Because of its general utility for normalizing absolute asymmetry distributions, the square root transformation was applied to all nine characters for analysis.

Analysis of covariance indicated that for each of the characters examined, the asymmetry versus size relationship did not differ between age classes (all age*size interactions, $P > 0.1$). Thus, the dependence of absolute asymmetry on character size and male age could be assessed simultaneously

by evaluating the significance of main effects. In general, there was little evidence of asymmetry differences between SY and ASY males (Tables 1-4 and 1-5). Only one of the nine age differences approached statistical significance (ulna asymmetry, $P = 0.07$); none was significant at $P \leq 0.05$ (Table 1-5). There was some suggestion that asymmetry and character size were inversely related in that seven of the nine partial coefficients for size were negative in sign (binomial test, $P = 0.09$; Table 1-5). However, none of the individual size effects even approached statistical significance (Table 1-5). Similarly, second order polynomial regressions (conducted separately by age and with age classes pooled) provided no evidence of a curvilinear relationship between size and asymmetry in any of the characters examined (all model P values > 0.1). Given that the effects of character size and male age were trivial at best, these factors were ignored in the remaining analyses.

Individual pairwise correlations among character asymmetries were generally weak (range: $-0.24 - 0.31$, mean = 0.06 ; Table 1-6), and only 3 of 36 were statistically significant ($P \leq 0.1$; Table 1-6). None of the correlations was significant after sequential Bonferroni adjustment (all adjusted P values > 0.1). Importantly, however, 25 of the 36 correlations were in the predicted direction (i.e., positive), indicating weak but statistically significant concordance overall (binomial test, $P = 0.01$). Similarly, Kendall's coefficient of concordance indicated significant agreement among ranks ($W = 0.15$, 62 df, $P < 0.025$). Thus, these data support the existence of an organism-wide asymmetry property.

To explore further the pattern of covariation among character asymmetries, I conducted PCA based on the correlation matrix presented in

Table 1-6. I chose correlation-based PCA over covariance-based PCA to prevent the outcome of the analysis from being dominated by a few characters that had particularly high variances (i.e., large external characters, see Table 1-4). Results of the PCA were consistent with those of the analysis presented above. First, the first principal axis (PC1) described positive covariation among most of the asymmetry measures: eight of the nine original variables were loaded in the same direction, and seven of the eight positive loadings were at least moderate in magnitude (Table 1-7). This is expected if the original variables are positively related (Rayment et al. 1984). Second, and perhaps more importantly, PC1 accounted for only 19% of the total original variance (Table 1-7), indicating that the analysis was largely ineffective at summarising asymmetry variation across characters. Indeed, the first three principal axes combined accounted for less than 50% (Table 1-7), a result attributable to relatively weak multivariate structure in the asymmetry data. Thus, although there was statistically significant concordance among character asymmetries (see above), no single linear combination of the original variables adequately described this pattern. This precluded development of an overall asymmetry index through use of PCA, which in turn reinforces the observation that the degree of concordance was weak.

My final objective was to test the prediction that epaulets (a secondary sexual character) exhibit high average levels of asymmetry relative to non-ornamental traits. In order to meet this aim, it was first necessary to determine the *among*-character relationship between asymmetry and size, as such a relationship would obviously complicate asymmetry comparisons. An

initial examination of this problem suggested that the relationship was positive, i.e., larger characters tended to show higher mean levels of absolute asymmetry (Fig. 1-1). Closer inspection of these data, however, revealed that this result may have been an artifact of size and asymmetry differences between particular types of characters. Specifically, the three feather characters measured (i.e., tail, wing, and epaulet) were on average both larger (Mann-Whitney $U = 17$, $n = 6,3$, $P = 0.05$) and more asymmetrical (Mann-Whitney $U = 18$, $n = 6,3$, $P < 0.05$) than the other characters examined. Thus, in the present analysis, effects of character size and character type (i.e., feather vs. non-feather) were confounded. Fortunately, this was inconsequential to the central aim of the analysis, because epaulets were clearly exceptional whether compared to other feather characters or to characters of similar size. Mean absolute asymmetry in epaulet length was 51-84% higher than that found in wing and tail (i.e., the other feather characters measured), and more than an order of magnitude higher than that found in five of six characters of comparable size (Fig. 1-1). Thus, although lack of replication precluded statistical testing (i.e., $n = 1$ sexual ornament), these data clearly support the prediction that epaulets show elevated levels of asymmetry relative to non-ornamental traits.

The observation that epaulets exhibited high levels of asymmetry is consistent with the hypothesis that sexual ornaments are particularly susceptible to the processes that tend to disrupt precise development (Møller and Pomiankowski 1993). This raises the possibility that asymmetry in epaulets might be a particularly good indicator of organism-wide developmental

competence, as some authors have suggested for secondary sexual characters in general (Møller and Pomiankowski 1993; Watson and Thornhill 1994). To explore this possibility, I assessed the relationship between epaulet asymmetry and a composite measure based on asymmetry levels exhibited at each of the other eight characters examined. Thus, for each non-ornamental character, individuals were ranked according to their absolute asymmetry levels, and the sum of these ranks was taken as a measure of "organism-wide" asymmetry. The relationship between this composite index and absolute epaulet asymmetry (sqrt-transformed) was positive but nonsignificant (simple linear correlation: $r = 0.19$, $n = 63$, $P = 0.14$). To gain some perspective on this result, I repeated the procedure for each of the other eight characters examined, and in each instance evaluated the relationship between asymmetry in the excluded character and the corresponding composite score. Only two of the resulting correlations were statistically significant (coracoid vs. composite asymmetry, $r = 0.30$, $n = 63$, $P = 0.02$; femur vs. composite asymmetry, $r = 0.29$, $n = 63$, $P = 0.02$). Perhaps more importantly, all correlations were decidedly weak (range: -0.06 - 0.30 , mean = 0.14), although three were nevertheless higher than that computed for epaulet asymmetry above. Collectively, these results indicate that no single character asymmetry accurately predicted asymmetry overall, and furthermore, that epaulet asymmetry was generally no more predictive than asymmetry in individual non-ornamental traits.

Table 1-1. Bilaterally-paired morphological characters used in the present study. External measurements generally follow those of Weatherhead and Clark (1994). Skeletal measurements follow Robins and Schnell (1971).

Character	Description
Tarsus length	Measured externally, from the proximate end of the tarsometatarsus to the distal end of the penultimate undivided scute (± 0.1 mm)
Wing chord	Measured with the wing folded against the body, from the arc of the wrist to the tip of the longest primary (± 1 mm)
Tail length	Length of the outer rectrix (± 1 mm)
Epaulet length	Measured with the wing folded against the body, from the arc of the wrist to the posterior-most extension of the yellow margin (± 0.1 mm)
Coracoid length	Maximum dimension (± 0.1 mm)
Femur length	Maximum dimension (± 0.1 mm)
Tibiotarsus length	Maximum dimension (± 0.1 mm)
Humerus length	Maximum dimension (± 0.1 mm)
Ulna length	Maximum dimension (± 0.1 mm)

Table 1-2. Within- and among-individual components of variance^a, percent measurement error^b (%ME), and repeatability^c (r_I) estimates for asymmetry measures (computed as the difference between the size of the left and right elements, in mm) made on four external and five skeletal paired morphological characters. Sample size indicates the number of individuals measured. Each individual was measured twice.

Character	n	VAR _{within}	VAR _{among}	%ME	r_I	F ^d
Tarsus	67	0.014	0.097	12.69	0.87	14.77
Wing	67	0.276	1.258	18.00	0.82	10.11
Tail	66	0.015	1.620	0.93	0.99	214.80
Epaulet	66	0.056	3.924	1.42	0.99	140.24
Coracoid	66	0.003	0.015	14.62	0.85	12.68
Femur	65	0.002	0.006	20.02	0.80	8.99
Tibiotarsus	67	0.004	0.025	13.27	0.87	14.07
Humerus	67	0.002	0.007	20.80	0.79	8.61
Ulna	67	0.002	0.008	15.93	0.84	11.56

^a Determined using one-way, Model II ANOVA (see text).

^b $[VAR_{within} / (VAR_{within} + VAR_{among})] \times 100$.

^c $[VAR_{among} / (VAR_{within} + VAR_{among})]$.

^d Test of H_0 : no significant among-individual variation. All F statistics are highly significant ($P < 0.0001$).

Table 1-3. Statistics describing the distribution of asymmetry levels (computed as the difference between the size of the left and right elements, in mm) exhibited at four external and five skeletal paired morphological characters.

Character	n	Mean Value			Skewness			Kurtosis		
		$\bar{x}$	SE	P ^a	g ₁	SE	P ^b	g ₂	SE	P ^c
Tarsus	67	0.05	0.039	0.203	0.20	0.374	ns	1.22	0.578	**
Wing	67	-0.22	0.144	0.139	-0.41	0.329	ns	-0.43	0.578	ns
Tail	66	-0.03	0.163	0.853	0.63	0.303	**	3.10	0.582	***
Epaulet	66	-0.46	0.245	0.065	-0.48	0.240	ns	1.16	0.582	**
Coracoid	66	-0.01	0.016	0.603	0.06	0.422	ns	-0.10	0.582	ns
Femur	65	-0.03	0.011	0.002	-0.36	0.045	ns	1.01	0.586	*
Tibiotarsus	67	0.00	0.020	0.911	-0.97	0.244	***	1.43	0.578	**
Humerus	67	-0.02	0.011	0.107	0.58	0.297	**	1.59	0.578	***
Ulna	67	-0.04	0.012	0.001	-0.17	0.032	ns	0.21	0.578	ns

^a Two-tailed t-test of H₀: $\mu = 0$.

^b Two-tailed t-test of H₀: $\gamma_1 = 0$. Exact probabilities unknown; *P < 0.1, **P < 0.05, ***P < 0.01, ns indicates P ≥ 0.1.

^c Two-tailed t-test of H₀: $\gamma_2 = 0$. Exact probabilities unknown; symbols as for skewness.

Table 1-4. Size and absolute asymmetry measures (mm) computed for four external and five skeletal paired morphological characters. Size is taken as the mean size of the left and right elements. Asymmetry is computed as the absolute value of the difference between the left and right sides.

Age	Character	n	Size		Asymmetry		
			Mean	SE	Mean	SE	Max
SY	Tarsus	34	27.75	0.127	0.25	0.040	0.85
	Wing	34	118.52	0.379	1.12	0.131	2.78
	Tail	33	89.28	0.424	0.73	0.180	4.53
	Epaulet	34	39.15	0.495	1.43	0.252	6.29
	Coracoid	34	26.56	0.089	0.10	0.013	0.31
	Femur	34	25.83	0.106	0.06	0.008	0.23
	Tibiotarsus	34	41.83	0.129	0.12	0.019	0.45
	Humerus	34	28.76	0.101	0.07	0.010	0.32
	Ulna	34	34.25	0.115	0.07	0.011	0.26
	Tarsus	33	28.15	0.113	0.22	0.037	1.00
ASY	Wing	33	122.38	0.431	0.80	0.093	2.28
	Tail	33	93.31	0.425	0.84	0.193	4.03

Table 1-4. (continued)

Age	Character	n	Size		Asymmetry		
			Mean	SE	Mean	SE	Max
ASY	Epaulet	32	44.31	0.332	1.47	0.218	4.76
	Coracoid	32	26.79	0.102	0.10	0.015	0.31
	Femur	31	25.93	0.092	0.07	0.010	0.27
	Tibiotarsus	33	42.36	0.160	0.12	0.019	0.55
	Humerus	33	28.80	0.087	0.06	0.009	0.18
	Ulna	33	34.35	0.114	0.09	0.008	0.16

Table 1-5. Analysis of covariance evaluating effects of male age (SY vs. ASY) and character size (taken as the mean size of the left and right elements, in mm) on the level of asymmetry (computed as the absolute value of the difference between the left and right sides, in mm, sqrt-transformed) exhibited at four external and five skeletal paired morphological characters. Interactions were not significant ($P > 0.1$) and were therefore removed from each model.

Model			Source	Coeff ^a	F	P
Character	n	R ²				
Tarsus	67	0.03	Age	0.002	0.00	0.951
			Size	-0.056	1.87	0.176
Wing	67	0.04	Age	-0.070	1.66	0.203
			Size	-0.001	0.00	0.965
Tail	66	0.03	Age	-0.044	0.22	0.640
			Size	0.038	1.65	0.204
Epaulet	66	0.02	Age	0.086	0.78	0.380
			Size	-0.027	0.99	0.325
Coracoid	66	0.04	Age	-0.003	0.03	0.866
			Size	-0.048	2.48	0.120
Femur	65	0.02	Age	0.011	0.93	0.338
			Size	0.004	0.04	0.844
Tibiotarsus	67	0.02	Age	0.018	0.66	0.420
			Size	-0.024	0.91	0.343
Humerus	67	0.01	Age	0.000	0.00	0.995
			Size	-0.019	0.70	0.405
Ulna	67	0.05	Age	0.021	3.31	0.074
			Size	-0.002	0.01	0.903

^a Partial coefficient. For age, add if ASY, subtract if SY.

Table 1-6. Product-moment correlations (above diagonal) and associated probability values (below diagonal) among asymmetry levels exhibited at four external and five skeletal paired morphological characters, based on a sample of 63 individual male red-winged blackbirds. Asymmetry is taken as the absolute value of the difference between the size of the left and right elements.

	Tarsus	Wing	Tail	Epaulet	Coracoid	Femur	Tibiotarsus	Humerus	Ulna
Tarsus	-	0.03	-0.14	0.05	0.14	0.08	-0.22	-0.11	-0.24
Wing	0.80	-	-0.03	-0.02	0.18	0.19	-0.02	-0.08	0.03
Tail	0.27	0.79	-	0.14	0.10	0.19	0.16	0.18	0.15
Epaulet	0.71	0.90	0.27	-	0.18	0.07	-0.01	-0.02	0.15
Coracoid	0.29	0.16	0.45	0.16	-	0.20	0.03	0.15	-0.03
Femur	0.52	0.14	0.13	0.57	0.11	-	0.01	0.07	0.07
Tibiotarsus	0.08	0.89	0.22	0.93	0.83	0.93	-	0.31	0.06
Humerus	0.40	0.55	0.15	0.87	0.23	0.57	0.01	-	0.00
Ulna	0.06	0.80	0.26	0.23	0.79	0.57	0.62	0.99	-

Table 1-7. Component loadings and percentage of the total variance explained by each of the first three principal axes (PCs) obtained from a correlation-based principal components analysis of asymmetry levels exhibited at four external and five skeletal paired morphological characters.

	PC1	PC2	PC3
Loadings			
Tarsus	-0.39	0.57	0.26
Wing	0.07	0.48	-0.08
Tail	0.64	0.02	-0.11
Epaulet	0.29	0.32	-0.42
Coracoid	0.34	0.62	0.23
Femur	0.39	0.54	-0.03
Tibiotarsus	0.50	-0.34	0.34
Humerus	0.57	-0.15	0.55
Ulna	0.40	-0.14	-0.68
Percent variance explained	19.0	16.6	13.3
Cumulative percent explained	19.0	35.6	48.8

Figure 1-1. Relationship between mean character size and mean character asymmetry, computed at the individual level as the average size of the left and right elements and as the absolute value of the difference between the left and right sides, respectively. Each observation is based on 65-67 individual male red-winged blackbirds, depending on the character. The relationship is statistically significant ($r_s = 0.68$, $P = 0.045$).

Discussion

A fundamental assumption inherent in current hypotheses regarding the role of asymmetry in female mate choice and male reproductive success is that some individuals have greater overall developmental competence than others. This, for instance, is a basic premise of the "male quality" hypothesis (Møller 1990a, 1992a; Thornhill 1992b). However, empirical evidence to support the existence of an organism-wide asymmetry property has been scant. Earlier authors dismissed the possibility based on repeated observations of poor agreement among asymmetry measures made on different characters (e.g., Van Valen 1962; Soule 1967; Soule and Baker 1968). More recently, it has been suggested that the general failure to detect concordance at the individual level may be a technical problem. For instance, Leamy (1993) suggested that any organism-wide "signal" is likely to be weak and therefore easily obscured by complicating factors such as measurement error and directionality. Other authors have argued that too few studies have examined a sufficient number of traits (Palmer 1994; Watson and Thornhill 1994). My results support this view. After reducing effects of measurement error and correcting directional biases, I demonstrated significant (albeit weak) concordance among character asymmetries in individual red-winged blackbirds. Thus, my results are at least consistent with the notion of organism-wide developmental competence.

A potential objection to my analysis is that I included characters exhibiting statistical departures from ideal FA. While all left-minus-right distributions were approximately normal in shape, and while there was clearly no evidence of antisymmetry in any of the characters examined, several

characters exhibited slight but significant directionality, such that for these characters the right element was significantly larger than the left element, on average. Palmer and Strobeck (1992) suggested that characters exhibiting such tendencies should be omitted from consideration, because such tendencies are thought to contaminate asymmetry measures as indices of developmental stability (see also Palmer and Strobeck 1986; Palmer 1994). This view, however, is predicated on the assumption that directional tendencies necessarily result from genetic predispositions toward greater development on one side. An alternative and perhaps more likely cause of directionality is bilateral measurement bias (e.g., a tendency to overestimate the size of a bilateral character on one particular side), in which case the problem is easily remedied through statistical correction (Palmer 1994). This seems a particularly plausible scenario in the present instance because all characters were measured by a right-handed investigator and most using right-handed callipers. Moreover, even if *all* of the observed directionality did indeed have a genetic basis, the tendency toward greater development on one side was clearly not absolute. At most, departure of the mean left-minus-right value was but 13% of the maximum deviation from perfect bilateral symmetry, and for most characters the corresponding value was considerably less. In no instance was the direction of bias uniform among all individuals sampled. In sum, the complicating influences of genetically based directionality in this study were minor at best and potentially nonexistent. For this reason, all characters were retained for analyses relating to the central objective.

The existence of an organism-wide asymmetry property in some animals

might have been inferred from previous studies. For instance, such a property is implied by multi-trait response to episodes of severe environmental or genetic stress (Watson and Thornhill 1994), and such a response has indeed been documented in a variety of animal species (see Parsons 1990 for a review). More directly, individual-level concordance among character asymmetries has been demonstrated in laboratory populations of house mice (*Mus musculus*; Bader 1965; Leamy 1993), but these studies have focused on localized suites of developmentally related characters (e.g., various dimensions of the mandible; Leamy 1993). My results indicate that individual-level concordance can also occur on a broader scale, emerging as a property of measurements made on characters from various regions of the body.

Given the apparent existence of an organism-wide asymmetry property in at least some species, it is of particular interest to determine whether asymmetry in any given character is likely to be good predictor of this property. My results indicate that in red-winged blackbirds, this is clearly not the case. Although I found statistically significant concordance among the character asymmetries examined, correlations among characters were generally weak. Thus, it was not possible to estimate overall asymmetry based on asymmetry in a single character. In this regard, my results have important implications for studies of asymmetry in relation to mate selection. Virtually all of the studies that have demonstrated associations between asymmetry and male mating success have been based on measurements made on a limited number of bilateral traits (e.g., Møller 1992a, 1993a; Thornhill 1992a,b; Harvey and Walsh 1993; Liggett et al. 1993; McLachlan and Cant 1995; Simmons

1995). In invoking the male quality hypothesis to explain their results, many authors have implicitly assumed that asymmetry in any given character is a reasonable measure of overall developmental competence (Møller 1992a, 1993a; Thornhill 1992a,b; Simmons 1995). My results add to a growing body of evidence to suggest that this assumption is tenuous (Evans et al. 1995; Ryan et al. 1995; see also Palmer and Strobeck 1986 and references therein).

It might be argued that the concern raised above does not apply to studies of asymmetry in sexual ornaments (e.g., Møller 1992a, 1993a) because, for reasons detailed by Møller and Pomiankowski (1993), sexual ornaments might be expected to be particularly revealing of overall developmental competence. Nevertheless, as several authors have recently emphasized, this premise needs to be verified (Watson and Thornhill 1994; Ryan et al. 1995). A straight-forward prediction of the premise is that asymmetry in sexual ornaments should be more predictive of composite (i.e., multi-trait) asymmetry than asymmetry in individual non-ornamental characters (Watson and Thornhill 1994). At present, there are few data available to assess this possibility. To my knowledge, this is the first study to address the issue explicitly, and I found no evidence to suggest that asymmetry in the sexually selected epaulets of male red-winged blackbirds was a better predictor of overall asymmetry than asymmetry in other traits. This occurred despite the fact that epaulets were exceptionally asymmetrical on average, an observation consistent with Møller and Pomiankowski's (1993) hypothesis. Interestingly, in a large-scale study of asymmetry variation in the barn swallow, Møller (1994) reported significant positive correlations among asymmetries exhibited at three of the four

characters he examined; the exceptional character was length of the elongated outer retriex, the sexual ornament that he studied. Clearly, more data are needed on patterns of asymmetry variation in ornamental and non-ornamental characters before it can be assumed that ornament asymmetry reflects overall developmental competence.

In sum, results of the present analysis support the existence of an individual-level, organism-wide asymmetry property in red-winged blackbirds. However, they also imply that asymmetry in any given character is likely to be a poor predictor of this property. This accords with the position recently taken by other authors (e.g., Palmer 1994; Ryan et al. 1995) that it is important to use a multiple-character approach when assessing potential reproductive consequences of asymmetry at the individual level. Nevertheless, it seems important to consider potential effects of individual character asymmetries as well, as there is some evidence indicating that asymmetry in particular characters (e.g., those associated with flight performance) might directly influence individual success in intra-sexual competition for mating opportunities (McLachlan and Cant 1995; see also Balmford and Thomas 1992; Palmer 1994). Collectively, these considerations suggest that it may be advisable to employ a dual approach in which components of reproductive success are evaluated in relation to both individual character asymmetries and to some composite measure (e.g., ranks of individual asymmetry scores summed across all characters) that should better reflect overall developmental competence (Palmer 1994). This is the approach adopted in the remaining chapters of this thesis.

CHAPTER 2

Bilateral symmetry as an indicator of male quality in
red-winged blackbirds: associations with measures
of health, viability, and parental effort

Introduction

Subtle departures from perfect symmetry in bilaterally-paired morphological characters have long been of interest to developmental and population biologists (for reviews, see Palmer and Strobeck 1986; Leary and Allendorf 1989; Parsons 1990, 1992; Zakharov 1992). This interest has stemmed primarily from the recognition that, where symmetry is the norm, departures from symmetry provide a convenient measure of the extent of disrupted development. Thus, asymmetry has often been used to characterize the condition or health of populations (Zakharov 1992). Indeed, at the population level, asymmetry has been linked to a variety of types of stress, including exposure to chemical pollutants and loss of genetic variation due to inbreeding (reviewed by Leary and Allendorf 1989; Parsons 1990, 1992).

More recently, it has become apparent that subtle developmental inconsistencies can have fitness consequences for individuals. Specifically, there is growing evidence to suggest that, in a variety of animal taxa, males exhibiting relatively high levels of asymmetry suffer reduced mating success (e.g., Markow and Ricker 1992; Møller 1992a, 1993a, 1996; Thornhill 1992a,b;

Harvey and Walsh 1993; Swaddle and Cuthill 1994a; McLachlan and Cant 1995), sometimes leading to a significant reduction in reproductive output (Møller 1992a, 1993a). While it is clear from these studies that asymmetry can influence individual reproductive success, the underlying mechanisms are poorly understood. The most frequently discussed possibility is that females discriminate against asymmetrical males when selecting among potential mates, the adaptive basis of which is that discriminating females obtain viability-enhancing genes for their offspring (Møller 1990a, 1992a; Thornhill 1992b; Swaddle and Cuthill 1994a,b). Alternatively, it has been suggested that females might selectively mate with males exhibiting low levels of asymmetry because such males are better able to provide material resources and/or parental care (Borgia and Wilkinson 1992; Thornhill 1992b). Both of these hypotheses are predicated on the assumption that asymmetry is a phenotypic indicator of overall male "quality", a premise that has received much theoretical attention (e.g., Møller 1993b; Møller and Pomiankowski 1993; Watson and Thornhill 1994), but for which empirical evidence is limited (see below). Here I present results of an analysis aimed at exploring whether bilateral asymmetry is a general quality indicator in male red-winged blackbirds (*Agelaius phoeniceus*).

To date, two principal lines of evidence have been offered in support of the suggestion that asymmetry reflects aspects of underlying individual quality. First, studies of naturally occurring patterns of asymmetry variation in the ornamental tail feathers of certain birds have revealed that ornament size and asymmetry are often inversely related (Møller 1990a; Manning and Hartley

1991; Møller and Høglund 1991). To the extent that ornament expression is a function of individual health or viability, this result is consistent with the suggestion that symmetry and quality are correlated (see Andersson 1994 for a review of evidence supporting quality indicator models of sexual selection). However, as several authors have recently stressed, there are difficulties with this interpretation. For instance, Evans and Hatchwell (1993) have argued that large ornaments might simply be constrained to develop more symmetrically, because the mechanical (e.g., aerodynamic) consequences of asymmetry are expected to increase with increasing size of the trait (see also Evans 1993; Thomas 1993; Evans et al. 1994). Thus, an inverse relationship between ornament size and asymmetry can occur in the absence of any direct link between asymmetry and quality. In addition, several recent investigations have failed to support the prediction (Balmford et al. 1993; Evans and Hatchwell 1993; Evans et al. 1995; Tomkins and Simmons 1995), suggesting limits to the generality of the pattern.

The second line of evidence for a link between asymmetry and individual quality has come from direct demonstration of associations between asymmetry and various fitness-related traits. For instance, Thornhill (1992a) reported that male Japanese scorpionflies (*Panorpa japonica*) exhibiting relatively low levels of forewing asymmetry were more likely to succeed in intra-sexual contests over food (see also Thornhill and Sauer 1992). Perhaps more importantly, symmetric individuals tended to survive longer under semi-natural conditions, suggesting that symmetry and inherent viability might be correlated in this species (Thornhill 1992a). Similar results have since been reported in

other insect taxa (Naugler and Leach 1994; Ueno 1994; see also Harvey and Walsh 1993). Finally, recent work on natural populations of *Drosophila* suggests that symmetry in certain characters might reflect heritable resistance to parasitic infection (Polak 1993). While results of these and related studies (too numerous to list here) support the suggestion that asymmetry provides information regarding overall quality, several authors have recently questioned this interpretation (e.g., Eggert and Sakaluk 1994; Palmer 1994; Ryan et al. 1995). The primary concern of these authors stems from the recognition that most of the relevant studies (e.g., all of those cited above) have been based on asymmetry measures made on one or two arbitrarily chosen traits. If the results of these studies are to be taken as evidence in support of the "individual quality" hypothesis, it follows that asymmetries exhibited at different characters should be correlated. However, there is growing evidence to suggest that such correlations are likely to be rare (see Chapter 1 and references therein), and thus, single character asymmetries are likely to be poor predictors of overall developmental competence (Palmer 1994). At the same time, however, few studies of the relationship between asymmetry and individual quality have employed a multiple-character approach. To my knowledge, no study has evaluated aspects of individual quality in relation to a composite measure of asymmetry that combines information across multiple characters, at least in the context of mate choice and sexual selection (for examples of other applications, see Leary et al. 1983; Manning and Ockenden 1994; Hartl et al. 1995). My central aim in this chapter is to provide such an analysis, using data assembled from free-living male red-winged blackbirds.

The red-winged blackbird is a socially polygynous passerine that breeds in open habitat, principally marsh, throughout much of North America (Orians 1980). In northern (i.e., migratory) populations, males arrive at breeding grounds in early spring, where they compete for and defend exclusive breeding territories (see Searcy and Yasukawa 1995). Female arrival and settlement follows, usually within a few weeks. Females, therefore, select among potential "breeding situations", each comprised of a particular male (i.e., social mate) and territory. Nevertheless, two considerations suggest that assessment of male quality in this species is unlikely to be complicated by associations with territory characteristics. First, extensive research on the factors influencing territory acquisition in red-winged blackbirds has shown that male and territory characteristics vary independently; high quality males (defined in terms of morphology and/or competitive ability) do not necessarily acquire high quality territories (Eckert and Weatherhead 1987a,b; see also Yasukawa 1979; Beletsky and Orians 1987a, 1989; Eckert and Weatherhead 1987c; Shutler and Weatherhead 1991, 1992). Second, recent DNA-based studies of parentage in red-winged blackbirds have revealed that females often copulate with, and produce young sired by, males other than their social mate (Gibbs et al. 1990; Westneat 1993; Weatherhead and Boag 1995; see also Chapter 3). This implies that female choice of a genetic sire in this species is not entirely constrained by her decision of where to nest (although see Weatherhead 1994). Taken together, these observations suggest that investigations of male "quality" in red-winged blackbirds are most appropriately restricted to characteristics of the males themselves.

If male morphological features are to influence female mating decisions, those features should be associated with characteristics that ultimately influence female fitness (Searcy 1979a). In other words, male quality is most appropriately defined in terms of benefits that might be accrued to discriminating females. In red-winged blackbirds, such benefits can be divided into two broad categories (Searcy and Yasukawa 1995). First, discriminating females might receive indirect benefits through the production of genetically superior offspring (see, for instance, Weatherhead 1984). Direct measurement of male genetic quality is naturally impossible, but if bilateral symmetry is a reliable indicator of overall genetic quality, asymmetry measures should correlate with measures of health and viability. Several such measures are readily quantified in free-living red-winged blackbirds. First, available evidence indicates that male red-winged blackbirds suffer a net energy deficit in spring and early summer (Searcy 1979b; Shutler and Weatherhead 1991). Thus, nutritional status (i.e., condition) provides one obvious measure of male health. Second, red-winged blackbirds are host to a wide variety of parasites, including endoparasitic haematzoa, ectoparasitic mites (Arachnida: Acari), and lice (Insecta: Phthiraptera). Parasitic infection varies considerably among individuals (Weatherhead and Bennett 1991; Weatherhead et al. 1993), and there is growing evidence that, contrary to conventional wisdom, parasites in general can have negative fitness consequences for their hosts (e.g., Booth et al. 1993; Brown et al. 1995; see also reviews by Møller et al. 1990; Reed 1990; Clayton 1991a). Thus, parasitic infection provides a second indirect measure of individual health and viability. Finally, male red-winged blackbirds exhibit

extremely high breeding site fidelity (Searcy 1979c; Beletsky and Orians 1987b), which allows for direct measurement of male viability through assessment of between-year survival (e.g., Searcy 1979b; Yasukawa 1987; Weatherhead and Clark 1994). My first objective in the present study, therefore, was to evaluate each of these measures of health and viability in relation to levels of bilateral asymmetry exhibited by individual males.

The second aspect of male quality that might be expected to influence female mating decisions is the extent to which particular males provide parental care (i.e., parental quality). In red-winged blackbirds, females alone perform most parental duties, including nest construction, incubation, and brooding of the young. Male provisioning of nestlings occurs to varying extents, but never comprises a major component of the total food delivery (Searcy and Yasukawa 1995). In fact, in lowland marshes of eastern Ontario (where the present study was conducted), male provisioning is negligible (Weatherhead 1990a; Hurd et al. 1991; Teather 1992). However, male red-winged blackbirds do provide significant parental care in the form of active nest defence. Nest defence effort varies widely among males (e.g., Eckert and Weatherhead 1987d), and there is empirical evidence that male nest defence influences female reproductive success (Knight and Temple 1988; Weatherhead 1990a; see also Searcy and Yasukawa 1995). My second objective, therefore, was to determine whether male nest defence effort might be predictable on the basis of bilateral asymmetry, and hence whether asymmetry might be a correlate of paternal quality in this species. For this objective, I used DNA-based methods to verify paternity of nestlings, which allowed me to eliminate potential effects of

paternity on patterns of parental care (e.g., Burke et al. 1989; Dixon et al. 1994; Weatherhead et al. 1994).

Methods

I evaluated associations between asymmetry and aspects of individual quality using two independent samples of free-living male red-winged blackbirds. The first sample was comprised of individuals collected during the spring of 1993 at a communal roost located approximately 10 km west of the Queen's University Biological Station (Chaffey's Locks, Ontario, 44°34'N; 76°20'W). The second sample consisted of males defending territories at selected sites within 8 km of the Biological Station during the breeding seasons of 1993 and 1994. Each of the two samples formed the basis of another major component of the thesis (Chapter 1 for roost-sampled individuals, Chapter 3 for breeding males), so only those methodological details that are directly relevant to the present analysis are given here.

Collected specimens

For analyses related to nutritional condition and parasitic infection, I focused exclusively on the point sample of individuals collected at the spring roost in 1993. Sixty-seven males were captured passively by mist net during a one-week period beginning 23 April. Captured individuals were transported immediately to the Biological Station, where they were classified according to age (second year vs. after second year, hereafter SY and ASY, respectively) and weighed to the nearest 0.5 g using a Pesola spring scale. A blood smear (for haematzoa analysis) was prepared for each individual following procedures outlined by Bennett (1970). Each individual was then suspended for five minutes in a polyethylene bag containing an absorbent pad treated with a small amount of

chloroform. In addition to killing the bird (for skeletal analysis, see below), the chloroform treatment provided a means of quantitatively assessing infestation by ectoparasites (Martin 1977; Fowler and Cohen 1983). Anesthetized ectoparasites were sorted and counted on site and then stored in absolute ethanol for later identification. Blood smears were sent to the International Reference Centre for Avian Haematozoa (Memorial University, St. John's, Newfoundland), where blood parasites were identified and infection intensities scored. Intensity of infection by *Haemoproteus* and *Plasmodium* was measured as the number of parasites per 100 fields at x100 (oil immersion). Intensity of infection by *Leucocytozoon* was assessed in a similar manner at x40.

Once all individuals had been collected and processed for parasites, I measured both the left and right elements of four external and five skeletal paired morphological characters. External characters included tarsus length, wing chord, and length of the outer rectrix (hereafter "tail length"), as well as total length of the epaulet, a bilaterally-paired plumage ornament (see Chapter 1, Table 1-1, for complete character descriptions). Skeletal characters included lengths of the coracoid, femur, tibiotarsus, humerus, and ulna. All characters except wing chord and tail length were measured to the nearest 0.1 mm using callipers; wing chord and tail length were measured to the nearest 1 mm using modified flat rulers. To improve precision of measurement, all characters were measured twice (but not in succession, see Chapter 1), and the mean of the two replicate measures used in analysis (see Bailey and Byrnes 1990; Yezerinac et al. 1992). Asymmetry for each character was taken as the absolute value of the difference between the left and right sides. Character size was

computed as the average size of the left and right elements (i.e., $[\text{left} + \text{right}] / 2$). Feathers showing evidence of breakage or wear were excluded from consideration, and skeletal elements damaged during specimen preparation were not measured. Consequently, sample sizes vary slightly among analyses.

I used body mass, corrected for structural size, as an index of nutritional condition. Body mass is typically correlated with total body lipids in birds (Blem 1990), and this correlation is generally improved by controlling body mass variation due to size differences (e.g., Bailey 1979; Johnson et al. 1985; Ringelman and Szymczak 1985). To obtain a measure of overall structural size for each individual, I first conducted principal components analysis (PCA) on the correlation matrix of size measures computed for each of the eight non-ornamental characters described above (see Rayment et al. 1984 for a general discussion of this application of PCA). This initial analysis was based on 64 individuals that had non-missing values for all eight characters. The first principal axis (PC1) described positive covariation among the five skeletal characters and tarsus (component loadings: 0.71 - 0.87), and accounted for 53.2% of the total original variance. Interestingly, wing chord and tail length were only moderately correlated with PC1 (loadings: 0.45 and 0.27, respectively). However, covariation between these two characters was clearly summarized by the second principal axis (loadings: 0.84 and 0.91 corresponding to wing chord and tail length, respectively; loadings for other variables: -0.26 - 0.02). Thus, PCA in this instance effectively extracted two "size" axes, with PC1 and PC2 primarily describing covariation among skeletal and feather characters, respectively. Because avian body size is perhaps best

equated with overall size of the skeleton (Freeman and Jackson 1990), I chose scores along the first principal axis (hereafter PC1 scores) as measures of overall size. For those individuals not included in the PCA (i.e., those missing a particular measurement), I estimated body size using a multiple linear regression equation describing the dependence of PC1 score on a subset of the original variables, specifically, those for which measures were available for all individuals in the sample (i.e., tarsus, wing, tibiotarsus, humerus, and ulna). In combination, these five measures were excellent predictors of PC1 score (model $R^2 = 0.98$, $n = 64$, $P < 0.0001$).

As expected, body mass varied with overall structural size ($r = 0.48$, $n = 67$, $P < 0.0001$). Thus, to control effects of size in analyses, I used residuals from the mass versus size regression as estimates of individual condition (see Sokal and Rohlf 1981: 494-496). Residuals for SY and ASY males were derived from a single regression equation under the assumption that the body mass versus size relationship was similar for these two groups of males. I confirmed that this was the case using analysis of covariance (age*size interaction: $F = 0.01$, $df = 1,63$, $P = 0.904$).

Breeding males

To address questions related to viability and parental quality, I monitored breeding activity and survival of individual males defending territories at four study sites during the breeding seasons (April - July) of 1993 and 1994. I also surveyed these same sites in the spring of 1995, with the aim of identifying returning males that had been banded in previous years. All sites were relatively

small (<10 ha) isolated lowland marshes characterized by stands of either willow (*Salix* sp.) or cattail (*Typha* sp.). Detailed descriptions of the study sites are provided elsewhere (Chapter 3). The four marshes supported breeding populations of 5-17 males in 1993 and 4-19 males in 1994. In each of the two years, 88% of breeding males were ultimately captured and processed, with many males banded in 1993 returning to defend the same territories in 1994 (see Chapter 3 for details). In all, morphological and breeding data were assembled for 52 individual males.

Monitoring of breeding activity began in early April of each year, soon after males had established territorial boundaries. Marshes were surveyed every 2-3 days and the area defended by each male recorded on a small-scale map. Males were captured by mist net using a model conspecific male and playback, processed on site, and released immediately back onto their territories. Each captured individual was fitted with a unique colour combination of aluminium leg bands, weighed (as above), and bilateral characters measured. Measurements were the same as those described for collected specimens (external characters only), but included one additional paired character, length of the red portion of the epaulet (Searcy 1979d). Measurement of both "red epaulet length" and "total epaulet length" was possible in this instance because all breeding males were at least two years old (i.e., ASY males), and thus, all were in full adult plumage (see Searcy and Yasukawa 1995). As with roost-caught individuals, all characters were measured twice (again, non-consecutively), and the average value of replicate measures used in analysis. Because skeletal measurements were not available

for breeding males, I used their external correlate, i.e., tarsus length, as a measure of overall body size (Freeman and Jackson 1990; see also results of the PCA reported above). Finally, in 1993 I obtained a blood sample from all males for subsequent paternity analysis (see Chapter 3). Blood sampling has no apparent deleterious effect on free-living red-winged blackbirds (Hoysak and Weatherhead 1991).

Prior to initiation of the present study, all four breeding populations had been monitored (and breeding adults banded) as part of a long-term investigation (1985 - 1992; Weatherhead and Boag 1997). As a result, and because male red-winged blackbirds are extremely site-faithful, I was able to obtain accurate estimates of the breeding experience of individual males. Because most males, if they breed at all, first establish territories when they are two or three years old (Orians and Beletsky 1989; Shutler and Weatherhead 1994), breeding experience provides a surrogate measure of age (e.g., Weatherhead and Boag 1995). Thus, I used the number of years of prior breeding experience at the outset of the breeding season as an index of the age of breeding males. Analysis based on a subsample of individuals for which exact ages were known (i.e., those initially banded as nestlings or SY males prior to 1993) confirmed that breeding experience and age were highly correlated ($r = 0.90$, $n = 18$, $P < 0.0001$).

Following female settlement and nest initiation, I conducted systematic nest searches of each marsh every 2-3 days. Most nests (90% of 194, years pooled) were discovered during nest construction or egg-laying; all were found before the eggs had hatched. For the few nests that were discovered with

complete clutches, I estimated date of clutch initiation by back-dating from hatch using an assumed incubation period of 11 days (i.e., the modal value for other nests; see also Searcy and Yasukawa 1995). Nests were checked every 2-3 days as long as they remained active, though the order in which visits were made to simultaneously active nests varied from one day of observation to the next. In 1993, blood samples (for parentage analysis) were obtained from all nestlings when they were 4-6 days old. In most instances, the attending female was captured and sampled as well (see Chapter 3).

To quantify male nest defence effort, I adopted a procedure that has been used extensively by other authors (e.g., Searcy 1979a; Eckert and Weatherhead 1987d; Weatherhead et al. 1994), in which aggressive response to a human intruder is scored during regular nest checks. Trials began with an observer (either myself or an assistant) approaching to within 1 m of an active nest. The attending male was given 2 minutes to respond. Males that did not respond (i.e., those that were not seen) during this period were assigned a score of zero. Once a male had responded, his aggressive behaviour was recorded over the next 2 minutes. Aggressive behaviour was rated on an objective scale that incorporated both the proximity of the male (i.e., approach distance) and the extent of vocalization (see Eckert and Weatherhead 1987d for a description of the categories used). Scores ranged from 1 (for males that remained silent at distances of >10 m) to 7 (physical attack on the observer). Trials were conducted at every nest visit following clutch completion, except during periods of rain. However, because nest defence effort is expected to vary with stage of the nest (i.e., offspring value; see Montgomerie

and Weatherhead 1988), I restricted analysis to those trials conducted when nestlings were 4-10 days old (see also Weatherhead et al. 1994).

I used multi-locus DNA fingerprinting to establish the true parentage of nestlings (Jeffreys et al. 1985a; Burke and Bruford 1987; see Burke 1989 for an overview of the technique). Fingerprinting protocols, gel scoring procedures, and criteria used to identify illegitimate young are described elsewhere (Chapter 3), so here I provide only a summary of the methods and overview of the main results. Fragments of *Alu* I-digested DNA were sorted according to size using agarose gel electrophoresis and transferred *in situ* by Southern Blotting to an Immobilon nylon membrane. Banding profiles (i.e., DNA fingerprints) were produced by hybridization of the transferred fragments with each of two radioactively labelled mini-satellite probes (Jeffreys et al. 1985a; Shin et al. 1985). Samples from nestlings and their putative parents were always run on the same gel. I used the presence of novel fragments (i.e., those that could not be ascribed to either parent), as well the degree of band-sharing between individuals, to identify illegitimate young (see Westneat 1990, 1993).

For logistic reasons, parentage analysis was restricted to samples obtained in 1993 and focussed exclusively on data collected at my two most productive study sites. All 26 resident males at the two sites were captured and included in the analysis, although broods of only 19 males survived to an age at which blood samples could be obtained. These broods ($n = 42$) collectively comprised 143 nestlings. All nestlings were found to be the true genetic offspring of the attending female (i.e., there was no evidence of intraspecific brood parasitism), but 21% of nestlings sampled were identified as

being sired by a male other than the territory owner (Chapter 3). Thirty-six percent of broods contained at least one illegitimate nestling. In the context of the present study, the significance of this result is that many nest defence trials were conducted at nests where the focal male had not secured full paternity in the brood. Importantly, however, reduced paternity has previously been shown to influence nest defence effort among male red-winged blackbirds (Weatherhead et al. 1994). I take these considerations into account in analysing the nest defence data.

Data analysis

Previous authors have identified a number of technical difficulties associated with quantifying asymmetry at the individual level (Palmer and Strobeck 1986, 1992; Palmer 1994; Swaddle et al. 1994). Potential complicating factors include: (1) high levels of measurement error; (2) genetic tendencies toward greater development on one side or the other (i.e., directional asymmetry and antisymmetry); and (3) size-dependence of asymmetry within characters (see Palmer 1994 for detailed treatment of these considerations). Analyses pertaining to these issues are presented elsewhere (Chapters 1 and 3), but it nevertheless seems appropriate here to review some of the key results. One-way analysis of variance based on replicate left-minus-right values revealed detectable levels of asymmetry (i.e., significant among-individual variability) at each of the characters measured. Measurement error of signed asymmetry values ranged from 0.9 to 20.8%, underscoring the value of making repeated measures on all individuals. There was no evidence of antisymmetry (i.e.,

bimodality or platykurtosis) in any of the characters examined, though many characters showed slight but statistically significant directionality (i.e., departures of the mean left-minus-right value from zero; see Palmer and Strobeck 1992). There was also some suggestion that directional tendencies occurred generally among characters (Chapter 1). Thus, before converting asymmetry scores to absolute values, individual left-minus-right values for each character were adjusted to a mean of zero (Palmer 1994; see Chapter 1 for details). Asymmetry scores for collected specimens and breeding males were adjusted separately, as individuals from the two samples were never included in the same analysis. Finally, because distributions of absolute asymmetry scores were positively skewed (as expected; see Swaddle et al. 1994), asymmetry measures for all characters were transformed to square roots for analysis (see Chapter 1). There was no apparent relationship between size and absolute asymmetry in any of the characters examined.

Previously I have shown that asymmetries exhibited at different characters are, at best, only weakly correlated in red-winged blackbirds (Chapter 1). Thus, to retain the maximum amount of information in analysis, I used a two-step analytical approach. First, I evaluated each response variable (i.e., each measure of individual quality) in relation to levels of asymmetry exhibited at each individual character. Second, I examined the relationship between each measure of individual quality and a composite asymmetry index that combined information across characters. Composite asymmetry was taken as the summed ranks of individual asymmetry scores, computed across all characters measured for a particular sample of males (i.e., asymmetry

scores for roost-caught individuals and breeding males were ranked independently). As a result, analyses involving composite asymmetry scores are necessarily restricted to those individuals having non-missing values for all characters ($n = 63$ and 46 for collected specimens and breeding males, respectively). For clarity, further analytical details are provided with the results. All analyses were conducted using JMP® (version 3.1) statistical software (SAS Institute Inc. 1994).

Results

Condition

As indicated above, analyses of nutritional condition were restricted to the sample of individuals collected at the spring roost in 1993. The basis for this decision was that, because collection was limited to a one-week period at the outset of the breeding season, it could reasonably be assumed that individuals in this sample had similar nutritional requirements. To evaluate the relationship between condition and individual character asymmetries, I developed separate analysis of covariance (ANCOVA) models for each character, treating condition (i.e., residual mass) as the response variable and specifying character asymmetry and male age (SY vs. ASY) as predictors. Age was included in each model because a preliminary analysis had revealed that SY males were in poor condition relative to ASY males ($t = 4.18$, $df = 65$, $P < 0.0001$). Initial models indicated that there were no significant interactions (all P values > 0.1); thus, only the results of reduced (i.e., main effects) models are reported here. While the partial coefficient describing the relationship between condition and asymmetry was in the predicted direction (i.e., negative) for seven of the nine characters examined (binomial test, $P = 0.09$; Table 2-1), in no instance did the relationship approach statistical significance (Table 2-1). Similarly, there was no detectable relationship between individual condition and the composite asymmetry index that combined information across all nine characters (ANCOVA, age*asymmetry interaction: $F = 1.97$, $df = 1,59$, $P = 0.17$; asymmetry effect, interaction removed: $F = 0.24$, $df = 1,60$, $P = 0.62$). Thus, I found little evidence to suggest that character asymmetries, either singly or in

combination, reflected the health of males as indicated by their nutritional status.

Parasitic infection

As expected, I detected a variety of both endo- and ectoparasites among the 67 roost-caught individuals surveyed (Table 2-2). Ectoparasites included two species of chewing lice (order Phthiraptera, formerly Mallophaga), as well as several species of haematophagous mites (suborder Acari). The lice encountered were *Philopterus agelaii* and *Brueelia ornatissima*, both of which are members of the suborder Ischnocera. Avian ischnocerans are obligate parasites that feed exclusively on feathers (Marshall 1981), with transmission occurring principally through direct contact between host individuals (Clayton 1991b; Clayton and Tompkins 1994). Mite samples were comprised primarily of *Ornithonyssus sylviarum* (Parasitiformes: Macronyssidae), a common avian blood-feeding parasite capable of both contact and independent transmission (DeVaney et al. 1980). Blood smears revealed three species of avian haematozoa: *Haemoproteus quisqualis*, *Leucocytozoon icterus*, and *Plasmodium vaughani* (see Atkinson and van Riper 1991 for a detailed description of the life cycles of these haemosporidians). The microfilariae of an unidentified nematode were also detected in the blood, but only two birds were infected. Because parasitism by microfilariae was rare, I did not consider this parasite any further.

For purposes of analysis, I treated infection by lice, mites, and haematozoa as independent components of parasitism. Most individuals were

found to be parasitized by lice, with relative louse loads among parasitized individuals ranging from 1 to 32 (Table 2-2). Similarly, variation in mite parasitism was described primarily by intensity of infestation, as most individuals were parasitized to some extent (Table 2-2). Thus, for both louse and mite parasitism, I assessed variation in intensity. As is typical of parasite data, intensity distributions were positively skewed. Accordingly, louse and mite intensities were transformed to square roots for analysis. A preliminary analysis had revealed that the square root transformation was the best transformation to normality (for both lice and mites) among those recommended by Sokal and Rohlf (1981:423-427).

The distribution of blood parasites among males suggested a somewhat different analytical approach. While parasitism by haematozoa was far from negligible, prevalences were generally low, and for a given parasite species the majority of males was found to be uninfected (Table 2-2). Thus, I combined data across blood parasite species and simply classified males according to whether they were infected or uninfected. This approach is consistent with the recommendations of Weatherhead and Bennett (1991), who have outlined a number of problems associated with the use of intensity estimates derived from blood parasite data (see also Weatherhead 1990b).

For the most part, infections by the three parasite taxa occurred independently of one another. The relationship between louse intensity and mite intensity was weak and nonsignificant ($r = 0.19$, $n = 67$, $P = 0.12$), and there was no difference between the louse intensities of individuals infected and those uninfected with haematozoa ($t = 0.23$, $df = 65$, $P = 0.82$). There was some

evidence of a negative association between the incidence of blood parasitism and intensity of mite infestation ($t = 1.79$, $df = 65$, $P = 0.08$), as was observed in a previous study of parasites in red-winged blackbirds (Weatherhead et al. 1993). However, one-way analysis of variance indicated that only 4.7% of the variation in mite intensity could be explained on the basis of blood parasite status (i.e., infected vs. uninfected). Given that associations among the various parasites were weak at best, I treated each parasite separately in subsequent analyses.

Louse intensities differed between the two recognisable age classes, with SY males supporting larger loads than older individuals ($t = 2.86$, $df = 65$, $P = 0.006$; Table 2-2). Thus, to control effects of male age in analyses of parasitism relative to asymmetry, I again used analysis of covariance, specifying louse intensity as the response variable and treating age and asymmetry as predictors. As with condition, models were developed separately for each character. Initial models again indicated that there were no significant interactions (all P values > 0.1). Analysis based on reduced models revealed that only one of the nine partial coefficients describing the relationship between louse intensity and character asymmetry was significant at $P \leq 0.1$; none was significant at $P \leq 0.05$ (Table 2-3). ANCOVA indicated a marginally significant relationship between louse intensity and composite asymmetry score, with the relationship occurring similarly among SY and ASY males (Fig. 2-1). Importantly, however, the relationship was in the direction opposite to that predicted: individuals with high levels of asymmetry were characterized by relatively low levels of parasitism (Fig. 2-1). Thus, these data suggest that asymmetry and

parasitic infection are indeed related in red-winged blackbirds, though in a manner different from that expected under the male quality hypothesis.

A limitation of the preceding analysis is that it does not permit a clear separation of the effects of individual character asymmetries and that of composite asymmetry *per se*. Of particular concern is the possibility that the relationship shown in Fig. 2-1 is entirely attributable to the marginally significant effect of tarsus asymmetry (Table 2-3), which in turn might be spurious, given the relatively large number of character asymmetries examined. To determine whether this was the case, I repeated the analysis using a revised composite measure that excluded information on tarsus asymmetry. Composite asymmetry was thus computed as the ranks of individual asymmetry scores summed across the other eight characters examined. Results of the reanalysis were consistent with those reported above. ANCOVA revealed a marginally significant inverse relationship between louse intensity and composite asymmetry score, with the relationship occurring independently of male age (age*asymmetry interaction: $F = 0.58$, $df = 1,59$, $P = 0.45$; asymmetry effect, interaction removed: $F = 2.98$, $df = 1,60$, $P = 0.09$). Thus, the association between louse parasitism and composite asymmetry (reported above) was not due solely to the potentially spurious effect of tarsus asymmetry.

As with infestation by ectoparasitic lice, mite intensities of SY males exceeded those of ASY males (Table 2-2), though the difference was only marginally significant ($t = 1.75$, $df = 65$, $P = 0.08$). Nevertheless, to ensure that any variation in mite parasitism due to male age was controlled in analyses of parasitism relative to asymmetry, I again used an ANCOVA approach (identical

to that described above), developing separate models for each character. Of the nine models developed, only one revealed a significant ($P \leq 0.1$) relationship between parasitism and asymmetry, and in this instance the direction of the relationship was again opposite to that predicted under the male quality hypothesis (Table 2-4). Perhaps more importantly, there was a significant inverse relationship between mite intensity and composite asymmetry score (Fig. 2-2). This relationship held when information on coracoid asymmetry (the one significant predictor among individual characters) was excluded from the composite measure (ANCOVA, age*asymmetry interaction: $F = 0.00$, $df = 1,59$, $P = 0.97$; asymmetry effect, interaction removed: $F = 4.49$, $df = 1,60$, $P = 0.04$). Collectively, these results imply that the observed association between mite parasitism and composite asymmetry cannot be ascribed to patterns of asymmetry variation in any one character.

In contrast to the situation for infestation by ectoparasites, there was no evidence of age-related variation in blood parasitism (2 x 2 contingency table analysis with age and blood parasite status as factors: $G = 0.419$, $df = 1$, $P = 0.52$; Table 2-2). Thus, to test for associations between blood parasitism and asymmetry, I combined data from the two age classes of males and simply compared asymmetry levels exhibited by individuals infected and those uninfected with haematzoa. In general, these two classes of individuals were indistinguishable based on either individual character asymmetries (Table 2-5) or asymmetry overall (i.e., composite asymmetry score, $t = 0.49$, $df = 61$, $P = 0.62$). Thus, I found no evidence to suggest that infection by haematzoa was associated with levels of asymmetry exhibited by

individual males.

Between-year survival

Of 35 breeding males captured and processed in 1993, 18 (51%) returned to defend territories in 1994. Of 35 males that bred in 1994 (i.e., 18 returning individuals and 17 new residents), 21 (60%) returned to breed in 1995. In both 1994 and 1995, breeding site fidelity was apparently absolute; territories of all returning males were at least contiguous with the areas that they had defended in the previous breeding season. It is noteworthy that the observed annual return rates are in agreement with a continent-wide survival rate estimate for male red-winged blackbirds based on band-recovery data (i.e., 54%; Searcy and Yasukawa 1981). This observation, in combination with the extremely high breeding site fidelity exhibited by returning individuals, suggests that few surviving males, if any, went undetected (see also Searcy and Yasukawa 1995). Thus, here I treat annual return and between-year survival as synonymous.

Because some males were present during both years of study, I evaluated asymmetry differences between surviving and non-surviving males separately by year. To ensure that these comparisons were not complicated by other uncontrolled determinants of survival, I first examined potential effects of male age (i.e., breeding experience) and overall body size (i.e., tarsus length). There was no evidence that either of these factors influenced between-year survival in this particular sample of males (t-test comparison of returning and non-returning individuals: age in 1993, $t = 0.74$, $df = 33$, $P = 0.46$; age in

1994, $t = 0.42$, $df = 33$, $P = 0.68$; size in 1993, $t = 0.35$, $df = 33$, $P = 0.73$; size in 1994, $t = 0.36$, $df = 33$, $P = 0.36$).

In general, there was little indication that between-year survival was consistently associated with asymmetry in any of the characters examined (Table 2-6). Among males that bred in 1993, there was some suggestion that those that survived to the subsequent breeding season had relatively low levels of total epaulet asymmetry ($P = 0.07$; Table 2-6). However, this difference was not apparent among males that bred in 1994 ($P = 0.55$; Table 2-6), though the trend in that year was in the same direction. Differences in asymmetries exhibited at other characters were, for the most part, inconsistent between 1993 and 1994, and generally did not approach statistical significance (Table 2-6). Additionally, there was no evidence that surviving and non-surviving males differed with respect to composite asymmetry in either 1993 ($t = 0.35$, $df = 29$, $P = 0.73$) or 1994 ($t = 0.06$, $df = 29$, $P = 0.95$). Thus, using a direct measure of individual viability, I found little evidence to suggest that viability and bilateral asymmetry are related in red-winged blackbirds.

Nest defence effort

Analyses presented here are based on 215 nest defence trials conducted at 87 nests during the two years of intensive study. Collectively, these trials involved a total of 26 males in 1993 and 25 males in 1994. These values include only those trials conducted when nestlings were 4-10 days old (see Methods), hence the reduction in the number of males included in the analysis (i.e., nests of some males did not survive to this stage of the nesting cycle). As with male survival,

analyses of nest defence were conducted separately by year because some males were present during both years of study. The nest defence score for a given nest was taken as the mean score for that nest computed across all trials included in the analysis.

In order to arrive at a single estimate of nest defence effort for each male, it was first necessary to evaluate other potential sources of variation in nest defence behaviour. Parental investment theory predicts that both re-nesting potential and offspring number should influence the intensity with which parent birds defend their nests (Montgomerie and Weatherhead 1988). Thus, I developed multiple linear regression models to predict male nest defence intensity based on date of clutch initiation and size of the brood. For this initial analysis, I treated nests as independent observations. In 1993, nest defence intensity increased as the season progressed (partial coeff = 0.05, $F = 7.46$, $df = 1,45$, $P = 0.009$), whereas there was no apparent effect of size of the brood (partial coeff = -0.12, $F = 7.46$, $df = 1,45$, $P = 0.76$). In 1994, neither date nor size of the brood appeared to be an important determinant of nest defence effort (model $R^2 = 0.04$, $F = 0.70$, $df = 2,36$, $P = 0.50$). A potential shortcoming of these analyses is that, because some males were associated with multiple nests, not all observations were independent. To ensure that this did not influence the main results, I repeated each analysis 25 times, each time selecting at random (with replacement) one observation per male. Results of the reanalyses confirmed an effect of date in 1993 (mean $F = 4.39$, $df = 1,23$, $P < 0.05$) but not in 1994 (mean $F = 1.47$, $df = 1,22$, $P > 0.1$), and no effect of brood size in either year (1993, mean $F = 0.43$, $df = 1,23$, $P > 0.25$; 1994,

mean $F = 0.39$, $df = 1,22$, $P > 0.25$).

To control the seasonal effects that were apparent in 1993, I adjusted nest defence scores obtained in that year using residuals from the simple linear regression equation describing the dependence of nest defence intensity on date of clutch initiation (see Sokal and Rohlf 1981:491-496). Thus, for each nest scored in 1993, adjusted nest defence (ND_{adj}) was computed according to the equation

$$ND_{adj} = (ND_{obs} - ND_{exp}) + \overline{ND},$$

where ND_{obs} is the observed nest defence score for a particular nest, ND_{exp} is the corresponding expected value estimated from the regression equation, and $\overline{ND}$ is the mean observed nest defence score for all nests included in the analysis. I then averaged adjusted values for individual nests (where appropriate) to arrive at a single nest defence score for each male. Overall nest defence was computed in a similar manner (but without adjustment, as none was necessary) for males scored in 1994.

Nest defence effort varied widely among individual males in both years of study (range of average scores: 1993, 0.0 - 6.7; 1994, 2.0 - 6.3). However, in neither year was this variation related to any of the male characteristics that I measured. There was no evidence that nest defence effort varied with male age (1993, $r = -0.28$, $n = 26$, $P = 0.16$; 1994, $r = 0.14$, $n = 25$, $P = 0.52$), body size (1993, $r = 0.18$, $n = 26$, $P = 0.38$; 1994, $r = 0.10$, $n = 25$, $P = 0.64$), or asymmetry in any of the characters examined (Table 2-7). Similarly, there was no relationship whatsoever between male nest defence effort and composite

asymmetry score (1993, $r = -0.08$, $n = 24$, $P = 0.72$; 1994, $r = 0.00$, $n = 22$, $P = 0.99$). Thus, using all available nest defence data, I found no evidence to suggest that nest defence effort was predictable on the basis of asymmetry levels exhibited by males.

One limitation of the preceding analysis is that it does not take into account potential effects of paternity on patterns of parental care. To verify that this potential confound did not influence the outcome of the central tests, I repeated the entire procedure as described above using only those nests for which parentage of nestlings had been determined through DNA fingerprinting (1993 only), and restricting analysis to broods that were found to contain no illegitimate young. Of the 19 males associated with nests that were assessed for parentage, 16 were found to have secured full paternity in at least one brood. Analysis based on these 16 males revealed no evidence of a relationship between mean nest defence score (computed as above) and asymmetries exhibited at any of the characters measured (correlation coefficients: $-0.31 - 0.18$; all P values ≥ 0.25). Similarly, there was no suggestion that male nest defence effort was related to composite asymmetry score ($r = 0.04$, $n = 15$, $P = 0.89$). Thus, results of the reanalysis were consistent with the conclusion that male nest defence effort and bilateral asymmetry are not related in red-winged blackbirds.

Table 2-1. Analysis of covariance evaluating effects of character asymmetry (asym, in mm, sqrt-transformed) and age (SY vs. ASY) on the condition (g) of individual male red-winged blackbirds. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements. Condition is taken as the residual from a simple linear regression of body mass on size (PC1 score, see text). Interactions were not significant ($P > 0.1$) and were therefore removed from each model.

Character	Model		Source	Coeff ^a	F	P
	n	R ²				
Tarsus	67	0.22	Asym	1.130	0.62	0.434
			Age	1.377	17.63	<0.001
Wing	67	0.22	Asym	0.684	0.49	0.487
			Age	1.415	17.80	<0.001
Tail	66	0.21	Asym	-0.188	0.10	0.748
			Age	1.363	16.61	<0.001
Epaulet	66	0.20	Asym	-0.323	0.27	0.604
			Age	1.313	15.96	<0.001
Coracoid	66	0.22	Asym	-0.847	0.12	0.736
			Age	1.396	17.62	<0.001
Femur	65	0.21	Asym	-0.948	0.07	0.798
			Age	1.351	16.33	<0.001
Tibiotarsus	67	0.22	Asym	-1.139	0.34	0.560
			Age	1.379	17.56	<0.001
Humerus	67	0.22	Asym	-1.920	0.33	0.567
			Age	1.365	17.28	<0.001
Ulna	67	0.21	Asym	-1.140	0.10	0.751
			Age	1.390	16.98	<0.001

^a Partial coefficient. For age, add if ASY, subtract if SY.

Table 2-2. Prevalence and intensity of various parasitic infections among 34 SY and 33 ASY male red-winged blackbirds.

Sample	Parasite	Prevalence		Intensity (among infected individuals)				
		No. Infected	Percent	Mean	SE	Median	Min	Max
SY males	Ectoparasites							
	Lice	33	97.1	8.6	1.25	6.0	1	32
	Mites	31	91.2	4.7	0.62	3.0	1	14
	Total	34	100.0	12.6	1.54	10.5	2	39
	Haematozoa							
ASY males	<i>Haemoproteus</i>	4	11.8	17.5	6.24	17.0	5	31
	<i>Leucocytozoon</i>	2	5.9	1.5	0.50	1.5	1	2
	<i>Plasmodium</i>	9	26.5	15.6	4.52	12.0	3	40
	Total	15	44.1	14.2	3.32	9.0	1	40
	Ectoparasites							
	Lice	24	72.7	7.0	1.53	3.5	1	31
	Mites	27	81.8	3.6	0.47	3.0	1	10
	Total	32	97.0	8.2	1.34	6.0	1	33
	Haematozoa							
	<i>Haemoproteus</i>	2	6.1	3.5	0.50	3.5	3	4
	<i>Leucocytozoon</i>	3	9.1	5.7	2.33	5.0	2	10
	<i>Plasmodium</i>	9	27.3	12.1	2.54	10.0	1	24
	Total	12	36.4	11.1	2.84	8.0	1	34

Table 2-3. Analysis of covariance evaluating effects of character asymmetry (asym, in mm, sqrt-transformed) and age (SY vs. ASY) on the intensity of ectoparasitic louse infestation (sqrt-transformed) among individual males. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements. Interactions were not significant ($P > 0.1$) and were therefore removed from each model.

Model			Source	Coeff ^a	F	P
Character	n	R ²				
Tarsus	67	0.16	Asym	-1.360	3.63	0.061
			Age	-0.487	8.94	0.004
Wing	67	0.13	Asym	-0.561	1.29	0.261
			Age	-0.515	9.22	0.004
Tail	66	0.10	Asym	0.033	0.01	0.907
			Age	-0.430	6.91	0.011
Epaulet	66	0.12	Asym	-0.198	0.38	0.538
			Age	-0.476	7.88	0.007
Coracoid	66	0.17	Asym	-1.404	1.42	0.239
			Age	-0.546	12.08	0.001
Femur	65	0.18	Asym	-1.206	0.48	0.491
			Age	-0.556	12.37	0.001
Tibiotarsus	67	0.11	Asym	-0.180	0.03	0.857
			Age	-0.472	7.93	0.007
Humerus	67	0.13	Asym	2.100	1.56	0.216
			Age	-0.473	8.19	0.006
Ulna	67	0.13	Asym	2.293	1.63	0.207
			Age	-0.522	9.49	0.003

^a Partial coefficient. For age, add if ASY, subtract if SY.

Figure 2-1. Relationship between intensity of ectoparasitic louse infestation and a composite asymmetry index based on measurements made on four external and five skeletal paired morphological characters (see text). Lines represent simple linear regressions conducted separately by age (SY males, $y = 3.32 - 0.003x$, $r^2 = 0.03$, $n = 33$; ASY males, $y = 3.29 - 0.006x$, $r^2 = 0.10$, $n = 30$). Slopes of the regression lines are not significantly different (analysis of covariance, age*asymmetry interaction: $F = 0.52$, $df = 1,59$, $P = 0.476$), but the elevation for SY males is greater than that for ASY males (age effect, interaction removed: $F = 11.13$, $df = 1,60$, $P = 0.002$). The common slope is significantly less than zero (asymmetry effect, interaction removed: $F = 3.64$, $df = 1,60$, $P = 0.061$).

Table 2-4. Analysis of covariance evaluating effects of character asymmetry (asym, in mm, sqrt-transformed) and age (SY vs. ASY) on the intensity of ectoparasitic mite infestation (sqrt-transformed) among individual males. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements. Interactions were not significant ($P > 0.1$) and were therefore removed from each model.

Model			Source	Coeff ^a	F	P
Character	n	R ²				
Tarsus	67	0.06	Asym	-0.460	0.88	0.353
			Age	-0.201	3.21	0.078
Wing	67	0.08	Asym	-0.494	2.22	0.142
			Age	-0.232	4.18	0.045
Tail	66	0.07	Asym	-0.263	1.79	0.186
			Age	-0.176	2.45	0.123
Epaulet	66	0.04	Asym	-0.138	0.42	0.517
			Age	-0.172	2.35	0.130
Coracoid	66	0.11	Asym	-1.823	4.80	0.032
			Age	-0.211	3.63	0.061
Femur	65	0.05	Asym	0.472	0.13	0.716
			Age	-0.210	3.23	0.077
Tibiotarsus	67	0.05	Asym	-0.309	0.21	0.645
			Age	-0.193	2.93	0.092
Humerus	67	0.05	Asym	-0.463	0.16	0.688
			Age	-0.197	3.05	0.085
Ulna	67	0.05	Asym	0.188	0.02	0.879
			Age	-0.201	3.01	0.088

^a Partial coefficient. For age, add if ASY, subtract if SY.

Figure 2-2. Relationship between intensity of ectoparasitic mite infestation and a composite asymmetry index based on measurements made on four external and five skeletal paired morphological characters (see text). Lines represent simple linear regressions conducted separately by age (SY males, $y = 3.21 - 0.005x$, $r^2 = 0.11$, $n = 33$; ASY males, $y = 2.59 - 0.004x$, $r^2 = 0.08$, $n = 30$). Neither the slopes nor the elevations of the regression lines are significantly different (analysis of covariance, age*asymmetry interaction: $F = 0.11$, $df = 1,59$, $P = 0.743$; age effect, interaction removed: $F = 1.58$, $df = 1,60$, $P = 0.213$). The slope of the coincident regression line is significantly less than zero (asymmetry effect, all other terms removed: $F = 6.81$, $df = 1,61$, $P = 0.011$).

Table 2-5. Levels of character asymmetry (mm) exhibited by males infected and those uninfected with haematozoa. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements.

Character	Status	n	Asymmetry		t ^a	P
			Mean	SE		
Tarsus	Infected	27	0.21	0.044	1.04	0.304
	Uninfected	40	0.25	0.034		
Wing	Infected	27	1.08	0.129	1.23	0.224
	Uninfected	40	0.89	0.106		
Tail	Infected	27	0.66	0.198	0.92	0.363
	Uninfected	39	0.87	0.175		
Epaulet	Infected	27	1.35	0.203	0.14	0.887
	Uninfected	39	1.52	0.245		
Coracoid	Infected	27	0.11	0.017	0.63	0.533
	Uninfected	39	0.10	0.012		
Femur	Infected	27	0.06	0.008	0.08	0.940
	Uninfected	38	0.07	0.010		
Tibiotarsus	Infected	27	0.12	0.021	0.04	0.967
	Uninfected	40	0.12	0.018		
Humerus	Infected	27	0.07	0.012	0.53	0.596
	Uninfected	40	0.06	0.008		
Ulna	Infected	27	0.08	0.011	0.87	0.387
	Uninfected	40	0.07	0.008		

^a Pooled variance t-test (two-tailed) based on sqrt-transformed asymmetry values.

Table 2-6. Levels of character asymmetry (mm) exhibited by males that bred in a given year and either survived or did not survive to the subsequent breeding season. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements.

Year	Character	Status	n	Asymmetry			p
				Mean	SE	ta	
1993	Tarsus	Surviving	18	0.26	0.050	0.38	0.707
		Non-surviving	17	0.28	0.045		
	Wing	Surviving	18	0.82	0.164	1.01	0.318
		Non-surviving	17	0.61	0.136		
	Tail	Surviving	16	1.62	0.403	1.69	0.101
		Non-surviving	16	0.79	0.121		
	Epaulet - red	Surviving	18	1.46	0.265	0.37	0.716
		Non-surviving	16	1.30	0.219		
1994	Epaulet - total	Surviving	18	0.81	0.171	1.85	0.073
		Non-surviving	17	1.44	0.311		
	Tarsus	Surviving	21	0.21	0.040	0.91	0.371
		Non-surviving	14	0.31	0.092		
	Wing	Surviving	21	0.63	0.101	0.02	0.983
		Non-surviving	14	0.72	0.225		

Table 2-6. (continued)

Year	Character	Status	n	Asymmetry			P
				Mean	SE	t ^a	
1994	Tail	Surviving	20	1.26	0.282	0.08	0.934
		Non-surviving	11	1.40	0.501		
	Epaulet - red	Surviving	21	1.25	0.225	0.37	0.712
		Non-surviving	14	1.32	0.295		
	Epaulet - total	Surviving	21	1.05	0.211	0.61	0.547
		Non-surviving	14	1.13	0.195		

^a Pooled variance t-test (two-tailed) based on sqrt-transformed asymmetry values.

Table 2-7. Simple linear regression models describing the relationship between intensity of male nest defence (rated on an objective scale from 1 to 7, see text) and asymmetry levels (mm, sqrt-transformed) exhibited at each of five bilaterally-paired characters. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements.

Year	Character	n	Intercept	Slope	r ²	F	P
1993	Tarsus	26	5.43	-2.221	0.08	1.96	0.174
	Wing	26	3.95	0.515	0.01	0.36	0.552
	Tail	24	3.83	0.424	0.02	0.46	0.506
	Epaulet - red	26	4.47	-0.082	0.00	0.01	0.927
	Epaulet - total	26	4.24	0.138	0.00	0.04	0.838
1994	Tarsus	25	5.13	-0.910	0.01	0.27	0.607
	Wing	25	4.49	0.347	0.01	0.13	0.724
	Tail	22	4.69	-0.091	0.00	0.02	0.895
	Epaulet - red	25	5.28	-0.529	0.03	0.70	0.411
	Epaulet - total	25	4.11	0.657	0.05	1.15	0.294

Discussion

It is now well established that, in many animal taxa, males characterized by low levels of bilateral asymmetry realize a mating advantage (Markow and Ricker 1992; Moller 1992a, 1996; Thornhill 1992a; Harvey and Walsh 1993; Liggett et al. 1993; McLachlan and Cant 1995; Simmons 1995). Moreover, experimental studies have confirmed that, in some instances, this advantage appears to be mediated by female mating preferences (Moller 1993a; Thornhill 1992b; see also Swaddle and Cuthill 1994a,b). While these results have often been interpreted as indicating female preference for males of high overall "quality" (e.g., Moller 1992a, 1993a; Thornhill 1992b; Swaddle and Cuthill 1994a; Simmons 1995), there has been little direct empirical verification of the underlying assumption that symmetry and quality are correlated. In the present study, I found little evidence to indicate that bilateral asymmetries (either singly or in combination) reflected the overall health, viability, or parental quality of individual male red-winged blackbirds. Asymmetries exhibited by males were apparently unrelated to nutritional condition, infection by haematzoa, or survivorship based on annual return to the breeding grounds. Multi-character (i.e., composite) asymmetry was associated with infestation by two types of ectoparasites (i.e., ischnoceran lice and haematophagous mites), but these associations occurred in the direction opposite to that expected under the male quality hypothesis. Finally, there was no indication that asymmetry covaried with male nest defence, the primary form of paternal care in my study population. Thus, in red-winged blackbirds, asymmetry appears to convey little or no information that might be of value to females selecting among potential

mates. This observation in turn suggests limits to the applicability of the male quality hypothesis.

In failing to provide support for the male quality hypothesis, my results differ from those of other studies that have identified associations between individual character asymmetries and various fitness-related traits, including nutritional status (Thornhill and Sauer 1992; Radesater and Halldorsdottir 1993; Swaddle and Witter 1994), parasitic infection (Polak 1993; Moller 1996), and longevity and/or survival (Thornhill 1992a; Packer and Pusey 1993; Moller 1994; Naugler and Leech 1994; Ueno 1994). While results of these studies are consistent with the suggestion that symmetry and quality are correlated, this interpretation is at odds with the observation that character asymmetries themselves tend to vary independently at the individual level (see Chapter 1 and references therein). Given that asymmetry in any one character is likely to be a poor predictor of overall developmental competence (Palmer 1994; Chapter 1), it seems premature to conclude that there exists a general link between developmental stability and individual quality.

Although results of the present study were largely inconsistent with the male quality hypothesis, there was some suggestion that asymmetry does covary with other male features in red-winged blackbirds. Specifically, I documented significant (or marginally significant) inverse associations between multi-trait asymmetry and infestation by each of two broad classes ectoparasites. That these associations occurred independently of one another and similarly among the two recognizable age classes suggests that the relationships were "real", and not spurious artifacts (i.e., Type I errors) arising

as a consequence of the fact that several measures of male health and viability were investigated. Importantly, both associations were generally not apparent when individual character asymmetries were considered in isolation. Moreover, analysis based on subsets of characters revealed that, in both instances, the association between multi-trait asymmetry and ectoparasite burden could not be attributed to asymmetry in any one trait. Rather, these patterns emerged as a result of considering several characters in combination. This observation affirms the importance of using a multiple-character approach when assessing asymmetry variation at the individual level (Palmer 1994; Ryan et al. 1995; Chapter 1).

I can only speculate as to why ectoparasite burdens were inversely associated with multi-trait asymmetry and, by inference, developmental instability. One possibility is that, despite the evidence summarized above, symmetry does in fact reflect individual quality in red-winged blackbirds, and that high quality individuals accrue benefits in certain social contexts at the cost of increased exposure to parasites. This point is perhaps best illustrated by example. During both the breeding and non-breeding seasons, red-winged blackbirds congregate in large numbers at communal roosts. Available evidence suggests that these roosts are not homogeneous assemblages of birds, but rather, that dominant individuals secure central positions that presumably afford greater protection from terrestrial predators (Weatherhead and Hoysak 1984). As central (i.e., preferred) roost sites are likely to be characterized by high roosting densities (and therefore, increased proximity of roosting individuals), the relative safety afforded by such sites might be

realized at the cost of increased exposure to contact-transmitted ectoparasites (see, for instance, Rozsa et al. 1996). Thus, if bilateral symmetry is a morphological correlate of social dominance in this species, symmetrical (i.e., dominant) individuals may well develop high ectoparasite burdens. However, this particular explanation appears unlikely because, while social dominance is apparently age-related in red-winged blackbirds (Searcy 1979d; Weatherhead and Hoysak 1984; Shutler and Weatherhead 1991), and while older individuals do indeed appear to occupy preferred roosting positions (Weatherhead and Hoysak 1984), in the present study there was no indication that older individuals were characterized by higher ectoparasite burdens. In fact, I found just the opposite: SY males supported higher louse loads (and possibly higher mite loads) than older males. Taken together, these observations argue against the possibility that preferred roost sites are associated with increased exposure to ectoparasites. More generally, available evidence is inconsistent with the premise that, in birds, symmetry and social dominance are positively related. In an independent investigation based on captive red-winged blackbirds, I found no evidence to suggest that males characterized by low levels of asymmetry were competitively superior (K.W. Dufour, unpublished data). Similar results have been reported for captive European starlings (*Sturnus vulgaris*; Swaddle and Witter 1994, 1995; Witter and Swaddle 1994), mallards (*Anus platyrhynchos*; Hoysak and Ankney 1996), and American black ducks (*Anus rubripes*; Hoysak and Ankney 1996). Thus, it appears unlikely that social factors can account for the associations between asymmetry and ectoparasitic infection observed in the present study.

In the preceding discussion, I assumed (for sake of argument) that observed variation in ectoparasitism was due, at least in part, to differential exposure to ectoparasites among individual males. If, on the other hand, ectoparasite burdens reflect genetically based resistance, an alternative explanation for the inverse association between asymmetry and parasitism is suggested. Polak and Trivers (1994) proposed that such an association might arise as a consequence of continuous host-parasite coevolution, which is expected to result in persistent selection for novel or rare, resistance-conferring alleles in the host population (Hamilton and Zuk 1982). The rapid incorporation of novel alleles is in turn expected to disrupt genomic coadaptation and reduce stability of development, as has been demonstrated for alleles conferring insecticide resistance in the Australian sheep blowfly (*Lucilia cuprina*; Clarke and McKenzie 1987; McKenzie and Clarke 1988; McKenzie and O'Farrell 1993). Applied to the results of the present study, this hypothesis requires (among other things) that ectoparasite burdens reflect individual resistance to infection, and that this resistance has a genetic basis. While there is some evidence that both of these requirements are met for avian haematophagous mites (e.g., Möller 1990b), the same cannot be said for ischnoceran lice, which are thought not to be susceptible to specific immunity (Clayton 1991a).

Regardless of the ultimate cause, an inverse association between asymmetry and ectoparasitism is, under the most straight-forward interpretation, clearly contrary to the male quality hypothesis. To the extent that females are expected to prefer males of high overall developmental

competence (Møller 1990a, Thornhill 1992b), results of the present study imply that, in red-winged blackbirds, females exhibiting such a preference would obtain mates with disproportionately *high* ectoparasite burdens. In this regard my results differ from those of other studies that have examined relationships between asymmetry and parasitism. For instance, Polak (1993) demonstrated a positive relationship between nematode infection and bristle asymmetry among wild-collected males of *Drosophila nigrospiracula*. However, this relationship was not evident when asymmetry in another character (i.e., wing length) was considered. More recently, Møller (1996) demonstrated directly that domestic flies (*Musca domestica*) exhibiting relatively high levels of wing length asymmetry were disproportionately susceptible to infection by an entomopathogenic fungus. Again, the relationship was apparently character-specific; susceptible and unsuitable individuals did not differ with respect to asymmetry in length of the tibia, the other character that Møller (1996) examined. These results, in conjunction with those of the present investigation, suggest that relationships between asymmetry and parasitism are likely to be complex and unpredictable. Clearly, more data are needed before generalizations regarding associations between developmental stability, bilateral symmetry, and parasitic infection can be made.

My central aim in the present chapter was to determine whether bilateral asymmetry might be a correlate of male quality in red-winged blackbirds, and hence, whether there might be potential for adaptive female choice of mates based on this particular aspect of morphology. While the results presented here are clearly inconsistent with this proposal, it seems premature to conclude that

asymmetry is unlikely to influence male reproductive success in this species. This caution is suggested by two considerations. First, although I included in the analysis a variety of male characteristics, I cannot exclude the possibility that I failed to consider some key variable that might influence female mate choice decisions. Second, it is important to recognize that female choice is not the only mechanism through which asymmetry might influence male reproductive success. For instance, some authors have argued that asymmetry in certain performance-related characters (e.g., those associated with flight) might directly influence the ability of individuals to compete intra-sexually for mating opportunities (Balmford and Thomas 1992; Harvey and Walsh 1993; Palmer 1994; McLachlan and Cant 1995). Thus, only through direct investigation of the reproductive consequences of asymmetry will it be possible to determine whether asymmetry influences male reproductive success in red-winged blackbirds. Such an investigation is provided in the remaining chapter of this thesis.

CHAPTER 3

Reproductive consequences of bilateral asymmetry for individual male red-winged blackbirds

Introduction

It has recently become apparent that subtle developmental inconsistencies can have fitness consequences (i.e., reproductive consequences) for individuals later in life. Specifically, departures from perfect symmetry in bilaterally-paired morphological characters have been shown to influence male mating success in a variety of animal taxa (e.g., Markow and Ricker 1992; Thornhill 1992a; Liggett et al. 1993; Radesater and Halldorsdottir 1993; Simmons 1995; Møller 1994, 1996). The mechanisms responsible for the disproportionate success of symmetrical males are poorly understood, but there is much interest in the possibility that females use symmetry as a criterion for mate selection. For the majority of paired characters, perfect symmetry represents the ideal developmental outcome (Palmer and Strobeck 1986). Thus, departures from symmetry are thought to reflect the inability of individuals to develop normally in the face of contingencies imposed by the environment (Palmer and Strobeck 1986; Parsons 1990, 1992). Individuals apparently vary in their ability to cope with these contingencies, and there is evidence that this variation can have a heritable basis (e.g., Mather 1953; Maynard Smith and Sondhi 1960; Hagen 1973; Thornhill and Sauer 1992; see

also Møller and Thornhill 1996). These observations led Møller (1990a) to suggest that the degree of asymmetry in certain characters (sexual ornaments in particular) might provide females with a reliable indication of male genotypic quality, and that females should therefore preferentially mate with symmetrical males to enhance the genetic quality, and hence the viability, of their offspring. Experimental manipulation of plumage asymmetries in free-living barn swallows (*Hirundo rustica*) and captive zebra finches (*Taeniopygia guttata*) have since confirmed that females of at least some species perceive individual differences in asymmetry and discriminate against asymmetrical males (Møller 1992a, 1993a; Swaddle and Cuthill 1994a).

Møller's (1990a) hypothesis actually describes but one of several ways in which the disproportionate success of symmetrical males might be mediated by female choice. In proposing that females use symmetry as an indicator of male genotypic quality, Møller (1990a) emphasized indirect benefits, accrued to discriminating females through the production of genetically superior offspring. Alternatively, it has been suggested that females might selectively mate with symmetrical (high quality) males because such males are better able to provide material resources (e.g., nuptial food items) and/or parental care (Borgia and Wilkinson 1992; Thornhill 1992b). Finally, it has been proposed that female preferences for symmetrical males might arise as a non-adaptive consequence of perceptual biases towards symmetry in general (Enquist and Arak 1994; Ryan et al. 1995), or as a result of preferences for the "average" phenotype, i.e., as a by-product of selection for mate recognition (Johnstone 1994).

As the discussion above might suggest, most speculation regarding the

influence of asymmetry on male reproductive success has focussed on potential effects of asymmetry on patterns of female mate selection. However, more direct reproductive consequences of asymmetry are also conceivable. For instance, theoretical work on the aerodynamic properties of avian wings and tails has suggested that even moderate departures from perfect symmetry in these structures can have a substantial impact on manoeuvrability and other aspects of flight performance (Balmford and Thomas 1992; Thomas 1993). Flight-cage experiments involving barn swallows and red-billed streamertails (*Trochilus polytmus*) have provided empirical evidence that this is indeed the case, at least for tail feather asymmetries (Møller 1991; Evans et al. 1994). As several authors have noted, such an effect might, either directly or indirectly, influence the ability of males to compete intra-sexually for mating opportunities (Balmford and Thomas 1992; Palmer 1994). This possibility has, in fact, been raised in connection with two recent studies that have identified inverse associations between wing-length asymmetry and male pairing success in insects (Harvey and Walsh 1993; McLachlan and Cant 1995).

Despite the varied ways in which asymmetry might influence male reproductive success, and despite the considerable attention that has been paid to the possibility, existing data on relationships between asymmetry and male success under natural conditions are limited in several important ways. First, although a number of field studies have demonstrated inverse associations between asymmetry and male mating success (Markow and Ricker 1992; Thornhill 1992a; Harvey and Walsh 1993; Liggett et al. 1993; McLachlan and Cant 1995; Simmons 1995; Møller 1994, 1996), in most

instances the underlying mechanisms have not been identified (see Polak 1996: Table 1). This limitation may be attributed in part to the fact that most studies have been cross-sectional in nature, restricted, for instance, to a comparison of mated and unmated males (see Møller 1994 for an important exception). Second, while studies of asymmetry in relation to male success have so far been limited to asymmetry measures made on one or two individual characters, there are theoretical reasons to expect single character asymmetries to be poor predictors of overall developmental competence (Palmer 1994; see also Chapter 1). This observation has led some authors to advocate the use of a multiple-character approach when quantifying asymmetry variation at the individual level (Palmer 1994; Ryan et al. 1995). At present, data on multiple-character asymmetry and male reproductive success are lacking. Finally, while a number of studies have provided support for the prediction that males exhibiting high levels of asymmetry suffer reduced mating success, other studies have not (e.g., Eggert and Sakaluk 1994; Ryan et al. 1995). Thus, additional data are needed to establish the generality of the phenomenon. Here I present the results of a two-year field study aimed at evaluating the reproductive consequences of asymmetry for individual male red-winged blackbirds (*Agelaius phoeniceus*). Specifically, using asymmetry data assembled on a number of paired characters, I test the hypothesis that males characterized by high levels of asymmetry suffer reduced reproductive success. The general approach adopted in this study was to assess variation in each of several distinct components of male success, including those stemming from direct intra-sexual (i.e., male-male) competition, as well as those presumably

under the influence of female mating decisions. I reasoned that such an approach would have potential to provide greater insight into the processes underlying any observed effects of asymmetry on male success.

The red-winged blackbird is a socially polygynous passerine that breeds in a variety of open habitat throughout much of continental North America (Orians 1980). Redwings are particularly well-suited to the study of phenotypic correlates of reproductive fitness, in part because they offer certain practical advantages for such study (Searcy and Yasukawa 1983), and in part because males of this species show pronounced among-individual variation in annual reproductive success (Payne 1979; Gibbs et al. 1990; Westneat 1993; Weatherhead and Boag 1997). This variation arises at a number of levels. First, in order to attract a social mate, males must establish and maintain a breeding territory (Orians 1961). Territories are apparently limited, however, and competition among males for territory ownership is intense (Orians 1961; Beletsky and Orians 1987a, Eckert and Weatherhead 1987c; Shutler and Weatherhead 1991). One outcome of this competition is that, in a given year, an estimated 35-80% of reproductively competent males fail to acquire a territory and become non-territorial "floaters" (Searcy and Yasukawa 1995). Because non-territorial males collectively account for <5% of all fertilizations (Gibbs et al. 1990; Westneat 1993; Weatherhead and Boag 1995; Gray 1996), acquisition of a territory is effectively prerequisite for successful reproduction, and territory acquisition thus constitutes a critical component of overall male success. My first specific objective in the present study, therefore, was to test the prediction that territory owners exhibit low levels of asymmetry relative to

their non-territorial counterparts. To this end, I conducted an experiment in which existing territory owners were removed from their territories and their morphology compared with that of the non-territorial males that could be expected to replace them (Eckert and Weatherhead 1987c; Shutler and Weatherhead 1991).

Additional variation in reproductive success among male red-winged blackbirds arises as a consequence of large-scale differences in territory quality. Specifically, researchers recognize two broad classes of habitat in which males of this species most often establish territories: (1) productive lowland marshes, particularly those dominated by cattail (*Typha* spp.); and (2) relatively marginal upland field habitat (Searcy and Yasukawa 1995). Marshes are generally regarded as the preferred habitat (e.g., Bent 1958; Searcy and Yasukawa 1995), and available evidence is largely consistent with this view. Breeding densities, whether computed as the number of male territories per unit area (Case and Hewitt 1963) or as the density of nests (Robertson 1972), are typically much higher in marsh habitat than in nearby upland areas (see also Searcy and Yasukawa 1995, Table 3.1). Perhaps more importantly, available evidence (though limited) suggests that males breeding in marsh habitat, on average, attract more social mates (Case and Hewitt 1963; Weatherhead et al. 1980; Eckert and Weatherhead 1987a). Nest success may or may not be higher in marsh habitat, depending on the specific locale (Searcy and Yasukawa 1995), but where such differences do occur, the increased success associated with marsh habitat can be substantial (Case and Hewitt 1963; Robertson 1972). On balance, then, the assumption that marshes

constitute preferred breeding habitat for red-winged blackbirds appears to be well-supported by existing data. Accordingly, my second objective was to test the prediction that, among established territory owners, those characterised by low levels of asymmetry would more often be found defending territories in high quality marsh habitat than in adjacent, presumably sub-optimal, upland field habitat.

Among males that succeed in establishing territories in high quality habitat, variation in individual reproductive success can also be substantial. Naturally, much of this variation arises as a consequence of polygyny (Weatherhead and Boag 1997), and indeed, red-winged blackbirds are among the most polygynous of birds (Searcy and Yasukawa 1995). In eastern Ontario (where the present study was conducted), the number of females simultaneously mated to a given male (i.e., harem size) ranges regularly from zero to four (mean = 2.3, $n = 103$ territory-years; Weatherhead and Boag 1997); in western populations, mean and maximum harem sizes are typically much higher (e.g., Orians and Beletsky 1989). This in itself provides ample opportunity for variable male success. However, recent DNA-based studies of parentage in red-winged blackbirds have revealed an additional source of variation. Specifically, it is now well-established that extra-pair mating is a regular component of reproduction in this species, and that some males realize a substantial proportion of their annual reproductive success through extra-pair fertilizations (Gibbs et al. 1990; Westneat 1993; Gray 1996; Weatherhead and Boag 1997). In the context of the present study, this observation has two implications. First, the existence of significant extra-pair mating provides an

additional avenue through which male success might be influenced by female mating decisions. That is, females might discriminate against particular male phenotypes, not during initial settlement, but rather, at the time of copulation (i.e., by choosing among potential within-pair and extra-pair sires; see Westneat et al. 1990). Second, that many males realize a net benefit from extra-pair mating affirms the importance of assessing parentage and including information on paternity when attempting to quantify male success in this species (Gibbs et al. 1990; Weatherhead and Boag 1997). Thus, my third objective in the present study was to combine field methods with DNA-based analysis of parentage to estimate each of the following components of male success: (1) recruitment of social mates (i.e., harem size); (2) average success of females within the harem; (3) within-pair paternity; and (4) success in achieving extra-pair fertilizations. My ultimate aim, of course, was to evaluate each component in relation to the levels of asymmetry exhibited by individual males. Finally, for a particular sub-sample of individuals, I also determined directly the relationship between asymmetry and true annual reproductive success (i.e., accounting for all four components above), confirmed through genetic analysis of parentage.

Methods

Study populations

This study was conducted at selected sites located within 20 km of the Queen's University Biological Station, Chaffey's Locks, Ontario, (44°34'N; 76°20'W). All data presented here were collected during the breeding seasons (April - July) of 1993 and 1994. Data derive from two main study areas, corresponding to the two broad categories of habitat in which red-winged blackbirds regularly breed (i.e., upland field and lowland marsh). In both habitats, males arrive from spring migration and establish territories in late March and early April. Female arrival and settlement follows, usually within a few weeks.

The Upland study area was characterized by isolated or semi-isolated territories distributed along approximately 35 km of paved highway (see Shutler and Weatherhead 1994 for details). Redwing activity on these territories typically centred on a small (<200 m²) patch of cattail adjacent to the highway, but most of the defended area was agricultural land, principally pasture or early successional old field. Isolated territories were separated from all other territories by areas uninhabited by red-winged blackbirds, whereas semi-isolated territories shared a common boundary with that of a single neighbouring male (i.e., semi-isolated territories, by definition, occurred in pairs). The Upland study area also included a number of small roadside marshes in which several males defended contiguous territories, but for reasons outlined below, these marshes were not used in the present study.

The Lowland study area was comprised of four relatively small (2-10 ha)

isolated marshes, each supporting a breeding population of 4-19 resident males. Two of the marshes were spring-fed beaver ponds characterized by dense stands of emergent vegetation, chiefly willow (*Salix* sp.) and sedge (*Cyperus* sp.). At a third beaver pond, males defended territories along the perimeter of a large open water area. Nesting substrate at this site was predominantly cattail. The fourth site (another cattail marsh) was located on the shore of Lake Opinicon. All four marshes had clearly defined perimeters and were surrounded by habitat unsuitable for nesting red-winged blackbirds. The four marshes were within 8 km of each other and occurred at distances of ≥ 8.5 km from the nearest site in the Upland study area.

Male removals

Assessing the potential influence of asymmetry on territory acquisition required comparable samples of territorial and non-territorial males. Accordingly, during the 1994 field season I conducted an experiment in which existing territory owners were removed from their territories and detained until the resulting vacancy had been filled by a (formerly non-territorial) replacement male. Such an approach has been used extensively in previous investigations of this nature (e.g., Beletsky and Orians 1987a; Eckert and Weatherhead 1987c; Shutler and Weatherhead 1991). For this part of the study, I focussed exclusively on the Upland study area and, to the extent possible, restricted removals to males defending isolated territories. This all but eliminated the possibility that experimentally created vacancies would be annexed by neighbouring territory owners. For the few cases in which the focal territory shared a boundary with

that of another male (i.e., semi-isolated territories), I determined during subsequent visits to the site whether the original neighbour had expanded his territory to include the newly created vacancy. If so, the site was excluded from further study.

Resident males were captured using decoy traps (Smith 1976) or mist nets (with model conspecific male and playback) on selected mornings between 6 May and 15 June. I chose not to remove males earlier than 6 May to ensure that initial territory ownership was firmly established at the outset of the experiment. Upon capture, each resident male was fitted with a numbered aluminum leg band, measured for bilateral asymmetry (see below), and weighed to the nearest 0.5 g using a hand-held Pesola spring scale. Captured residents were then transported to the Biological Station, where they were housed in an outdoor aviary and provided with food and water *ad libitum*. Experimentally created vacancies were visited the following morning and each subsequent morning until a replacement male had been captured and processed, or until repeated attempts to capture the replacement male had failed. At this point, the original resident was fitted with a unique colour combination of aluminium leg bands and released. All males involved in the removal study (both resident and replacement) were at least two years old based on plumage (Searcy and Yasukawa 1995), but otherwise their ages were unknown.

Breeding data

Field methods. - Redwing breeding activity was monitored continuously at all four lowland study sites during both the 1993 and 1994 field seasons.

Beginning 1 April, each site was surveyed every 2-3 days and the area defended by each resident male recorded on a small-scale map. Territory boundaries were determined by noting the location of territorial displays and by observing male movements and aggressive interactions. Resident males were captured by mist net, uniquely colour-banded for individual recognition, measured, weighed (as above), and released immediately at the site of capture. In 1993, I also obtained a blood sample (80-120 μ l) from each individual using jugular venipuncture (Hoysak and Weatherhead 1991). Blood samples were stored in 900 μ l of lysis buffer (Seutin et al. 1991) and maintained at 4°C until the end of the field season. In each of the two years, approximately 90% of resident males were ultimately captured and included in the study.

All breeding males were in full adult plumage and were therefore at least two years old. However, because all four breeding populations had previously been monitored (and breeding adults banded) as part of a long term investigation (Weatherhead and Boag 1997), and because male red-winged blackbirds exhibit extremely high breeding site fidelity (Searcy 1979c; Beletsky and Orians 1987b), I had at my disposal complete breeding histories for all males included in this part of the study. Moreover, because most male redwings first establish territories when they are two or three years old (Orians and Beletsky 1989; Shutler and Weatherhead 1994), breeding experience provides a surrogate measure of age (see also Chapter 2). Thus, for this particular sample of males, I measured male age as the amount of breeding experience (in years) accrued by the beginning of the appropriate breeding season.

Following female settlement and nest initiation, I conducted systematic searches of each marsh every 2-3 days to locate new nests and to monitor the progress of nests already found. Most nests (90% of 194, years pooled) were discovered during nest construction or egg-laying; all were found before the eggs had hatched. That no nests were discovered beyond the incubation stage suggests that few nests, if any, went undetected. Nests were initially assigned to resident males on the basis of location. In all but one instance, the identity of the putative male parent was later confirmed (often repeatedly) through direct observation of nest defence behaviour (Chapter 2). Nests were checked every 2-3 days and, in 1993, blood samples (50-70 μ l) were obtained from all nestlings when they were 4-6 days old. In both years, I continued to monitor nests as long as they remained active. Nestlings were assumed to have fledged if (1) fledglings were observed at or near the nest at the appropriate stage of the nesting cycle (i.e., 9-12 days post-hatch); or (2) the nest was found empty after a minimum brood-rearing period of 9 days had elapsed, and there was no indication that the nest had been disturbed by a predator.

During the 1993 field season, I also endeavoured to capture, colour band, and obtain blood samples from all females associated with active nests. Some females were captured opportunistically during the pre-nesting period (i.e., during attempts to capture males), but most were caught in nets set near their nests during incubation or brood rearing. In all, 58 of 72 nesting females (81%) were captured in 1993. For purely logistic reasons, I made no attempt to capture females in 1994.

I defined harem size as the total number of individual females nesting on the territory of a given male during the course of the breeding season (e.g., Weatherhead 1995; cf. Searcy and Yasukawa 1995). For data collected in 1993, harem size could be determined directly because, in that year, most females were individually marked. For data collected in 1994, I used nesting chronologies to estimate harem size indirectly, as the maximum number of simultaneously active nests (e.g., Weatherhead and Boag 1995). Analysis based on the 1993 data set confirmed that my indirect measure was an excellent predictor of true harem size as defined herein (simple linear correlation: $r = 0.91$, $n = 35$, $P < 0.0001$). Average success of females within the harem was taken as the total number of fledglings raised per female on the territory of a given male (Weatherhead 1995).

Parentage analysis. - I determined the true parentage of nestlings sampled in 1993 using standard multi-locus DNA fingerprinting techniques (Jeffreys et al. 1985a,b; Burke and Bruford 1987; see Burke 1989 for an overview). Fingerprinting protocols and gel scoring procedures were virtually identical to those described by Yezerinac et al. (1995), so here I simply review those methods and provide additional detail specific to my own analysis. Due to time and financial constraints associated with the laboratory component of the procedure (Weatherhead and Montgomerie 1991), I restricted the analysis to samples obtained at my two most productive study sites. The resulting subsample was comprised of 143 nestlings from 42 broods, collectively reared on the territories of 26 males. For all but three of the broods, the attending

female had been sampled and was included in the analysis as well.

Nuclear DNA was isolated by first suspending each blood sample in 2.5 ml 1X Applied Biosystems (AB) lysis buffer and 500 μ l AB proteinase-K. Each suspension was subjected to two phenol:chloroform (70:30) extractions, followed by a third extraction using chloroform only. DNA was precipitated by adding 3 M sodium acetate and 100% isopropanol, washed in 70% ethanol, air-dried, and resuspended in 350-750 μ l 1X TNE₂. The quantity and quality of the extracted DNA was determined by electrophoresis of *Eco* R1-digested samples, corresponding undigested samples, and a standard containing a known quantity of DNA (see Bruford et al. 1992). Having determined the concentration of DNA in each suspension, I digested 15 μ g of each DNA sample using the restriction endonuclease *Alu* I (chosen based on preliminary work for Gibbs et al. 1990). Digested DNA was precipitated with sodium acetate and ethanol, air-dried, and resuspended in 30 μ l 1X TNE₂. After readjusting estimates of DNA concentrations using a second quantification gel, I combined 5 μ g of DNA from each individual with a loading buffer containing lambda size markers (2 ng *Bst* EII-digested and 4 ng *Hind* III/*Eco* R1-digested lambda DNA). DNA fragments were then sorted according to size by running the samples on a 30-cm 0.8% agarose gel at 65-75 V for 42-46 hours. Subsequently, gels were depurinated, denatured, and neutralized (see Yezerinac et al. 1995 for details), and the DNA transferred by Southern Blotting to an Immobilon nylon membrane. Each fingerprint gel contained DNA from 11-18 individuals, with samples arranged such that nestlings were always flanked by their putative parents. To achieve this, samples from males associated with >1 brood were

occasionally run twice on the same gel.

DNA profiles (i.e., "fingerprints") were produced by hybridization of the transferred fragments with each of two radioactively labelled mini-satellite probes: Jeffreys 33.15 (Jeffreys et al. 1985a) and *per* (Shin et al. 1985). In brief, membranes were "prehybridized" following Westneat et al. (1988) while the probe DNA was simultaneously labelled with ^{32}P -dCTP using random primer extension (see Bruford et al. 1992). Prehybridized membranes were then exposed to the labelled probe for approximately 24 hours at 65°C. Exposed membranes were washed in 2X SSC, 0.1% SDS, sealed in plastic, and placed on Cronex 4 x-ray film for 1-13 days at -70°C. Once the resulting autoradiographs had been developed, each membrane was stripped and neutralized (see Yezerinac et al. 1995), and the process repeated for the second mini-satellite probe. Finally, each membrane was stripped and neutralized a second time, and probed with lambda DNA to reveal the in-lane size markers.

DNA profiles were compared with the aid of a computerized scoring system developed specifically for the analysis of electrophoretic gels (National Centre for Supercomputing Applications, Champagne, Illinois). The chief advantage of the system, which has been used in other DNA-based studies of parentage (e.g., Hill et al. 1994; Weatherhead et al. 1994; Yezerinac et. al. 1995), is that the molecular weights of the electrophoretically separated fragments are estimated, by reference to a digitized image of the appropriate size-marker autoradiograph. These estimates in turn provide an objective basis for the comparison of fingerprints, including those generated from different fingerprint gels. This last feature is particularly useful for assigning true genetic

parentage once illegitimate young have been identified (e.g., Weatherhead et al. 1994; Yezerinac et al. 1995).

Autoradiographs were digitized using an Apple One flatbed scanner and Ofoto (version 2.0) imaging software for the Macintosh. Images were analysed using NCSA GelReader (version 2.0.5). For purposes of analysis, I determined the molecular weights of all bands detected by GelReader in the 3.5 - 21.2 kb range. This yielded 4-15 bands per individual for Jeffreys 33.15 (mean = 9.3, SE = 0.18, n = 212), and 4-19 bands per individual for the *per* probe (mean = 10.6, SE = 0.22, n = 212). When results from the two probes were combined, the number of bands scored per individual ranged from 9 to 34 (mean = 19.9, SE = 0.34, n = 212). Bands from different individuals were considered "shared" if they were of similar intensity and if their molecular weights were indistinguishable based on 99% confidence limits. Confidence limits were computed as the molecular weight of each band $\pm$ 1.066%, a figure derived empirically from an analysis of DNA samples run repeatedly on the same and on different gels (R. Montgomerie and T. Poldmaa, unpublished data). Because different multi-locus probes typically detect independent sets of genetic markers (e.g., Burke and Bruford 1987; Piper and Parker Rabenold 1992), I combined results from the two probes for analysis.

To assess parentage, I used information on both the frequency of novel bands (i.e., nestling bands not present in the DNA profile of either social parent), as well as the degree of band-sharing between individuals. Band-sharing coefficients (D values) were computed according to

$$D = 2(N_{ab}) / (N_a + N_b),$$

where N_{ab} is the number of bands shared by individuals a and b, and N_a and N_b represent the total number of bands scored for individuals a and b, respectively (Wetton et al. 1987). Because DNA fingerprint fragments are inherited in a Mendelian fashion (e.g., Burke and Bruford 1987; Burke et al. 1989; Gibbs et al. 1990), and because the loci involved are exceptionally variable (Jeffreys et al. 1985a; Burke and Bruford 1987), offspring are expected to share approximately 50% of their bands with each of their true genetic parents (Wetton et al. 1987). In practice, however, bands-sharing coefficients between first order relatives vary (see Westneat 1990 for a discussion of the factors responsible). In other avian studies that have used the same enzyme-probe combinations as those employed here, band-sharing coefficients between offspring and their true parents have typically ranged from 0.40 to 0.70 (e.g., Poldmaa et al. 1995; Yezerinac et al. 1995). Similarly, while Mendelian inheritance implies that all bands in the DNA profile of a given individual should be ascribable to one or the other parent, novel bands do arise as result of mutation (Jeffreys et al. 1985a; Burke and Bruford 1987). Thus, in the present investigation, I adopted a conservative, dual criterion for parentage exclusions, similar to that used in previous studies of parentage in red-winged blackbirds: nestlings were assumed to be the true descendants of their social parents unless (1) the nestling's DNA profile contained >3 novel bands; and (2) the band-sharing coefficient between the nestling and at least one of its social parents (i.e., the excluded parent) was < 0.40 (see Westneat

1993; Weatherhead et al. 1994; Gray 1996). For the few cases in which only the putative male parent was sampled ($n = 9$ nestlings), I determined whether the paternal band-sharing coefficient fell within 99% confidence limits of the corresponding distribution of observations for established parent-offspring dyads. If not, I assumed true maternity and concluded that the nestling was sired by an extra-pair male. Because previous genetic studies have shown intra-specific brood parasitism to be virtually absent in red-winged blackbirds (Gibbs et al. 1990; Westneat 1993; Weatherhead et al. 1994; Gray 1996), my assumptions regarding maternity in these instances were probably correct.

Male morphology

To assess variation in asymmetry, I measured on all individual males both the left and right elements of five bilaterally-paired morphological characters: tarsus length, wing chord, "tail length" (i.e., length of the outer rectrix), and both the length of the red portion and total length of the epaulet, a bilaterally-paired plumage ornament (see Chapter 1, Table 1-1, for complete character descriptions). Tarsus and epaulet measures were made to the nearest 0.1 mm using callipers, whereas wing chord (± 1 mm) and tail length (± 1 mm) were measured with modified rulers. To improve precision of measurement, all characters were measured twice (non-consecutively), and the mean of the replicate measures used in analysis (Bailey and Byrnes 1990; Yezerinac et. al 1992). Measurements made on feather characters showing evidence of breakage or wear were excluded from analysis, resulting in slightly different sample sizes among the various tests.

Asymmetry for each character was initially taken as the signed difference between the size of the left and right elements (i.e., with information on the direction of departure from perfect symmetry retained). This measure was used, for instance, to determine the extent to which the character asymmetries studied conformed to "ideal fluctuating asymmetry" (ideal FA; Palmer and Strobeck 1992). For subsequent analysis, I used the absolute value of the difference between the two sides, after first adjusting individual signed asymmetry values to a mean of zero (see Results). Because the distribution of absolute asymmetry scores for each character was positively skewed (as expected; see Swaddle et al. 1994), all scores were transformed to square roots for analysis. A preliminary analysis had revealed that the square root transformation was, for all five characters, clearly the most useful transformation to normality among those recommended by Sokal and Rohlf (1981; see also Chapter 1).

Elsewhere I have shown that, in red-winged blackbirds, there exists statistically significant concordance among asymmetry measures made on different characters (Chapter 1). While this suggests that the effects of developmental stability are, to some extent, "organism-wide" in this species, correlations among characters are nonetheless typically weak (Chapter 1). Thus, in addition to evaluating asymmetry variation at each individual character, I also computed a composite index that should better reflect overall developmental competence (Palmer 1994). Specifically, for each character, I ranked individuals according to their absolute asymmetry scores and, for each individual, took the sum of these ranks as a measure of asymmetry overall. As

such, composite asymmetry scores were only available for those individuals having non-missing values for all five characters. Composite scores were normally distributed (Shapiro-Wilk $W = 0.98$, $n = 108$, $P = 0.37$) and ranged from 121 to 471, with high values indicating high levels of asymmetry relative to other individuals in the sample.

In addition to asymmetry, I also considered several other male characteristics that might be expected to influence male reproductive success. Two attributes that have previously been identified as important determinants of male success in my study population are male age and overall body size (Weatherhead and Boag 1995). Methods for estimating male age (where possible) have already been described. To determine the most appropriate measure of body size for males included here, I first conducted principal components analysis (PCA) on the correlation matrix of size measures made on each of the three non-ornamental characters described above, i.e., tarsus, wing, and tail (for this and all other analyses reported herein, the size of each character was taken as the mean size of the left and right elements; see Cuthill et al. 1993). Consistent with the results of a similar analysis based on an independent sample of males (Chapter 2), PCA effectively extracted two "size" axes, one describing positive covariation among feather characters (component loadings: 0.11, 0.93, and 0.92 corresponding to tarsus, wing, and tail, respectively), and the other describing variation in "structural size", in this case, tarsus length (loading = 0.99; loadings for wing and tail: 0.00 and -0.12, respectively). Given the failure of PCA in this instance to extract a single multivariate size measure, and because evidence from my study population

indicates that tarsus length covaries with size of the skeleton (Chapter 2), I chose tarsus length as my measure of overall body size for this particular sample of males (see also Rising and Somers 1989; Freeman and Jackson 1990). Finally, because there is some suggestion that energy balance might influence the ability of male red-winged blackbirds to defend territories and/or perform epigamic displays (Searcy 1979b), I also considered nutritional condition as a potential source of variation in male success. Condition for each individual was taken as the residual from a multiple linear regression equation describing the dependence of body mass on both date of capture (days since 31 March) and overall body size (model: $\text{Mass} = 49.9 - 0.09 [\text{Date}] + 0.74 [\text{Tarsus}]$; model $R^2 = 0.19$, $n = 119$, $P < 0.0001$).

Data analysis

All analyses were performed using JMP® (version 3.1) statistical software (SAS Institute Inc. 1994). With the exception of analyses relating to territory acquisition (where paired-sample comparisons were required), my basic analytical approach was to evaluate each component of male success in relation to character or composite asymmetry using generalized linear modelling procedures (SAS Institute Inc. 1985), controlling effects of additional variables (i.e., age, size, and/or individual condition) where appropriate. Thus, where the response variable was continuous (e.g., harem size), I used multiple linear regression, specifying asymmetry and other male characteristics as predictors. For categorical response variables (e.g., marsh vs. upland habitat), I developed binary logistic regression models and evaluated the significance of

-115-

predictors using likelihood ratio tests (SAS Institute Inc. 1994). All models were developed separately by character. Further details are provided with individual results. All means are presented in original units ± 1 SE.

Results

Patterns of asymmetry variation

In order to meet the central aims of the study, it was first necessary to address a number of technical issues related to quantifying asymmetry at the individual level. Palmer and Strobeck (1992) have argued that genetic tendencies toward greater development on one side or the other can compromise the use of asymmetry as a measure of developmental competence, and that tests for directional asymmetry and antisymmetry should be routinely employed. The authors further stressed that choice of an appropriate asymmetry index depends critically on the relationship between asymmetry and character size (see also Palmer 1994). For the characters used here, both of these issues have already been addressed in a separate analysis based on an independent sample of males (Chapter 1). Thus, here I present only the key results of a similar analysis based on the sample of individuals included in the present investigation. This preliminary analysis was based on all 119 territorial males (both resident and replacement) captured over the two years of study.

In brief, all character asymmetries were in qualitative agreement with the criteria for ideal FA: frequency distributions of left-minus-right values were, at best, only slightly non-normal (based on inspection of normal probability plots; SAS Institute Inc. 1994), and all were centred on a mean of approximately zero. Formal testing revealed no evidence of antisymmetry (i.e., platykurtosis) in any of the characters measured (one-tailed t-tests of $H_0: \gamma_2 \geq 0$, all P

values > 0.25; see Sokal and Rohlf 1981). However, three of the characters showed slight but significant ($P < 0.05$) directionality, that is, departures of the mean left-minus-right value from zero (tarsus, mean = 0.09 ± 0.052 , $t = 2.67$, $df = 118$, $P = 0.009$; red epaulet, mean = -0.85 ± 0.150 , $t = 5.68$, $df = 117$, $P < 0.001$; total epaulet, mean = -0.64 ± 0.150 , $t = 4.27$, $df = 118$, $P < 0.001$). A fourth departure was significant at $P < 0.1$ (tail, mean = -0.35 ± 0.200 , $t = 1.77$, $df = 108$, $P = 0.08$). For all characters, mean deviations from perfect symmetry were moderate, ranging from 3.2 to 12.7% of the maximum individual value. Nevertheless, to eliminate the biasing effects of these directional tendencies, I adjusted individual signed asymmetry scores to a mean of zero before converting them to absolute values (Palmer 1994; see Chapter 1 for details). Absolute asymmetry did not covary with size in any character (simple linear regressions based on sqrt-transformed asymmetry values, all P values > 0.30), so correction for size-dependence was not necessary (Palmer 1994).

Because males were captured throughout each breeding season, it was important to determine whether the measurements I made varied according to the date upon which particular individuals were caught. Thus, for males breeding in upland habitat ($n = 67$; sampled in 1994 only), I used simple linear regression to assess the effect of capture date on both size and asymmetry measures made on each individual character. In general, there was little indication that either of these measures varied seasonally in this particular sample of males (Appendix 2). For males breeding in marsh habitat ($n = 52$), I used analysis of covariance (ANCOVA), specifying both date and year of capture as predictors. As with upland males, there was no evidence to suggest

that size or asymmetry measures were influenced by seasonal effects (Appendix 3). The ANCOVA models also indicated a general lack of size or asymmetry differences between males sampled from marsh habitat in 1993 and those captured in 1994 (Appendix 3).

Territory acquisition

Between 6 May and 15 June 1994, I removed and detained a total of 41 resident males that had been defending isolated or semi-isolated territories in upland habitat. Of the resulting 41 vacancies, 33 were subsequently reoccupied, with replacement usually occurring within 48 hours (two of the remaining eight vacancies were annexed by neighbouring resident males, one was reoccupied by a former resident that had been removed from another territory, and five vacancies, all created after 5 June, were never filled). Of the 33 replacement males, 24 were eventually captured and processed. Consistent with previous studies of territory acquisition in red-winged blackbirds (e.g., Yasukawa 1979; Eckert and Weatherhead 1987c; Shutler and Weatherhead 1991), there was no indication that territory owners were larger than their non-territorial counterparts (paired-sample comparison of residents and replacements based on tarsus length: $t = 0.12$, $df = 23$, $P = 0.91$). There was some suggestion that residents were in better condition than replacement males, but the difference was only marginally significant (paired-sample t-test based on residual body mass: $t = 1.48$, $df = 23$, $P = 0.07$). Furthermore, simple logistic regression (with resident vs. replacement as the binary response variable) revealed that condition explained only 5.1% of the "uncertainty" in territorial status (see SAS

Institute Inc. 1994). Given that the influence of condition was apparently weak and only marginally significant, and because statistical control in this instance would have required that I ignore the paired nature of the data, I elected not to control for condition in analyses of territory ownership relative to asymmetry.

Paired-sample comparisons provided little evidence that territory owners were more symmetrical than their non-territorial counterparts (Table 3-1). Although two of the five comparisons (by character) revealed marginally significant ($P \leq 0.1$) asymmetry differences between residents and replacements, in both of these instances, the direction of the difference was opposite to that expected (i.e., for these characters, resident males had higher rather than lower levels of asymmetry than replacement males; Table 3-1). Similarly, among resident-replacement pairs in which both members had non-missing values for all characters, there was no indication that residents were more symmetrical overall (paired-sample t-test based on composite asymmetry scores: $t = 0.61$, $df = 19$, $P = 0.55$). Thus, I found little evidence to suggest that asymmetry and success in competition for a territory are associated in male red-winged blackbirds.

Territory quality (major habitat type)

I predicted that, among males that succeed in establishing a territory, those characterised by low levels of asymmetry would more often be found defending territories in high quality marsh habitat. To test this prediction, I compared the morphology of males that held territories in the Lowland study area (marsh

habitat) with that of the original territory owners involved in the removal experiment (upland habitat). For males from marsh habitat, I included only those individuals that held territories in 1994 ($n = 35$), because only in that year were males sampled from the Upland study area. The upland sample included all 41 residents from the removal study, as well as one additional territory owner that had been captured opportunistically. Males from the two habitats were of similar size ($t = 0.76$, $df = 75$, $P = 0.45$), but those defending territories in marsh habitat were in superior condition, on average ($t = 3.40$, $df = 75$, $P = 0.001$).

To assess habitat-related variation in asymmetry while controlling for differences in individual condition, I developed multiple logistic regression models, specifying habitat as the binary response variable and treating character asymmetry and residual body mass as predictors. In each of the five models (developed separately by character), the effect of asymmetry on the probability of holding a territory in marsh habitat was nonsignificant (Table 3-2). Similarly, analysis based on composite asymmetry scores ($n = 71$ males) revealed no relationship between the probability of holding a territory in marsh habitat and asymmetry overall (binary logistic regression with asymmetry and residual body mass as predictors, asymmetry effect: $G = 1.20$, $df = 1$, $P = 0.27$). Thus, I found no evidence to support the prediction that males characterized by low levels of asymmetry more often establish territories in high quality habitat.

Success among territory owners in high quality habitat

Of 40 males that held territories in the Lowland study area in 1993, 35 (88%) were ultimately captured and included in the study. Eighteen of these individuals returned to defend the same territories in 1994. Of 22 previously unbanded males that also held territories in 1994 (presumed to be first-time breeders), 17 were ultimately captured and processed. Thus, morphological and breeding data were assembled for a total of 52 individual males. Because some males were present during both years of study, all analyses were conducted separately by year. Data from the four focal marshes were combined for analysis because preliminary tests had indicated that there were no between-site differences in measures of morphology or breeding performance in either 1993 or 1994.

Recruitment of mates. - In 1993, harem size varied from zero (for males that failed to recruit any social mates) to five (mean = 2.1 ± 0.22 , $n = 35$). Harem sizes were somewhat smaller in 1994 (mean = 1.4 ± 0.16 , $n = 35$), but still showed appreciable variation among males (range: 0 - 4). Contrary to the results of a long-term study of the same breeding population (Weatherhead and Boag 1995), larger males did not attract more social mates during the two years of the present investigation (1993, $r = -0.06$, $n = 35$, $P = 0.72$; 1994, $r = -0.26$, $n = 35$, $P = 0.13$). However, harem size did increase with increasing male age (i.e., breeding experience), at least among males that bred in 1993 (Fig. 3-1). There was no detectable relationship between harem size and male condition in either 1993 ($r = 0.21$, $n = 35$, $P = 0.22$) or 1994 ($r = 0.13$, $n = 35$,

$P = 0.45$).

To test the prediction that symmetrical males attract more social mates, I examined the relationship between harem size and asymmetry in each character, controlling for male age in each instance using multiple linear regression (MLR). In 1993, partial coefficients describing the relationship between harem size and asymmetry were significant ($P \leq 0.05$) or marginally significant ($P \leq 0.1$) for two of the five characters measured (Table 3-3). In both of these instances, however, the direction of the relationship was opposite to that predicted: for both wing length and red epaulet length, departures from perfect symmetry were *positively* related to success in attracting social mates (Table 3-3). Neither of these relationships was apparent among males that bred in 1994, nor were effects of other character asymmetries evident in that year (Table 3-3). Finally, there was no apparent relationship between harem size and composite asymmetry in either of the two years of study (MLR with age and asymmetry as predictors, asymmetry effect: 1993, partial coeff = 0.00, $F = 0.02$, $df = 1,28$, $P = 0.89$; 1994, partial coeff = 0.00, $F = 0.08$, $df = 1,28$, $P = 0.78$). Thus, I found no evidence to suggest that males characterized by low levels of asymmetry attract disproportionately high numbers of social mates.

Reproductive success of mates. - In polygynous species, male reproductive success is naturally expected to increase with increasing average success of females within the harem (note, however, that this relationship is weakened to some extent by extra-pair mating, see below). To determine whether this

component of male success was related to male morphology (i.e., asymmetry). I first computed the number of fledglings raised per female on the territory of each male (i.e., average female reproductive success). The analysis was thus restricted to those males that had recruited ≥ 1 social mate, and each male was represented once in a given test. Average female success was unrelated to male age (1993, $r = 0.04$, $n = 30$, $P = 0.81$; 1994, $r = -0.02$, $n = 28$, $P = 0.91$) or condition (1993, $r = -0.20$, $n = 30$, $P = 0.30$; 1994, $r = 0.10$, $n = 28$, $P = 0.60$), but was positively related to overall male size (i.e., tarsus length), at least for males that bred in 1993 (Fig. 3-2). To control the effects of male size in analyses of asymmetry variation, I again used an MLR approach (similar to that described above), with average female success as the response variable and male size and asymmetry as predictors. Of the 10 models developed (by character and year), only one was suggestive of a relationship between female success and male character asymmetry (Table 3-4), and in this instance (wing asymmetry in 1994) the relationship was only marginally significant ($P = 0.06$). Similarly, there was no relationship between female success and male composite asymmetry in either 1993 (partial coeff = 0.04, $F = 0.02$, $df = 1,24$, $P = 0.88$) or 1994 (partial coeff = 0.01, $F = 0.00$, $df = 1,21$, $P = 0.95$). Thus, I found little evidence to suggest that females mated to symmetrical males realize higher annual reproductive success.

Within-pair paternity. - To facilitate paternity analysis, I first sought to verify that nestlings were the true descendants of the female attending the nest. Band-sharing coefficients for female-offspring dyads (D_f values) varied more or

less continuously from 0.32 to 0.80 (mean = 0.51 ± 0.007 , $n = 134$; Fig. 3-3).

Of the 134 nestlings assessed for maternity, only three met the dual criterion for parentage exclusion, i.e., $D_f < 0.40$ and >3 novel bands (Fig. 3-3).

Furthermore, two observations suggest that these three individuals, in common with the other nestlings, were the true descendants of their respective social mothers. First, under the assumption that all other nestlings were legitimate (with respect to the attending female), band-sharing coefficients for the three "excluded" nestlings fell within 99% confidence limits of the distribution of observations for established mother-offspring dyads ($L_1 = 0.30$, $L_2 = 0.73$, $n = 131$; D_f for the three nestlings in question: 0.32, 0.37, and 0.38; see also Fig. 3-3). Second, paternity analysis subsequently identified all three nestlings as having been sired by a male other than the social father. This in itself could account for the occurrence of novel bands in the DNA profiles of these nestlings, and indeed, once the true genetic sires had been identified (see below), only one novel band, detected in the profile of only one of the three nestlings, remained unaccounted for. Based on these results, I concluded that all 134 nestlings were the true descendants of the female attending the nest. Thus, consistent with the results of other studies of parentage in red-winged blackbirds (e.g., Gibbs et al. 1990; Westneat 1993; Gray 1996), I found no evidence of intra-specific brood parasitism.

In contrast to the situation for nestlings and their social mothers, the distribution of band-sharing coefficients for male-offspring dyads (D_m values) was distinctly bimodal (range for each of two non-overlapping distributions: 0.05 - 0.24 and 0.31 - 0.71; $n = 29$ and 105, respectively). The separation of

observations into two distinct clusters was particularly evident when band-sharing coefficients were plotted in relation to the number of novel fragments (Fig. 3-3). Of the 134 nestlings for which both types of information were available, 28 met the dual criterion for parentage exclusion (i.e., $D_m < 0.40$ and >3 novel bands). Accordingly, I concluded that these individuals were sired by an extra-pair male. An additional seven nestlings had D_m values of < 0.40 but fewer than four novel fragments (Fig. 3-3); these cases were therefore initially ambiguous. However, six of the seven individuals had DNA profiles with very few novel fragments (0 or 1) and paternal band-sharing coefficients ranging from 0.31 to 0.39 (Fig. 3-3). Because these values were comparable to those of nestlings that were clearly legitimate (i.e., $D_m \geq 0.40$ and ≤ 3 novel bands), I concluded that these six individuals were the true genetic offspring of the attending male. The other questionable nestling had a very low paternal band-sharing coefficient ($D_m = 0.07$), and yet its DNA profile contained only three novel bands. However, this individual also had an exceptionally faint fingerprint (indicating that comparatively little DNA had been prepared for profiling), so it is perhaps not surprising that so few novel bands were detected. Given the low degree of similarity between the nestling's DNA profile and that of its social father, I concluded that this individual was sired by an extra-pair male. Thus, among nestlings for which I had information on both band-sharing and novel fragments, 29 were identified as illegitimate. Paternal band-sharing coefficients for legitimate and illegitimate nestlings averaged $0.53 (\pm 0.008, n = 105)$ and $0.12 (\pm 0.010, n = 29)$, respectively.

For an additional nine nestlings, DNA was available from the putative

male parent only. Of these nestlings, eight had paternal band-sharing coefficients ranging from 0.44 to 0.57, all well within the 99% confidence limits of observations for established father-offspring dyads ($L_1 = 0.31$, $L_2 = 0.74$, $n = 105$). The other nestling had a paternal band-sharing coefficient of 0.18. Because this value fell outside the 99% confidence limits for established father-offspring dyads (but well within the range of observed values for excluded nestlings; see Fig. 3-3), I concluded that this one nestling was the result of an extra-pair fertilization. Thus, in total, 30 of 143 sampled nestlings (21%) were identified as having been sired by an extra-pair male. Expressed another way, 15 of 42 sampled broods (36%) contained at least one extra-pair-sired nestling. While these rates of extra-pair paternity are slightly lower than a long-term average based on the same study population (Weatherhead and Boag 1997), they nevertheless underscore the importance of assessing parentage when attempting to quantify components of male reproductive success in this species.

To assess variation in within-pair paternity, I computed for each male the proportion of sampled nestlings that were found to be legitimate (e.g., Gibbs et al. 1990; Westneat 1993). Although all 26 males resident on the two focal marshes were sampled and included in the parentage analysis, broods of only 19 males survived to an age at which blood samples could be obtained (mean number of nestlings sampled per male = 7.5 ± 0.81). Of these 19 males, nine secured full within-pair paternity, eight obtained partial paternity (proportion of nestlings legitimate: 0.64 - 0.93), and two males suffered complete loss of paternity as a result of extra-pair mating. Complete loss of

paternity, however, was not an artifact of there being few nestlings available for analysis, as the two males in question were assessed for parentage based on samples of 4 and 13 nestlings, from one and four complete broods, respectively.

The observation that almost half of all males suffered no loss of paternity whatsoever (in combination with the limited overall sample size) suggested that the most appropriate analysis for these data would be a comparison of males that secured full within-pair paternity and those that suffered reduced paternity (either partial or complete) as a result of extra-pair mating. These two groups of males were indistinguishable based on age (i.e., breeding experience; $t = 0.28$, $df = 17$, $P = 0.78$), body size (i.e., tarsus length; $t = 0.40$, $df = 17$, $P = 0.69$), or nutritional condition (i.e., residual mass; $t = 0.88$, $df = 17$, $P = 0.39$), indicating that statistical control of these variables was not required. Thus, to determine whether males with high levels of asymmetry were more likely to suffer reduced paternity, I developed simple logistic regression models for each character, in each instance specifying paternity status (i.e., full vs. reduced) as the binary response variable. While there was some suggestion that males characterized by high levels of red epaulet asymmetry were more likely to suffer reduced paternity (Table 3-5), the relationship was only marginally significant ($P = 0.07$). Effects of other character asymmetries were decidedly nonsignificant (Table 3-5), as was the effect of asymmetry overall (simple logistic regression of paternity status on composite asymmetry: $G = 0.95$, $df = 1$, $P = 0.33$). Thus, in general, I found little evidence to suggest that asymmetry and loss of paternity are associated in

male red-winged blackbirds. Clearly, however, sample sizes for this analysis were limited, so conclusions here should be viewed as somewhat tentative.

Extra-pair mating success. - I identified the true genetic sires of excluded nestlings using a two-step parentage assignment procedure. First, with the aid of acetate overlays, I screened the DNA profiles of all males resident on the appropriate marsh to identify individuals that might account for most or all of the novel bands detected in the excluded nestling's fingerprint (note that this was only possible for the 29 excluded nestlings for which I had blood samples from both social parents). Initial screening was done without reference to the location of male territories within the marsh, and typically identified 1-3 candidate fathers. DNA profiles of these males were then compared with that of the nestling in question as for parentage exclusions, using both band-sharing and novel fragments for diagnosis. With one exception, this procedure unambiguously identified a single male as the true genetic sire (i.e., $D_m \geq 0.40$ and ≤ 3 novel bands). The exceptional nestling could not be assigned to any resident male, and was therefore presumably sired by a non-territorial floater (see Weatherhead and Boag 1995). Finally, for the one excluded nestling whose mother was not sampled (i.e., for which I lacked information on novel fragments), I simply omitted the initial screen and computed band-sharing coefficients between the nestling and all males resident on the marsh. One male (later identified as an immediate neighbour of the cuckolded male) had a band-sharing coefficient with the excluded nestling of 0.43, whereas band-sharing coefficients for the other residents ranged from 0.00 to 0.24. Accordingly, I

concluded that the male with $D_m = 0.43$ was the true sire of this particular nestling. In sum, I was able to identify the males responsible for 29 of 30 extra-pair fertilizations. A retrospective analysis revealed that, in common with the results other studies of parentage in red-winged blackbirds (Gibbs et al. 1990, Westneat 1993, Gray 1996), most extra-pair sires (77%) defended adjacent territories. Band-sharing coefficients between assigned nestlings and their true fathers averaged $0.51 (\pm 0.013, n = 29)$ and did not differ from those computed for legitimate father-offspring pairs identified in the earlier exclusion analysis (mean = $0.53 \pm 0.008, n = 113; t = 0.69, df = 140, P = 0.49$).

Resident males varied considerably in the extent to which they achieved extra-pair fertilizations. Although more than half of sampled residents (18 of 26) were apparently unsuccessful in this regard, some males realized substantial gains through extra-pair reproduction (number of extra-pair nestlings sired per successful male = $3.6 \pm 1.66, n = 8$ extra-pair sires). Indeed, one male sired a total of 15 extra-pair nestlings, these distributed among six broods reared on the territories of four different males (notably, this male also secured full paternity in each of two broods reared on his own territory). Despite the variable success of extra-pair sires, however, their low frequency precluded the possibility of relating this variation to male morphology. Thus, for purposes of analysis, I simply classified males according to whether they were known to have sired extra-pair young.

Known extra-pair sires and unsuccessful males were similar with respect to overall body size ($t = 0.31, df = 24, P = 0.75$) and individual condition ($t = 0.14, df = 24, P = 0.89$). However, consistent with previous work based on the

same study population (Weatherhead and Boag 1995), older, experienced males were more likely to achieve extra-pair fertilizations. Known extra-pair sires had, on average, 2.1 years of prior breeding experience, whereas the corresponding value for unsuccessful males was only 0.39 (i.e., most were first-time breeders). This difference was highly significant ($t = 2.91$, $df = 24$, $P = 0.008$). Accordingly, to control the effects of male age in analyses of asymmetry variation, I again used logistic regression, specifying extra-pair mating status as the binary response variable and male age and character asymmetry as predictors. Of the five models developed (by character) only one revealed a significant ($P \leq 0.10$) asymmetry effect (Table 3-6), and in this instance the direction of the relationship was opposite to that predicted. That is, males characterized by low levels of red epaulet asymmetry were less rather than more likely to achieve extra-pair mating success (Table 3-6). Similarly, the probability of achieving extra-pair mating success was unrelated to asymmetry overall (logistic regression with male age and composite asymmetry as predictors, asymmetry effect: $G = 0.00$, $df = 1$, $P = 0.99$). Also noteworthy is the observation that the exceptionally successful extra-pair sire (identified above) was not particularly symmetrical. For instance, the composite asymmetry score for this individual was 218.5, a value only 0.76 standard deviations from the sample mean (281.3 ± 17.25 , $n = 23$). Overall, then, I found little evidence to suggest that symmetrical males are more likely to realize extra-pair mating success.

Annual reproductive success. - The consistent lack of association between

asymmetry and specific components of male success suggested that asymmetry was unlikely to be an important determinant of male success overall. Nevertheless, to address the issue directly, I computed for each male included in the parentage analysis ($n = 26$) true annual reproductive success (annual RS), defined here as the total number of fledglings sired by a given male, either on his own territory or through extra-pair mating. Perhaps not surprisingly, there was a highly significant positive relationship between age (i.e., breeding experience) and the number of fledglings sired (Fig. 3-4), reflecting the influence of age on both recruitment of social mates and extra-pair fertilization success (see above). On the other hand, there was no detectable relationship between annual RS and male size ($r = 0.18$, $n = 26$, $P = 0.39$) or individual condition ($r = 0.06$, $n = 26$, $P = 0.75$).

To assess variation in annual RS relative to asymmetry, I developed separate regression models for each character (with annual RS as the response variable), in each instance controlling the effects of male age by including breeding experience as a predictor. As expected, there was little indication that annual RS was related to asymmetry in any of the characters examined (Table 3-7). Similarly, there was no relationship whatsoever between annual RS and asymmetry overall (MLR with age and composite asymmetry as predictors, asymmetry effect: partial coeff = 0.00, $F = 0.05$, $df = 1, 20$, $P = 0.83$). Thus, using a comprehensive measure of reproductive success, I found no evidence to suggest that asymmetry influences reproductive performance among individual male red-winged blackbirds.

Table 3-1. Comparison of resident (territorial) and replacement (floater) male red-winged blackbirds with respect to asymmetry levels (mm) exhibited at each of five bilaterally-paired morphological characters. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements.

Character	Status	n	Asymmetry		t ^a	P
			Mean	SE		
Tarsus	Resident	24	0.23	0.037	0.57	0.575
	Replacement	24	0.30	0.074		
Wing	Resident	24	0.83	0.133	1.79	0.087
	Replacement	24	0.53	0.104		
Tail	Resident	20	1.17	0.276	0.49	0.631
	Replacement	20	1.32	0.270		
Epaulet: red	Resident	24	1.31	0.182	0.11	0.913
	Replacement	24	1.45	0.241		
Epaulet: total	Resident	24	1.41	0.223	1.86	0.076
	Replacement	24	0.97	0.170		

^a Paired sample t-test (two-tailed) with resident males and their respective replacements as paired observations, based on sqrt-transformed asymmetry values.

Table 3-2. Levels of character asymmetry (mm) exhibited by males defending territories in high quality marsh habitat and those defending territories in relatively marginal upland field habitat. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements.

Character	Habitat	n	Asymmetry		G ^a	P
			Mean	SE		
Tarsus	Marsh	35	0.25	0.044	0.33	0.565
	Upland	42	0.20	0.025		
Wing	Marsh	35	0.66	0.107	0.51	0.475
	Upland	42	0.78	0.088		
Tail	Marsh	31	1.31	0.250	0.00	0.376
	Upland	40	1.18	0.271		
Epaulet: red	Marsh	35	1.28	0.177	0.22	0.637
	Upland	42	1.23	0.133		
Epaulet: total	Marsh	35	1.08	0.147	2.48	0.115
	Upland	42	1.50	0.174		

^a Likelihood-ratio test of the effect of character asymmetry (sqrt-transformed) on the probability of securing a territory in marsh habitat (binary logistic regression with asymmetry and individual condition [i.e., residual mass, see text] as predictors; SAS Institute Inc. 1994).

Figure 3-1. Relationship between the number of social mates (harem size, see text) and prior breeding experience among individual males in each of two years of study. Lines represent simple linear regressions conducted separately by year (1993, $y = 1.8 + 0.28x$, $r^2 = 0.12$; 1994, $y = 1.2 + 0.13x$, $r^2 = 0.05$). Numbers indicate coincident observations. The relationship is significant for 1993 ($F = 4.53$, $df = 1,33$, $P = 0.041$) but not for 1994 ($F = 1.83$, $df = 1,33$, $P = 0.186$).

Table 3-3. Multiple linear regression models evaluating effects of character asymmetry (asym, in mm, sqrt-transformed) and age (breeding experience, in yrs) on the number of social mates recruited by individual males. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements.

Model							
Year	Character	n	R ²	Source	Coeff ^a	F	P
1993	Tarsus	35	0.17	Asym	-1.397	1.78	0.191
				Age	0.303	5.29	0.028
	Wing	35	0.20	Asym	0.973	3.17	0.084
				Age	0.264	4.20	0.049
	Tail	32	0.14	Asym	-0.197	0.18	0.678
				Age	0.298	4.41	0.044
	Epaulet: red	34	0.26	Asym	1.108	6.53	0.016
				Age	0.257	4.53	0.041
	Epaulet: total	35	0.13	Asym	-0.273	0.38	0.543
				Age	0.281	4.42	0.044
1994	Tarsus	35	0.10	Asym	0.907	1.54	0.224
				Age	0.121	1.52	0.227
	Wing	35	0.05	Asym	-0.076	0.03	0.872
				Age	0.137	1.77	0.193
	Tail	31	0.10	Asym	-0.364	1.25	0.273
				Age	0.148	2.03	0.165
	Epaulet: red	35	0.06	Asym	0.183	0.26	0.613
				Age	0.126	1.58	0.218
	Epaulet: total	35	0.12	Asym	-0.582	2.57	0.118
				Age	0.121	1.56	0.220

^a Partial regression coefficient.

Figure 3-2. Number of fledglings raised per female on the territory of a given male (i.e., average female reproductive success) in relation to overall male size (measured as length of the tarsus, see text). Lines represent simple linear regressions conducted separately by year (1993, $y = -26.6 + 1.01x$, $r^2 = 0.15$; 1994, $y = -14.6 + 0.60x$, $r^2 = 0.06$). The relationship is significant for 1993 ($F = 4.96$, $df = 1,28$, $P = 0.034$) but not for 1994 ($F = 1.79$, $df = 1,26$, $P = 0.192$).

Table 3-4. Multiple linear regression models evaluating effects of character asymmetry (asym, in mm, sqrt-transformed) and male size (measured as length of the tarsus, in mm) on the number of fledglings raised per female on the territory of a given male. Asymmetry for each character is taken as the absolute value of the difference between the size of the left and right elements.

Model							
Year	Character	n	R ²	Source	Coeff ^a	F	P
1993	Tarsus	30	0.16	Asym	-0.465	0.15	0.701
				Size	0.961	4.11	0.053
	Wing	30	0.15	Asym	-0.223	0.12	0.733
				Size	1.050	4.85	0.036
	Tail	27	0.15	Asym	-0.289	0.33	0.571
				Size	1.075	4.18	0.052
	Epaulet: red	30	0.15	Asym	-0.187	0.10	0.759
				Size	1.021	4.88	0.036
	Epaulet: total	30	0.18	Asym	0.431	0.83	0.371
				Size	0.916	3.89	0.059
1994	Tarsus	28	0.06	Asym	-0.168	0.01	0.916
				Size	0.596	1.66	0.210
	Wing	28	0.19	Asym	-1.389	3.96	0.058
				Size	0.630	2.19	0.152
	Tail	24	0.11	Asym	-0.380	0.42	0.524
				Size	0.757	2.48	0.130
	Epaulet: red	28	0.07	Asym	0.095	0.03	0.875
				Size	0.603	1.73	0.200
	Epaulet: total	28	0.06	Asym	0.053	0.01	0.931
				Size	0.592	1.56	0.223

^a Partial regression coefficient.

Figure 3-3. Proportion of multi-locus DNA fingerprint bands shared by nestlings and their putative parents (band-sharing coefficients, see text for details), shown in relation to the number of novel bands detected in nestling fingerprints. Data derive from 134 nestlings for which both putative parents were sampled. Dashed lines indicate initial criteria used to identify illegitimate young (i.e., >3 novel bands and a band-sharing coefficient of <0.40).

Table 3-5. Levels of character asymmetry (mm) exhibited by males that secured full within-pair paternity and those that suffered reduced paternity as a result of extra-pair mating. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements.

Character	Paternity	n	Asymmetry		G ^a	P
			Mean	SE		
Tarsus	Full	9	0.28	0.068	0.54	0.461
	Reduced	10	0.20	0.042		
Wing	Full	9	0.65	0.152	0.06	0.813
	Reduced	10	0.78	0.217		
Tail	Full	9	0.77	0.164	0.73	0.392
	Reduced	9	1.38	0.579		
Epaulet: red	Full	9	1.23	0.188	3.23	0.072
	Reduced	10	2.00	0.349		
Epaulet: total	Full	9	1.43	0.545	0.09	0.769
	Reduced	10	1.36	0.238		

^a Likelihood-ratio test of the effect of character asymmetry (sqrt-transformed) on the probability of securing full paternity (binary logistic regression; SAS Institute Inc. 1994).

Table 3-6. Levels of character asymmetry (mm) exhibited by males that were known to have sired extra-pair young and those that were apparently unsuccessful in this regard. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements.

Character	Status of male	n	Asymmetry		G ^a	P
			Mean	SE		
Tarsus	Extra-pair sire	8	0.24	0.060	0.11	0.742
	Unsuccessful	18	0.23	0.044		
Wing	Extra-pair sire	8	0.69	0.208	0.19	0.659
	Unsuccessful	18	0.65	0.125		
Tail	Extra-pair sire	8	1.42	0.648	0.28	0.599
	Unsuccessful	16	0.99	0.152		
Epaulet: red	Extra-pair sire	8	1.95	0.431	3.34	0.068
	Unsuccessful	17	1.27	0.234		
Epaulet: total	Extra-pair sire	8	0.77	0.211	2.12	0.145
	Unsuccessful	18	1.42	0.301		

^a Likelihood-ratio test of the effect of character asymmetry (sqrt-transformed) on the probability of siring ≥ 1 extra-pair nestling (binary logistic regression with asymmetry and male age [i.e., breeding experience] as predictors; SAS Institute Inc. 1994).

Figure 3-4. Relationship between annual reproductive success (annual RS, computed as the total number of fledglings sired, both on and off the territory) and prior breeding experience among individual males. The slope of the simple linear regression line (shown, $y = 2.4 + 1.75x$, $r^2 = 0.35$) is significantly greater than zero ($F = 13.04$, $df = 1,24$, $P = 0.001$). Numbers indicate coincident observations.

Table 3-7. Multiple linear regression models evaluating effects of character asymmetry (asym, in mm, sqrt-transformed) and age (breeding experience, in yrs) on the annual reproductive success of individual males. Asymmetry for each character is computed as the absolute value of the difference between the size of the left and right elements. Reproductive success is taken as the total number of fledglings sired, both on and off the territory.

Model			Source	Coeff ^a	F	P
Character	n	R ²				
Tarsus	26	0.36	Asym	-2.488	0.37	0.549
			Age	1.766	12.85	0.002
Wing	26	0.36	Asym	-0.961	0.17	0.683
			Age	1.786	12.74	0.002
Tail	24	0.37	Asym	1.270	0.47	0.502
			Age	1.789	12.11	0.002
Epaulet: red	25	0.36	Asym	1.180	0.46	0.503
			Age	1.710	11.62	0.003
Epaulet: total	26	0.39	Asym	-1.873	1.42	0.246
			Age	1.700	12.35	0.002

^a Partial regression coefficient.

Discussion

Recent interest in bilateral symmetry as a potential source of variation in individual reproductive performance has been substantial (for discussions, see Møller and Pomiankowski 1993; Brooks and Pomiankowski 1994; Polak and Trivers 1994; Watson and Thornhill 1994; Markow 1995). This interest has stemmed in large part from the novel suggestion that symmetry might act as a reliable indicator of individual phenotypic or genotypic quality, and that females might therefore use symmetry as a criterion for mate selection (Møller 1990a; Thornhill 1992b). This possibility is of particular interest to behavioural ecologists because of its obvious connection to quality indicator models of sexual selection (see Andersson 1994 for a review), and experimental studies have indeed confirmed that females of at least some species perceive individual differences in asymmetry and discriminate against asymmetrical males (Møller 1992a, 1993a; Swaddle and Cuthill 1994a,b). Additionally, both theory and evidence suggests that asymmetry in certain characters might also have a direct impact on the ability of males to compete for mating opportunities, via effects on mechanical efficiency, for example (e.g., Balmford and Thomas 1992; McLachlan and Cant 1995). Despite these and other developments, however, there have been few comprehensive empirical investigations of the reproductive consequences of asymmetry for individual males under natural conditions. My aim in the present study was to provide as complete an analysis as was logistically possible for the system under study, by evaluating each of several components of male reproductive success in relation to asymmetry measures made on a variety of characters. To broaden the scope of analysis, I included

characters that have an obvious signalling function (i.e., epaulet measures), those that might be expected to influence aerodynamic performance (i.e., wing and tail), and a composite asymmetry measure that should better reflect overall developmental competence. Significantly, perhaps the most salient result to emerge from the analysis relates not to any one component of male success or individual character, but rather becomes evident upon inspection of the results overall. That is, results of the present investigation were notably consistent in their failure to support the prediction that males characterized by low levels of asymmetry realize a reproductive advantage. To summarize, results of a male removal experiment provided little evidence to suggest that asymmetry influences territory acquisition among male red-winged blackbirds; established territory owners and non-territorial replacement males were effectively indistinguishable in this regard. Similarly, I found no evidence to suggest that, among territory owners, those characterized by low levels of asymmetry were more likely to establish territories in high quality habitat. Finally, intensive monitoring of breeding activity in high quality habitat revealed that variable male reproductive success due to differences in harem size, average success of females within the harem, within-pair paternity, and extra-pair fertilization success was generally unrelated to asymmetry levels exhibited by resident males. Thus, contrary to prediction, bilateral symmetry (and, by inference, developmental stability) appears not to be an important determinant of reproductive success among individual male red-winged blackbirds.

One obvious limitation of the present study is that, for certain reproductive components, the number of males included in the analysis was

limited, and hence, some tests had low statistical power. This was particularly true of analyses related to within-pair paternity and extra-pair mating success, where logistic considerations required that I include data from only a subsample of available males. However, given that the effects of individual character asymmetries on these components of success rarely even approached statistical significance, and because there was no suggestion whatsoever that within-pair paternity or extra-pair mating success might be associated with multi-character asymmetry (arguably the most informative measure of asymmetry used here; see Palmer 1994), it appears unlikely that additional data from my study population would alter my conclusions regarding the importance of asymmetry in this regard. Moreover, because asymmetry was not predictive of other components of success among territorial males, any subtle (i.e., undetected) effects of asymmetry on within-pair or extra-pair mating success apparently would have had little substantive impact on male success overall. Still, the paucity of data on asymmetry and extra-pair mating in general suggests scope for further investigation. Given the growing realization that extra-pair mating is an important component of reproduction in many avian species (for reviews, see Westneat et al. 1990; Birkhead and Møller 1992), and because there is now convincing evidence that females of at least some species exercise control over extra-pair copulations (e.g., Smith 1988; Kempenaers et al. 1992; Sheldon 1994; Gray 1996), additional studies of extra-pair mating success in relation to this aspect of male morphology may be worthwhile.

Another potential concern in analyses of asymmetry variation,

particularly those that yield negative results, is the level of measurement error associated with asymmetry scores. While precision of measurement is a relevant consideration in any morphometric study (Lougheed et al. 1991; Yezerinac et al. 1992), high measurement error can be particularly problematic for studies of asymmetry, because departures from perfect symmetry are typically subtle, and individual differences are therefore easily obscured (Palmer 1994; Merila and Bjorklund 1995). Indeed, in the present investigation, the maximum individual departure from perfect symmetry (expressed as percentage of character size) varied from as low as 2.1% (range among all five characters: 2.1 - 12.3%; see also Chapter 1, Table 1-4). For several reasons, however, it appears unlikely that the effects of measurement error can account for the lack of association between asymmetry and components of male reproductive success reported here. First, in an analysis of within- and among-individual variability based on an independent sample of males (Chapter 1), asymmetry measures made on the same characters as those used here showed levels of measurement error ranging from 0.9 to 18.0% (Chapter 1, Table 1-2). These values are comparable to those of other studies that have detected inverse associations between asymmetry and male reproductive success (e.g., Møller 1994, 1996). Second, it is important to recognize that the use of mean values computed across replicate measures increases precision of measurement and effectively reduces the amount of measurement error introduced in the analysis (Bailey and Byrnes 1990, Yezerinac et al. 1992). Because all individuals included in the present study were measured twice (and the mean value used in analysis), initially moderate levels of measurement error

were reduced even further in all tests related to the central objectives. Thus, imprecision of measurement is unlikely to have been an important source of error in the present investigation.

Given that the lack of association between asymmetry and male reproductive success in red-winged blackbirds appears genuine, it is of interest to consider the extent to which this result conforms to those of similar studies involving other avian species. The best data available derive from a series of studies conducted on natural populations of barn swallows (Møller 1992a, 1993a, 1994). In the most extensive of these, Møller (1994) demonstrated that males characterized by relatively low levels of wing and outer tail feather asymmetry were more likely to obtain a mate, a result which the author attributed to female mating preferences for symmetrical males (see also Møller 1992a, 1993a). While I can only speculate as to why Møller's (1994) results differ from those reported here, one possibility is that, contrary to Møller's interpretation, the advantages accrued to symmetrical male barn swallows are realized not through female preferences, but rather arise as a result of the mechanical consequences of asymmetry for aerodynamic performance (Balmford and Thomas 1992). If so, asymmetry might be expected to have a substantial impact on the reproductive performance of aerial insectivores such as barn swallows, whereas for species that rely less heavily on aerial agility (e.g., red-winged blackbirds) the consequences of asymmetry should be less severe (Balmford et al. 1993). However, this interpretation, at least insofar as it applies to tail feather asymmetries, is difficult to reconcile with the recent demonstration that even the appearance of an asymmetrical tail (created via

experimental colour manipulation) can influence the reproductive performance of male barn swallows (Møller 1993a). For barn swallows, then, available evidence supports the interpretation that the mating advantage realized by symmetrical males is mediated by female choice and occurs independently of any mechanical effects of asymmetry on aerial agility (see also Swaddle and Cuthill 1994a,b). Aerodynamic considerations, therefore, are unlikely to account for the differences between Møller's (1994) results and those reported here.

If Møller's (1994) results indeed reflect a genuine preference on the part of female barn swallows for symmetrical males, why might such preferences not also exist among female red-winged blackbirds? Conceivably, there might be inter-specific differences in the extent to which asymmetry conveys useful information regarding the quality of potential mates. Noteworthy in this regard are the findings reported earlier, that character asymmetries exhibited by male red-winged blackbirds appear, for the most part, to be unrelated to measures of overall health, viability, or parental effort (Chapter 2). Because these results are inconsistent with the premise that asymmetry indicates individual phenotypic or genotypic quality, it is perhaps not surprising that female red-winged blackbirds do not appear to use symmetry as a criterion for mate selection. At the same time, however, the nature of the benefits accrued to discriminating female barn swallows have not yet been identified, nor is it clear why symmetry should be indicative of male quality in some species and not in others (see, for instance, Leung and Forbes 1996). Both of these issues will require closer scrutiny before predictions regarding the reproductive consequences of asymmetry are likely to be accurate.

To my knowledge, only two other avian studies have examined the reproductive consequences of asymmetry for individual males under natural conditions. In common with the results of the present investigation, Yezerinac (1995) found that male yellow warblers (*Dendroica petechia*) characterized by low levels of tarsal or wing asymmetry were no more likely than other males to secure full within-pair paternity, achieve extra-pair mating success, or realize higher reproductive success overall. Similarly, Lanctot (1996) reported that in the lek-breeding buff-breasted sandpiper (*Tryngites subruficollis*), male mating success (inferred from behavioural observations and/or genetic analysis of parentage) was apparently unrelated to asymmetry measures made on a variety of traits. These recent studies, in combination with the results of the present investigation, suggest that the influence of asymmetry on male success may be considerably less ubiquitous than initially suggested (e.g., Møller and Pomiankowski 1993; Watson and Thornhill 1994), at least among natural populations of birds.

The prediction that symmetry should be associated with male reproductive success has received broader support from studies of invertebrates. In particular, inverse relationships between asymmetry and male pairing success have been reported in a variety of insect taxa (Markow and Ricker 1992; Thornhill 1992a,b; Harvey and Walsh 1993; Liggett et al. 1993; Radesater and Halldorsdottir 1993; McLachlan and Cant 1995; Simmons 1995; Møller 1996; although see Ueno 1994). Although these results are consistent with Møller's (1990a) male quality/female choice hypothesis, several authors have noted that there are difficulties with this interpretation (Eggert and

Sakaluk 1994; Palmer 1994; Ryan et al. 1995). Specifically, while virtually all of the studies cited above were based on asymmetry measures made on one or two individual characters, it is becoming increasingly apparent that single character asymmetries are likely to be poor predictors of overall developmental competence. This suggestion stems from the recognition that asymmetry measures made on different characters are, at best, only weakly correlated at the individual level (see Chapter 1 and references therein). Thus, unless the authors cited above fortuitously measured particularly revealing characters, it is unclear how the male quality/female choice hypothesis might account for these results. An alternative possibility, and that clearly favoured by some authors (e.g., McLachlan and Cant 1995), is that asymmetry has a direct mechanical impact on the functioning of certain traits, leading to a reduction in male competitive ability. Suggestively, most of the studies cited above were based on asymmetry measures made on wings or other functional appendages. However, explanations based on mechanical considerations clearly cannot account for all of the observed associations. For instance, through a series of mate choice experiments, Thornhill (1992b) demonstrated directly that female Japanese scorpionflies (*Panorpa japonica*) actively discriminate against males characterized by high levels of forewing asymmetry. Again, whether discriminating females in this system actually receive either material or genetic benefits remains to be determined.

In conclusion, results of the present investigation generally failed to support the prediction that male red-winged blackbirds characterized by high levels of bilateral symmetry realize a reproductive advantage. While this finding

does not does negate the fact that such associations do indeed appear to exist in other sexual systems, it does add to the growing suggestion (e.g., Eggert and Sakaluk 1994; Ueno 1994; Ryan et al. 1995) that asymmetry-related reproductive consequences may be considerably less ubiquitous than initially supposed. Future studies should seek to identify the specific mechanisms underlying established associations between asymmetry and male mating success (e.g., Polak 1993). Until such information becomes available, it will be difficult to determine why developmental stability and bilateral symmetry appear to have individual-level fitness consequences in some species and not in others.

Summary and Conclusions

Chapter 1

My aim in the first chapter was to explore naturally occurring patterns of asymmetry variation in several external and skeletal paired morphological characters, and in particular, to evaluate the extent to which asymmetries exhibited at different characters are correlated. Analysis based on repeated measurements revealed detectable departures from perfect symmetry (i.e., significant among-individual variability) in all characters examined, and the distribution of individual asymmetry scores for each character generally conformed to the pattern expected if departures from symmetry result from random developmental accidents (i.e., left-minus-right values normally distributed and centred on a mean of zero). Absolute asymmetry scores did not differ between the two recognizable age classes of males, nor was there evidence of a relationship between size and asymmetry in any of the characters measured. Overall concordance of asymmetry among characters was weak but statistically significant, providing evidence of an "organism-wide" asymmetry property in red-winged blackbirds. Nevertheless, composite (i.e., multi-trait) asymmetry was poorly predicted by asymmetry measures made on individual traits. Male epaulets, a bilaterally-paired plumage ornament, exhibited high levels of asymmetry relative to non-ornamental traits, but there was little indication that epaulet asymmetry was more predictive of asymmetry overall, contrary to the suggestion that secondary sexual characters should be particularly revealing of overall developmental competence. Collectively, these

results suggest a clear need for caution when interpreting single character asymmetries as indices of developmental competence and/or individual quality. This observation in turn has implications for the interpretation of previous work on asymmetry and male mating success, much of which has been based on measurements made on a rather limited number of traits.

Chapter 2

A principal goal of this study was to determine the extent to which symmetry conveys information that might be useful to females engaged in mate selection. Thus, I investigated relationships between asymmetry levels exhibited by males and measures of overall health, viability and parental effort. There was little evidence that character asymmetries, either singly or in combination, covaried with nutritional condition (body mass corrected for structural size). Similarly, I found no differences in asymmetry levels exhibited by males infected and those uninfected with avian haematzoa. Composite asymmetry was significantly and independently related to the intensity of infestation by ectoparasitic mites and ischnoceran lice. Further, these relationships were generally not apparent when individual characters were considered in isolation, lending additional support to the position that it may be advisable to use multiple characters when assessing correlates of asymmetry at the individual level. However, in the present instance, relationships between composite asymmetry and ectoparasite burdens were relatively weak and occurred in the direction opposite to that predicted by current theory. Finally, there was little indication that character asymmetries reflected either the survival prospects or parental quality of

individual males. Overall, these results are inconsistent with the proposal that symmetry provides a reliable indication of male phenotypic or genotypic quality. In red-winged blackbirds, benefits that would accrue to females that might discriminate against asymmetrical males appear to be minimal, suggesting that selection for female choice based on this aspect of morphology is probably weak or non-existent.

Chapter 3

A central aim of the present study was to evaluate directly the reproductive consequences of asymmetry for individual males under natural conditions. To provide a more comprehensive analysis than has been typical of studies of this nature, I evaluated each of several distinct components of male reproductive success in relation to asymmetry measures made on a variety of characters. Results of a male removal experiment generally failed to support the prediction that symmetry confers an advantage in (or is at least associated with) success in competition for access to breeding territories. Similarly, I found no evidence to suggest that males characterized by relatively low levels of asymmetry were more likely to acquire territories in high quality (i.e., marsh) habitat. Finally, among males resident in high quality habitat, symmetry was generally unrelated to recruitment of social mates (i.e., harem size), the productivity of those mates (i.e., average female success), within-pair paternity, or extra-pair mating success. Thus, symmetry appears not to be an important determinant of reproductive success among individual male red-winged blackbirds, at least under the conditions that prevailed during the

present study.

To conclude, results of the present investigation affirm the importance of using multiple characters when attempting to estimate developmental competence at the individual level. They also indicate, however, that subtle developmental asymmetries may play less of a role in determining patterns of female mate selection and/or male reproductive success than the recent surge of interest in this area might suggest. At the least, my results suggest limits to the general significance of symmetry as a quality indicator and as a fitness correlate at the individual level. Future studies should seek to clarify the mechanisms responsible for previously established associations between asymmetry and male reproductive fitness.

Literature Cited

- Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton.
- Atkinson, C.T., and van Ripper III, C. 1991. Pathogenicity and epizootiology of avian haematozoa: *Plasmodium*, *Leucocytozoon*, and *Haemoproteus*. In Bird-parasite interactions: ecology, evolution and behaviour. Edited by J.E. Loye and M. Zuk. Oxford University Press, Oxford. pp. 19-48.
- Bader, R.S. 1965. Fluctuating asymmetry in the dentition of the house mouse. *Growth* **29**: 291-300.
- Bailey, R.C., and Byrnes, J. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. *Syst. Zool.* **39**: 124-130.
- Bailey, R.O. 1979. Methods of estimating total lipid content in the redhead duck (*Aythya americana*) and an evaluation of condition indices. *Can. J. Zool.* **57**: 1830-1833.
- Balmford, A., Jones, I.L., and Thomas, A.L.R. 1993. On avian asymmetry: evidence of natural selection for symmetrical tails and wings in birds. *Proc. R. Soc. Lond. (Series B)* **252**: 245-251.
- Balmford, A., and Thomas, A.L.R. 1992. Swallowing ornamental asymmetry. *Nature* **359**: 487.
- Beletsky, L.D., and Orians, G.H. 1987a. Territoriality among male red-winged blackbirds II. Removal experiments and site dominance. *Behav. Ecol. Sociobiol.* **20**: 339-349.
- Beletsky, L.D., and Orians, G.H. 1987b. Territoriality among male red-winged

- blackbirds I. Site fidelity and movement patterns. *Behav. Ecol. Sociobiol.* **20**: 21-34.
- Beletsky, L.D., and Orians, G.H. 1989. Territoriality among male red-winged blackbirds III. Testing hypotheses of territorial dominance. *Behav. Ecol. Sociobiol.* **24**: 333-339.
- Bennett, G.F. 1970. Simple techniques for making avian blood smears. *Can. J. Zool.* **48**: 585-586.
- Bent, A.C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.
- Birkhead, T.R., and Møller, A.P. 1992. *Sperm competition in birds: evolutionary causes and consequences*. Academic Press, London.
- Blem, C.R. 1990. Avian energy storage. *In Current Ornithology. Vol. 7. Edited by D.M. Power*. Plenum Press, New York. pp. 59-113.
- Booth, D.T., Clayton, D.H., and Block, B.A. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proc. R. Soc. Lond. (Series B)* **253**: 125-129.
- Borgia, G., and Wilkinson, G. 1992. Swallowing ornamental asymmetry. *Nature* **359**: 487-488.
- Brookes, M., and Pomiankowski, A. 1994. Symmetry is in the eye of the beholder. *Trends Ecol. Evol.* **9**: 201-202.
- Brown, C.R., Brown, M.B., and Rannala, B. 1995. Ectoparasites reduce long-term survival of their avian host. *Proc. R. Soc. Lond. (Series B)*. **262**: 313-319.
- Bruford, M.W., Hanotte, O., Brookfield, J.F.Y., and Burke, T. 1992. Single-locus and multilocus DNA fingerprinting. *In Molecular genetic analysis of*

- populations: a practical approach. *Edited by* A.R. Hoelzel. Oxford University Press, Oxford. pp. 225-269.
- Burke, T. 1989. DNA fingerprinting and other methods for the study of mating success. *Trends Ecol. Evol.* 4: 139-144.
- Burke, T., and Bruford, M.W. 1987. DNA fingerprinting in birds. *Nature* 327: 149-152.
- Burke, T., Davies, N.D., Bruford, M.W., and Hatchwell, B.J. 1989. Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* 338: 249-251.
- Case, N.A., and Hewitt, O.H. 1963. Nesting and productivity of the red-winged blackbird in relation to habitat. *Living Bird* 2: 7-20.
- Clarke, G.M., and McKenzie, J.A. 1987. Developmental stability of insecticide resistant phenotypes in blowfly: a result of canalizing natural selection. *Nature* 325: 345-346.
- Clayton, D.H. 1991a. The influence of parasites on host sexual selection. *Parasitology Today* 7: 329-334.
- Clayton, D.H. 1991b. Coevolution of avian grooming and ectoparasite avoidance. *In* Bird-parasite interactions: ecology, evolution and behaviour. *Edited by* J.E. Loye and M. Zuk. Oxford University Press, Oxford. pp. 258-289.
- Clayton, D.H., and Tompkins, D.M. 1994. Ectoparasite virulence is linked to mode of transmission. *Proc. R. Soc. Lond. (Series B)* 256: 211-217.
- Clutton-Brock, T.H. 1988. Reproductive success. *In* Reproductive success: studies of individual variation in contrasting breeding systems. *Edited by*

- T.H. Clutton-Brock. University of Chicago Press, Chicago. pp. 472-485.
- Cuthill, I.C., Swaddle, J.P., and Witter, M.S. 1993. Fluctuating asymmetry. *Nature* **361**: 217-218.
- Darwin, C. 1871. The descent of man and selection in relation to sex. John Murray, London.
- DeVaney, J.A., Quisenberry, J.H., Doran, B.H., and Bradley, J.W. 1980. Dispersal of the northern fowl mite, *Ornithonyssus sylviarum* (Canestrini and Fanzago), and the chicken body louse, *Menacanthus stramineus* (Nitzsch), among thirty strains of egg-type hens in a caged laying house. *Poultry Sci.* **59**: 1745-1749.
- Dixon, A., Ross, D., O'Malley, S.L.C., and Burke, T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* **371**: 698-699.
- Eckert, C.G., and Weatherhead, P.J. 1987a. Ideal dominance distributions: a test using red-winged blackbirds (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.* **20**: 43-52.
- Eckert, C.G., and Weatherhead, P.J. 1987b. Competition for territories in red-winged blackbirds: is resource-holding potential realized? *Behav. Ecol. Sociobiol.* **20**: 369-375.
- Eckert, C.G., and Weatherhead, P.J. 1987c. Owners, floaters and competitive asymmetries among territorial red-winged blackbirds. *Anim. Behav.* **35**: 1317-1323.
- Eckert, C.G., and Weatherhead, P.J. 1987d. Male characteristics, parental quality and the study of mate choice in the red-winged blackbird (*Agelaius*

- phoeniceus*). Behav. Ecol. Sociobiol. **20**: 35-42.
- Eggert, A., and Sakaluk, S.K. 1994. Fluctuating asymmetry and variation in the size of courtship food gifts in decorated crickets. Am. Nat. **144**: 708-716.
- Enquist, M., and Arak, A. 1994. Symmetry, beauty and evolution. Nature **372**: 169-172.
- Evans, M.R. 1993. Fluctuating asymmetry and long tails: the mechanical effects of asymmetry may act to enforce honest advertisement. Proc. R. Soc. Lond. (Series B) **253**: 205-209.
- Evans, M.R., and Hatchwell, B.J. 1993. New slants on ornament asymmetry. Proc. R. Soc. London. (Series B) **251**: 171-177.
- Evans, M.R., Martins, T.L.F., and Haley, M.P. 1994. The asymmetrical cost of tail elongation in red-billed streamertails. Proc. R. Soc. London. (Series B) **256**: 97-103.
- Evans, M.R., Martins, T.L.F., and Haley, M.P. 1995. Inter- and intra-sexual patterns of fluctuating asymmetry in the red-billed streamertail: should symmetry always increase with ornament size? Behav. Ecol. Sociobiol. **37**: 15-23.
- Fowler, J.A., and Cohen, S. 1983. A method for the quantitative collection of ectoparasites from birds. Ringing Migration **4**: 185-189.
- Fox, S.F. 1975. Natural selection on morphological phenotypes of the lizard *Uta stansburiana*. Evolution **29**: 95-107.
- Freeman, S., and Jackson, W.M. 1990. Univariate metrics are not adequate to measure avian body size. Auk **107**: 69-74.

- Gibbs, H.L., Weatherhead, P.J., Boag, P.T., White, B.N., Tabak, L.M., and Hoysak, D.J. 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. *Science* **250**: 1394-1397.
- Grafen, A. 1988. On the uses of data on lifetime reproductive success. *In* Reproductive success: studies of individual variation in contrasting breeding systems. *Edited by* T.H. Clutton-Brock. University of Chicago Press, Chicago. pp. 454-471.
- Graham, J.H., Freeman, D.C., and Emlen, J.M. 1993. Antisymmetry, directional asymmetry, and chaotic morphogenesis. *Genetica* **89**: 121-137.
- Gray, E.M. 1996. Female control of offspring paternity in a western population of red-winged blackbirds (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.* **38**: 267-278.
- Hagen, D.W. 1973. Inheritance of numbers of lateral plates and gill rakers in *Gasterosteus aculeatus*. *Heredity* **30**: 303-312.
- Hamilton, W.D., and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* **218**: 384-387.
- Hartl, G.B., Suchentrunk, F., Willing, R., and Petznek, R. 1995. Allozyme heterozygosity and fluctuating asymmetry in the brown hare (*Lepus europaeus*): a test of the developmental homeostasis hypothesis. *Phil. Trans. R. Soc. Lond. (Series B)* **350**: 313-323.
- Harvey, I.F. and Walsh, K.J. 1993. Fluctuating asymmetry and lifetime mating success are correlated in males of the damselfly *Coenagrion puella* (Odonata: Coenagrionidae). *Ecol. Entomol.* **18**: 198-202.
- Hill, G.E., Montgomerie, R., Roeder, C., and Boag, P.T. 1994. Sexual selection and

- cuckoldry in a monogamous songbird: implications for sexual selection theory. *Behav. Ecol. Sociobiol.* **35**: 193-199.
- Hoysak, D.J., and Ankney, C.D. 1996. Correlates of behavioural dominance in mallards and American black ducks. *Anim. Behav.* **51**: 409-419.
- Hoysak, D.J., and Weatherhead, P.J. 1991. Sampling blood from birds: a technique and assessment of its effect. *Condor* **93**: 746-752.
- Hurd, P.L., Weatherhead, P.J., and McRae, S.B. 1991. Parental consumption of nestling feces: good food or sound economics. *Behav. Ecol.* **2**: 69-76.
- Jeffreys, A.J., Wilson, V., and Thein, S.L. 1985a. Hypervariable 'minisatellite' regions in human DNA. *Nature* **314**: 67-73.
- Jeffreys, A.J., Wilson, V., and Thein, S.L. 1985b. Individual specific 'fingerprints' of human DNA. *Nature* **316**: 76-79.
- Jennions, M.D., and Oakes, E.J. 1994. Symmetry and sexual selection. *Trends Ecol. Evol.* **9**: 440.
- Johnson, D.H., Krapu, G.L., Reinecke, K.J., and Jorde, D.G. 1985. An evaluation of condition indices for birds. *J. Wildl. Manage.* **49**: 569-575.
- Johnstone, R.A. 1994. Female preference for symmetrical males as a by-product of selection for mate recognition. *Nature* **372**: 172-175.
- Kempenaers, B., Verheyen, G.R., Van der Broeck, M., Burke, T., Van Broeckhoven, C., and Dhondt, A.A. 1992. Extra-pair paternity results from female preference for high quality males in the blue tit. *Nature* **357**: 494-496.
- Knight, R.L., and Temple, S.A. 1988. Nest defence behaviour in the red-winged blackbird. *Condor* **90**: 193-200.

- Lake, P.E. 1981. Male genital organs. *In* Form and function in birds. Vol. 2.
Edited by A.S. King and J. McLelland. Academic Press, London. pp. 1-61.
- Lancot, R.B. 1996. Variable mating behaviour and reproductive success in the lek-breeding buff-breasted sandpiper, *Tryngites subruficollis*. Ph.D. thesis, Carleton University, Ottawa.
- Leamy, L. 1984. Morphometric studies of inbred and hybrid house mice V. Directional and fluctuating asymmetry. *Am. Nat.* **123**: 579-593.
- Leamy, L. 1993. Morphological integration of fluctuating asymmetry in the mouse mandible. *Genetica* **89**: 139-153.
- Leary, R.F., and Allendorf, F.W. 1989. Fluctuating asymmetry as an indicator of stress: implications for conservation biology. *Trends Ecol. Evol.* **4**: 214-217.
- Leary, R.F., Allendorf, F.W., and Knudsen, K.L. 1983. Developmental stability and enzyme heterozygosity in rainbow trout. *Nature* **301**: 71-72.
- Lessells, C.M., and Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**: 116-121.
- Leung, B., and Forbes, M.R. 1996. Fluctuating asymmetry in relation to stress and fitness: effects of trait type as revealed by meta-analysis. *Ecoscience*. In Press.
- Liggett, A.C., Harvey, I.F., and Manning, J.T. 1993. Fluctuating asymmetry in *Scatophaga stercoraria* L.: successful males are more symmetrical. *Anim. Behav.* **45**: 1041-1043.
- Lougheed, S.C., Arnold, T.W., and Bailey, R.C. 1991. Measurement error of external and skeletal variables in birds and its effect on principal

- components. *Auk* **108**: 432-436.
- Manning, J.T., and Hartley, M.A. 1991. Symmetry and ornamentation are correlated in the peacock's train. *Anim. Behav.* **42**: 1020-1021.
- Manning, J.T., and Ockenden, L. 1994. Fluctuating asymmetry in racehorses. *Nature* **370**: 185-186.
- Markow, T.A. 1995. Evolutionary ecology and developmental stability. *Ann. Rev. Entomol.* **40**: 105-120.
- Markow, T.A., and Ricker, J.P. 1992. Male size, developmental stability, and mating success in natural populations of three *Drosophila* species. *Heredity* **69**: 122-127.
- Marshall, A.G. 1981. The ecology of ectoparasitic insects. Academic Press, London.
- Martin, J.E.H. 1977. The insects and arachnids of Canada, part I: collecting preparing and preserving insects, mites, and spiders. Biosystematics Research Institute Publ. 1643, Ottawa.
- Mather, K. 1953. Genetical control of stability in development. *Heredity* **7**: 297-336.
- Maynard Smith, J., and Sondhi, K.C. 1960. The genetics of a pattern. *Genetics* **45**: 1039-1050.
- McKenzie, J.A., and Clarke, G.M. 1988. Diazinon resistance, fluctuating asymmetry and fitness in the Australian sheep blowfly, *Lucilia cuprina*. *Genetics* **120**: 213-220.
- McKenzie, J.A., and O'Farrell, K. 1993. Modification of developmental stability and fitness: malathion resistance in the Australian sheep blowfly, *Lucilia*

- cuprina*. *Genetica* **89**: 67-76.
- McLachlan, A., and Cant, M. 1995. Small males are more symmetrical: mating success in the midge *Chironomus plumosus* L. (Diptera: Chironomidae). *Anim. Behav.* **50**: 841-846.
- Merila, J., and Bjorklund, M. 1995. Fluctuating asymmetry and measurement error. *Syst. Biol.* **44**: 97-101.
- Mitton, J.B. 1993. Enzyme heterozygosity, metabolism, and developmental stability. *Genetica* **89**: 47-65.
- Mitton, J.B., and Grant, M.C. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Ann. Rev. Ecol. Syst.* **15**: 479-499.
- Møller, A.P. 1990a. Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. Behav.* **40**: 1185-1187.
- Møller, A.P. 1990b. Effects of a haematophagous mite on the barn swallow (*Hirundo rustica*): a test of the Hamilton and Zuk hypothesis. *Evolution* **44**: 771-784.
- Møller, A.P. 1991. Sexual ornament size and the cost of fluctuating asymmetry. *Proc. R. Soc. Lond. (Series B)* **243**: 59-62.
- Møller, A.P. 1992a. Female swallow preference for symmetrical male sexual ornaments. *Nature* **357**: 238-240.
- Møller, A.P. 1992b. Patterns of fluctuating asymmetry in weapons: evidence for reliable signalling of quality in beetle horns and bird spurs. *Proc. R. Soc. Lond. (Series B)* **248**: 199-206.
- Møller, A.P. 1993a. Female preference for apparently symmetrical male sexual

- ornaments in the barn swallow *Hirundo rustica*. Behav. Ecol. Sociobiol. **32**: 371-376.
- Møller, A.P. 1993b. Developmental stability, sexual selection, and speciation. J. Evol. Biol. **6**: 493-509.
- Møller, A.P. 1994. Sexual selection in the barn swallow (*Hirundo rustica*) IV. Patterns of fluctuating asymmetry and selection against asymmetry. Evolution **48**: 658-670.
- Møller, A.P. 1996. Sexual selection, viability, selection, and developmental stability in the domestic fly *Musca domestica*. Evolution **50**: 746-752.
- Møller, A.P., Allander, K., and Dufva, R. 1990. Fitness effects of parasites on passerine birds: a review. In Population biology of passerine birds. Edited by J. Blondel, A. Gosler, J.D. Lebreton, and R. McCleery. Springer-Verlag, Berlin. pp. 269-280.
- Møller, A.P., and Hoglund, J. 1991. Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. Proc. R. Soc. Lond. (Series B) **245**: 1-5.
- Møller, A.P., and Pomiankowski, A. 1993. Fluctuating asymmetry and sexual selection. Genetica **89**: 267-279.
- Møller, A.P., and Thornhill, R. 1996. A meta-analysis of the heritability of developmental stability. J. Evol. Biol. In Press.
- Montgomerie, R.D., and P.J. Weatherhead. 1988. Risks and rewards of nest defence by parent birds. Quart. Rev. Biol. **63**: 167-187.
- Naugler, C.T., and Leech, S.M. 1994. Fluctuating asymmetry and survival ability in the forest tent caterpillar moth *Malacosoma disstria*: implications for

- pest management. *Entomol. Exp. Appl.* **70**: 295-298.
- Orians, G.H. 1961. The ecology of blackbird (*Agelaius*) social systems. *Ecol. Monogr.* **31**: 285-312.
- Orians, G.H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton University Press, Princeton.
- Orians, G.H., and Beletsky, L.D. 1989. Red-winged blackbird. *In* Lifetime reproduction in birds. *Edited by* I. Newton. Academic Press, London. pp. 183-197.
- Orians, G.H., and Christman, G.M. 1968. A comparative study of the behaviour of red-winged, tricoloured, and yellow-headed blackbirds. *Univ. Calif. Publ. Zool.* **84**: 1-81.
- Packer, C., and Pusey, A.E. 1993. Should a lion change its spots? *Nature* **362**: 595.
- Palmer, A.R. 1994. Fluctuating asymmetry analyses: a primer. *In* Developmental stability: it's origins and evolutionary implications. *Edited by* T.A. Markow. Kluwer Academic Publishers, Dordrech. pp. 335-364.
- Palmer, A.R. 1996. Waltzing with asymmetry. *Bioscience* **46**: 518-532.
- Palmer, A.R., and Strobeck, C. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Ann. Rev. Ecol. Syst.* **17**: 391-421.
- Palmer, A.R., and Strobeck, C. 1992. Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests. *Acta Zool. Fenn.* **191**: 57-72.
- Parsons, P.A. 1990. Fluctuating asymmetry: an epigenetic measure of stress. *Biol. Rev.* **65**: 131-145.

- Parsons, P.A. 1992. Fluctuating asymmetry: a biological monitor of environmental and genomic stress. *Heredity* **68**: 361-364.
- Payne, R.B. 1979. Sexual selection and intersexual differences in variance of breeding success. *Am. Nat.* **114**: 447-452.
- Piper, W.H., and Parker Rabenold, P. 1992. Use of fragment-sharing estimates from DNA fingerprinting to determine relatedness in a tropical wren. *Molecular Ecol.* **1**: 69-79.
- Polak, M. 1993. Parasites increase fluctuating asymmetry of male *Drosophila nigrospiracula*: implications for sexual selection. *Genetica* **89**: 255-265.
- Polak, M. 1996. Parasites, fluctuating asymmetry, and sexual selection. *In* Parasites: effects on host hormones and behaviour. *Edited by* N.E. Beckage. Chapman and Hall, New York.
- Polak, M., and Trivers, R. 1994. The science of symmetry in biology. *Trends Ecol. Evol.* **9**: 122-124.
- Poldmaa, T., Montgomerie, R., and Boag, P.T. 1995. Mating system of the cooperatively breeding noisy miner *Manorina melanocephala*, as revealed by DNA profiling. *Behav. Ecol. Sociobiol.* **37**: 137-143.
- Radesater, T., and Halldorsdottir, H. 1993. Fluctuating asymmetry and forceps size in earwigs, *Forficula auricularia*. *Anim. Behav.* **45**: 626-628.
- Rayment, R.A., Blackith, R.E., and Campbell, N.A. 1984. Multivariate morphometrics (Second edition). Academic Press, London.
- Reed, A.F. 1990. Parasites and the evolution of host sexual behaviour. *In* Parasitism and host behaviour. *Edited by* C.J. Bernard and J.M. Behnke. Taylor and Francis, London. pp. 117-157.

- Rice, W.R. 1989. Analysing tables of statistical tests. *Evolution* **43**: 223-225.
- Ringelman, J.K., and Szymczak, M.R. 1985. A physiological condition index for wintering mallards. *J. Wildl. Manage.* **49**: 564-568.
- Rising, J.D., and Somers, K.M. 1989. The measurement of overall body size in birds. *Auk*. **106**: 666-674.
- Robertson, R.J. 1972. Optimal niche space of the red-winged blackbird (*Agelaius phoeniceus*) I. Nesting success in marsh and upland habitat. *Can. J. Zool.* **50**: 247-263.
- Robins, J.D., and Schnell, G.D. 1971. Skeletal analysis of the *Ammodramus-Ammospiza* grassland sparrow complex: a numerical taxonomic study. *Auk* **88**: 567-590.
- Rozsa, L., Rekasi, J. and Reiczigel, J. 1996. Relationship of host coloniality to population ecology of avian lice (Insecta: Phthiraptera). *J. Anim. Ecol.* **65**: 242-248.
- Ryan, M.J., Warkentin, K.M., McClelland, B.E., and Wilczynski, W. 1995. Fluctuating asymmetries and advertisement call variation in the cricket frog, *Acris crepitans*. *Behav. Ecol.* **6**: 124-131.
- SAS Institute Inc. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary.
- SAS Institute Inc. 1994. JMP statistics and graphics guide. SAS Institute Inc., Cary.
- Searcy, W.A. 1979a. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). *Am. Nat.* **114**: 77-100.

- Searcy, W.A. 1979b. Sexual selection and body size in male red-winged blackbirds. *Evolution* **33**: 649-661.
- Searcy, W.A. 1979c. Male characteristics and pairing success in red-winged blackbirds. *Auk* **96**: 353-363.
- Searcy, W.A. 1979d. Morphological correlates of dominance in captive male red-winged blackbirds. *Condor* **81**: 417-420.
- Searcy, W.A., and Yasukawa, K. 1981. Sexual size dimorphism and survival of male and female blackbirds (Icteridae). *Auk* **98**: 457-465.
- Searcy, W.A., and Yasukawa, K. 1983. Sexual selection and red-winged blackbirds. *Am. Sci.* **71**: 166-174.
- Searcy, W.A., and Yasukawa, K. 1995. Polygyny and sexual selection in red-winged blackbirds. Princeton University Press, Princeton.
- Seutin, G., White, B.N., and Boag, P.T. 1991. Preservation of avian blood and tissue samples for DNA analysis. *Can. J. Zool.* **69**: 82-90.
- Sheldon, B.C. 1994. Sperm competition in the chaffinch: the role of the female. *Anim. Behav.* **47**: 163-173.
- Shin, H.S., Bargiello, T.A., Clark, B.T., Jackson, F.R., and Young, M.W. 1985. An unusual coding sequence from a *Drosophila* clock gene is conserved in vertebrates. *Nature* **317**: 445-448.
- Shutler, D., and Weatherhead, P.J. 1991. Owner and floater red-winged blackbirds: determinants of status. *Behav. Ecol. Sociobiol.* **28**: 234-241.
- Shutler, D., and Weatherhead, P.J. 1992. Surplus territory contenders in male red-winged blackbirds: where are the desperados? *Behav. Ecol. Sociobiol.* **31**: 97-106.

- Shutler, D., and Weatherhead, P.J. 1994. Movement patterns and territory acquisition by male red-winged blackbirds. *Can. J. Zool.* **72**: 712-720.
- Simmons, L.W. 1995. Correlates of male quality in the field cricket, *Gryllus campestris* L.: age, size, and symmetry determine pairing success in field populations. *Behav. Ecol.* **6**: 376-381.
- Smith, D.G. 1976. An experimental analysis of the function of red-winged blackbird song. *Behaviour* **56**: 136-156.
- Smith, S.M. 1988. Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour* **107**: 15-23.
- Sokal, R.R., and Rohlf, F.J. 1981. *Biometry: the principles and practice of statistics in biological research* (Second edition). W.H. Freeman and Company, New York.
- Soule, M.E. 1967. Phenetics of natural populations II. Asymmetry and evolution in a lizard. *Am. Nat.* **101**: 141-160.
- Soule, M.E., and Baker, B. 1968. Phenetics of natural populations IV. The population asymmetry parameter in the butterfly *Coenonympha tullia*. *Heredity* **23**: 611-614.
- Soule, M.E., and Cuzin-Roudy, J. 1982. Allometric variation 2. Developmental instability of extreme phenotypes. *Am. Nat.* **120**: 765-786.
- Swaddle, J.P., and Cuthill, I.C. 1994a. Female zebra finches prefer males with symmetric chest plumage. *Proc. R. Soc. Lond. (Series B)* **258**: 267-271.
- Swaddle, J.P., and Cuthill, I.C. 1994b. Preference for symmetric males by female zebra finches. *Nature* **367**: 165-166.
- Swaddle, J.P., and Witter, M.S. 1994. Food, feathers, and fluctuating

- asymmetries. Proc. R. Soc. Lond. (Series B) **255**: 147-152.
- Swaddle, J.P., and Witter, M.S. 1995. Chest plumage, dominance and fluctuating asymmetry in female starlings. Proc. R. Soc. Lond. (Series B) **260**: 219-223.
- Swaddle, J.P., Witter, M.S., and Cuthill, I.C. 1994. The analysis of fluctuating asymmetry. Anim. Behav. **48**: 986-989.
- Teather, K.L. 1992. An experimental study of competition for food between male and female nestlings of the red-winged blackbird. Behav. Ecol. Sociobiol. **31**: 81-87.
- Thomas, A.L.R. 1993. The aerodynamic costs of asymmetry in the wings and tails of birds: asymmetric birds can't fly round tight corners. Proc. R. Soc. Lond. (Series B) **254**: 181-189.
- Thornhill, R. 1992a. Fluctuating asymmetry and the mating system of the Japanese scorpionfly *Panorpa japonica*. Anim. Behav. **44**: 867-879.
- Thornhill, R. 1992b. Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). Behav. Ecol. **3**: 277-283.
- Thornhill, R. 1992c. Fluctuating asymmetry, interspecific aggression and male mating tactics in two species of Japanese scorpionflies. Behav. Ecol. Sociobiol. **30**: 357-363.
- Thornhill, R., and Sauer, P. 1992. Genetic sire effects on the fighting ability of sons and daughters and mating success of sons in a scorpionfly. Anim. Behav. **43**: 255-264.
- Tomkins, J.L., and Simmons, L.W. 1995. Patterns of fluctuating asymmetry in

- earwig forceps: no evidence for reliable signalling. Proc. R. Soc. Lond. (Series B) **259**: 89-96.
- Ueno, H. 1994. Fluctuating asymmetry in relation to two fitness components, adult longevity and male mating success in a ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Ecol. Entomol. **19**: 87-88.
- Van Valen, L. 1962. A study of fluctuating asymmetry. Evolution **16**: 125-142.
- Vrijenhoek, R.C., and Lerman, S. 1982. Heterozygosity and developmental stability under sexual and asexual breeding systems. Evolution **36**: 768-776.
- Waddington, C.H. 1957. The strategy of the genes. George Allen Unwin, London.
- Watson, P.J., and Thomhill, R. 1994. Fluctuating asymmetry and sexual selection. Trends Ecol. Evol. **9**: 21-25.
- Weatherhead, P.J. 1984. Mate choice in avian polygyny: why do females prefer older males? Am. Nat. **123**: 873-875.
- Weatherhead, P.J. 1990a. Nest defence as shareable paternal care in red-winged blackbirds. Anim. Behav. **39**: 1173-1178.
- Weatherhead, P.J. 1990b. Secondary sexual traits, parasites, and polygyny in red-winged blackbirds, *Agelaius phoeniceus*. Behav. Ecol. **1**: 125-130.
- Weatherhead, P.J. 1994. Mixed mating strategies by females may strengthen the sexy son hypothesis. Anim. Behav. **47**: 1210-1211.
- Weatherhead, P.J. 1995. Effects on female reproductive success of familiarity and experience among male red-winged blackbirds. Anim. Behav. **49**: 967-976.
- Weatherhead, P.J., and Bennett, G.F. 1991. Ecology of red-winged blackbird

- parasitism by haematozoa. *Can. J. Zool.* **69**: 2352-2359.
- Weatherhead, P.J., Bider, J.R., and Clark, R.G. 1980. Surfactants and the management of red-winged blackbirds in Quebec. *Phytoprotection* **61**: 39-47.
- Weatherhead, P.J., and Boag, P.T. 1995. Pair and extra-pair mating success relative to male quality in red-winged blackbirds. *Behav. Ecol. Sociobiol.* **37**: 81-91.
- Weatherhead, P.J., and Boag, P.T. 1997. Genetic estimates of annual and lifetime reproductive success in male red-winged blackbirds. *Ecology*. In Press.
- Weatherhead, P.J., and Clark, R.G. 1994. Natural selection and sexual size dimorphism in red-winged blackbirds. *Evolution* **48**: 1071-1079.
- Weatherhead, P.J., and Hoysak, D.J. 1984. Dominance structuring of a red-winged blackbird roost. *Auk* **101**: 551-555.
- Weatherhead, P.J., Metz, K.J., Bennett, G.F., and Irwin, R.E. 1993. Parasite faunas, testosterone and secondary sexual traits in male red-winged blackbirds. *Behav. Ecol. Sociobiol.* **33**: 13-23.
- Weatherhead, P.J., and Montgomerie, R. 1991. Good news and bad news about DNA fingerprinting. *Trends Ecol. Evol.* **6**: 173-174.
- Weatherhead, P.J., Montgomerie, R., Gibbs, H.L., and Boag, P.T. 1994. The cost of extra-pair fertilizations to female red-winged blackbirds. *Proc. R. Soc. Lond. (Series B)* **258**: 315-320.
- Westneat, D.F. 1990. Genetic parentage in the indigo bunting: a study using DNA fingerprinting. *Behav. Ecol. Sociobiol.* **27**: 67-76.
- Westneat, D.F. 1993. Polygyny and extra-pair fertilizations in eastern red-

- winged blackbirds (*Agelaius phoeniceus*). Behav. Ecol. **4**: 49-60.
- Westneat, D.F., Noon, W.A., Reeve, H.K., and Aquadro, C.F. 1988. Improved hybridization conditions for DNA "fingerprints" probed with M13. Nucleic Acids Res. **16**: 4161.
- Westneat, D.F., Sherman, P.W., and Morton, M.L. 1990. The ecology and evolution of extra-pair copulations in birds. In Current Ornithology. Vol. 7. Edited by D.M. Power. Plenum Press, New York. pp. 331-369.
- Wetton, J.H., Carter, R.E., Parkin, D.T., and Walters, D. 1987. Demographic study of a wild house sparrow population by DNA fingerprinting. Nature **327**: 147-149.
- Witter, M.S., and Swaddle, J.P. 1994. Fluctuating asymmetries, competition, and dominance. Proc. R. Soc. Lond. (Series B) **256**: 299-303.
- Yamaguchi, T. 1977. Studies on the handedness of the fiddler crab, *Uca lactea*. Biol. Bull. **152**: 424-436.
- Yasukawa, K. 1979. Territory establishment in red-winged blackbirds: importance of aggressive behaviour and experience. Condor **81**: 258-264.
- Yasukawa, K. 1987. Breeding and nonbreeding season mortality of territorial male red-winged blackbirds (*Agelaius phoeniceus*). Auk **104**: 56-62.
- Yezerinac, S.M. 1995. Extra-pair mating in yellow warblers: sexual selection and reproductive strategies. Ph.D. thesis, Carleton University, Ottawa.
- Yezerinac, S.M., Loughheed, S.C., and Handford, P. 1992. Measurement error and morphometric studies: statistical power and observer experience. Syst. Biol. **41**: 471-482.

- Yezerinac, S.M., Weatherhead, P.J., and Boag, P.T. 1995. Extra-pair paternity and the opportunity for sexual selection in a socially monogamous bird (*Dendroica petechia*). *Behav. Ecol. Sociobiol.* **37**: 179-188.
- Zakharov, V.M. 1992. Population phenogenetics: analysis of developmental stability in natural populations. *Acta Zool. Fenn.* **191**: 7-30.
- Zakharov, V.M., Pankakoski, E., Sheftel, B.I., Peltonen, A., and Hanski, I. 1991. Developmental stability and population dynamics of the common shrew, *Sorex araneus*. *Am. Nat.* **138**: 797-810.
- Zar, J.H. 1984. *Biostatistical analysis* (Second edition). Prentice-Hall, Englewood Cliffs.

Appendix 1

Figure A1-1 (a - e). Distribution of individual male red-winged blackbirds relative to asymmetry levels (left - right, in mm) exhibited at four external and five skeletal paired morphological characters (see Table 1-1 for character descriptions). Sample size = 67, except for epaulet and coracoid length (n = 66) and for femur length (n = 65).

Figure A1-1a. Tarsus and wing asymmetry

Figure A1-1b. Tail and epaulet asymmetry

Figure A1-1c. Coracoid and femur asymmetry

Figure A1-1d. Tibiotarsus and humerus asymmetry

Figure A1-1e. Ulna asymmetry

Appendix 2

Table A2-1. Simple linear regression models describing the dependence of (a) character size (mm) and (b) character asymmetry (mm, sqrt-transformed) on date of capture for males sampled from upland habitat. Size for each character is taken as the mean size of the left and right elements. Asymmetry is computed as the absolute value of the difference between the left and right sides. Date is measured as days since 31 March.

(a) Character size

Character	n	Intercept	Slope	r ²	F	P
Tarsus	67	28.55	-0.007	0.02	1.61	0.209
Wing	67	122.86	0.005	0.00	0.05	0.819
Tail	62	87.05	-0.007	0.00	0.05	0.818
Epaulet: red	67	41.11	-0.031	0.06	4.35	0.041
Epaulet: total	67	44.62	-0.003	0.00	0.03	0.855

(b) Character asymmetry

Character	n	Intercept	Slope	r ²	F	P
Tarsus	67	0.47	-0.001	0.00	0.07	0.797
Wing	67	0.64	0.002	0.01	0.49	0.486
Tail	62	0.67	0.006	0.02	0.98	0.325
Epaulet: red	67	1.35	-0.005	0.02	1.50	0.226
Epaulet: total	67	1.32	-0.005	0.02	1.16	0.285

Appendix 3

Table A3-1. Analysis of covariance evaluating the dependence of (a) character size (mm) and (b) character asymmetry (mm, sqrt-transformed) on both date and year of capture for males sampled from marsh habitat. Size for each character is taken as the mean size of the left and right elements. Asymmetry is computed as the absolute value of the difference between the left and right sides. Date is measured as days since 31 March. Year (1993 vs. 1994) is treated as a categorical variable.

(a) Character size

Model						
Character	n	R ²	Source	Coeff ^a	F	P
Tarsus	52	0.00	Date	0.000	0.01	0.940
			Year	0.018	0.04	0.834
Wing	52	0.05	Date	-0.006	0.11	0.738
			Year	0.600	2.57	0.115
Tail	47	0.00	Date	0.004	0.04	0.843
			Year	-0.075	0.03	0.875
Epaulet: red	51	0.01	Date	0.003	0.08	0.777
			Year	0.167	0.46	0.503
Epaulet: total	52	0.03	Date	-0.011	1.05	0.311
			Year	0.165	0.51	0.480

^a Partial coefficient. For year, add if 1993, subtract if 1994.

Table A3-1. (continued)

(b) Character asymmetry

Model						
Character	n	R ²	Source	Coeff ^a	F	P
Tarsus	52	0.01	Date	-0.001	0.36	0.554
			Year	-0.010	0.10	0.749
Wing	52	0.03	Date	0.003	1.19	0.281
			Year	0.022	0.17	0.680
Tail	47	0.02	Date	-0.004	1.01	0.320
			Year	0.002	0.00	0.982
Epaulet: red	51	0.02	Date	0.001	0.14	0.712
			Year	0.047	0.50	0.484
Epaulet: total	52	0.02	Date	-0.003	0.83	0.367
			Year	-0.030	0.19	0.661

^a Partial coefficient. For year, add if 1993, subtract if 1994.