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Sexual selection and reproductive strategies in songbirds

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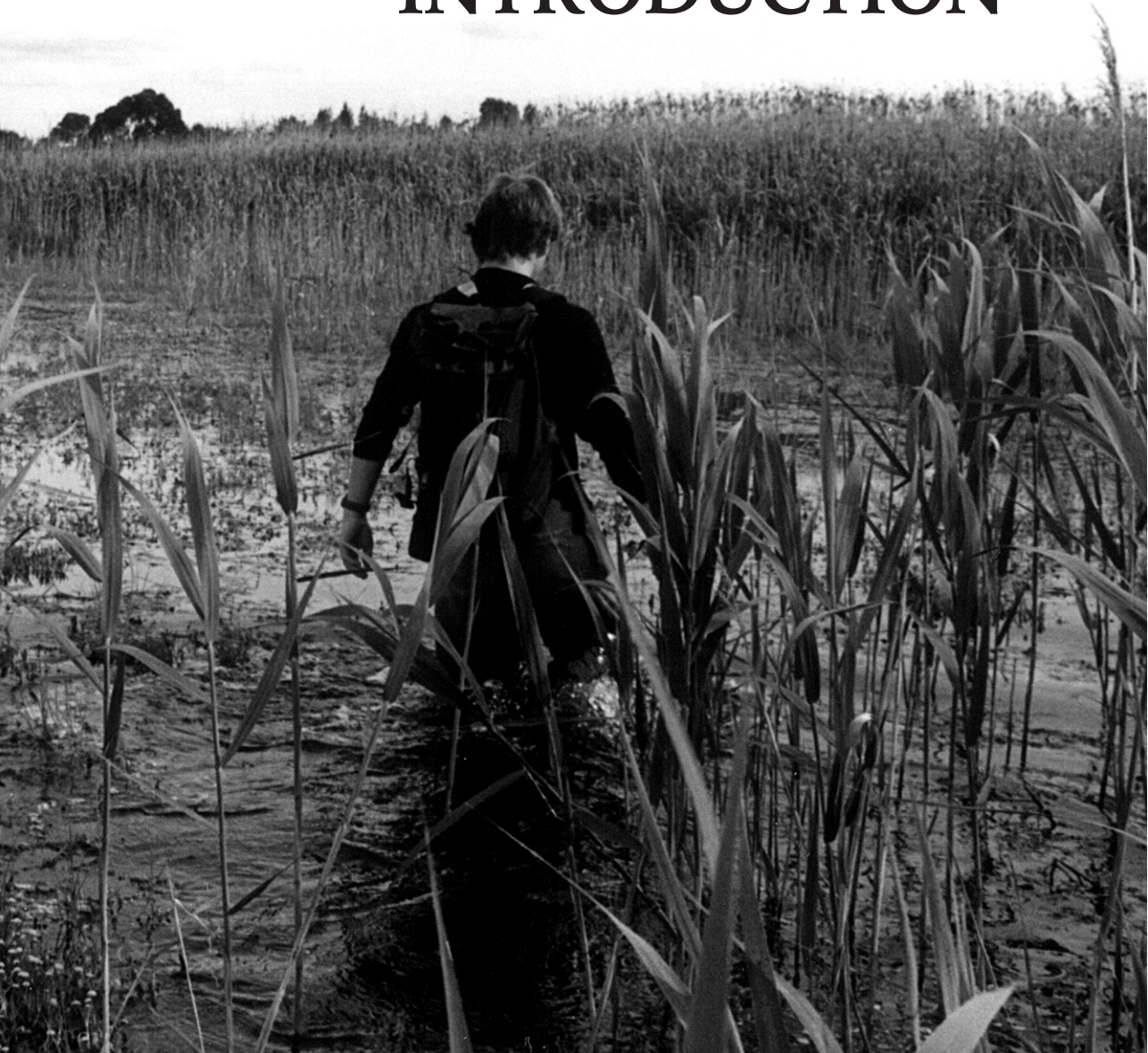
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Part I

INTRODUCTION



Chapter **1**

**Sexual selection and reproductive strategies:
a general introduction**

Mathew L. Berg

FITNESS AND INDIVIDUAL OPTIMIZATION

The study of life-histories is concerned with strategic actions of an organism over the course of its lifetime. Ever since Darwin's (1859) seminal publication on evolution by natural selection, biologists have recognised that organisms are selected to evolve life history traits and act in such a way as to maximise their fitness (i.e. their genetic contribution to future generations). Therefore, evolutionary theory predicts that animals will evolve strategies¹ that maximize their fitness (e.g. Maynard Smith 1978). This can be accomplished by adopting strategies that enable them to compete with conspecifics for territories and mates, avoid predation and ill-health, and raise successful offspring. However, the best strategy to follow may vary between different time periods, locations and individuals. Consequently, how individuals allocate resources such as time and energy to various aspects of reproduction is central to understanding life history strategies. The resultant adjustment in the strategies of individuals according to their circumstances is referred to as individual optimisation (e.g. Maynard Smith 1978; Drent & Daan 1980; Högstedt 1980; Kisdi *et al.* 1998). One of the main implications of this notion is that individuals must differ in their phenotypic 'quality', and that this can result from both environmental and genetic variation.

The presence of trade-offs between different life-history strategies is pivotal to the study of individual optimization (e.g. Clutton-Brock 1991). These may include trade-offs between survival and reproduction, but may also include trade-offs within those two broad components of fitness. For instance, an individual may trade-off its allocation to current reproduction with its allocation to future reproduction (Trivers 1972). Such trade-offs arise because animals are not able to simultaneously pursue all strategies that might enhance their fitness. If potential costs are involved, individuals are expected to adopt particular strategies only if the costs are outweighed by the benefits, which may be either direct (e.g. benefits of providing more care to offspring) or indirect (e.g. benefits of breeding with a high quality mate).

Males and females are expected to experience many of these trade-offs in different ways, leading to potential conflicts between the sexes (Trivers 1972). For example, in species with internal fertilization, certainty of offspring parentage tends to be higher for females than for males (Trivers 1972; Clutton-Brock 1991), and this is likely to have a large influence on individual reproductive strategies in such species (Queller 1997; Wade & Shuster 2002; Kokko 2003). Uncertain paternity is likely to diminish the potential fitness gains of care-giving males below that of females. As a consequence, males are expected to implement strategies in order to enhance their certainty of paternity and improve their fitness without relying on offspring of uncertain paternity. This is likely to be especially true in organisms such as the oscine passerines (songbirds), where most species are genetically promiscuous (see Box 1.1). The ways in which individuals vary

¹ 'Strategies' can be considered a rule that specifies how an organism should react in a given circumstance (McNamara & Houston 1996). In general terms, this may refer any traits displayed by an individual, including morphological, genetic, physiological or behavioural characteristics. However, in this thesis I am primarily concerned with behavioural strategies for reproduction.

their reproductive strategies in the face of such competition and conflict are major themes in this thesis.

COMPETITION AND CONFLICT: SEXUAL SELECTION AND REPRODUCTIVE STRATEGIES

Natural selection (Darwin 1859; Fisher 1930) is not the only form of selection through which evolution may act on individuals in the wild. Another process, sexual selection, deals with the advantage individuals have over others of the same sex, in exclusive relation to reproduction (Darwin 1871; Andersson 1994). This form of evolution operates through two main processes, where strategies are favoured that make males good at competing with other males (intra-sexual selection), or that make males more attractive to females (inter-sexual selection)². Competition and conflict for reproductive advantages (e.g. territories, mates or paternity) are at the heart of sexual selection. Thus, sexual selection provides an explanation for sexually dimorphic characteristics that do not provide any obvious survival advantage (or indeed may be deleterious to survival). It can operate throughout the life cycle of an individual and at all stages of reproduction.

In this thesis, we are primarily concerned with behavioural strategies associated with reproduction, which may be expected to impinge on an individual's reproductive success (and hence fitness). Reproductive strategies may be intended to bolster pre-copulatory competition (e.g. competition for a breeding position or a mate) or to promote post-copulatory reproductive success (e.g. paternity assurance or offspring care). In general, males (or the sex with smallest gametes) are expected to invest most heavily in the former while females (or the sex with the largest gametes) are expected to invest most heavily in the latter (e.g. Maynard Smith 1977). Many of the same arguments that are applied to parental investment in gametes can also be applied to post-fertilization offspring care (Wade & Shuster 2002).

ENVIRONMENTAL INFLUENCES & FLEXIBLE STRATEGIES

In natural systems, there is often considerable variation within and between individuals in the behaviour they express. This variation is often attributed to corresponding variation in environmental circumstances (Clark & Ehlinger 1987; Wilson 1998). Members of a population often experience different environmental conditions, and individuals may be expected to react differently to different environments. Specifically, their strategies should be individually tailored to their individual circumstances. Thus, whenever possible, strategies should be flexible, i.e. individuals should be 'phenotypically plastic' (Nur & Hasson

² Broadly speaking, the words 'male' and 'female' are interchangeable in this context. However, in most species it is males that compete for females, and females that are choosy (e.g. Trivers 1972; Kokko & Jennions 2003), and songbirds are no exception (Lack 1968). Therefore, I use the terminology applicable to this particular case for simplicity.

1984; Schlichting & Pigliucci 1998; Piersma & Drent 2003). Such flexibility may be constrained by physiological processes or the ability to perceive environmental variation (Kisdi *et al.* 1998). Accordingly, plasticity in traits itself may be one of the most important traits under selection, particularly in more variable or unpredictable environments.

In this context, environment encompasses a broad meaning, and includes not only external variables (e.g. food availability, predator abundance or climate), but also variation in the internal state of the individual (e.g. size, health, condition or energy reserves), and social or population variables (e.g. density, sex ratio or pairing status). Environmental variation may be largely stochastic, or fixed and predictable. Furthermore, it may exert an influence on an individual basis (e.g. predation or parasite infection) or on the population as a whole (e.g. climate or population density).

It is therefore crucial to consider environmental variation when ascribing observed individual behaviour to reproductive strategies. In order to quantify the relationship between observed behaviour, strategies and the environment, we can investigate phenotypic variation between and within individuals in relation to natural variation in the individual's environment. Where possible, an even better approach is to manipulate the environmental factors of interest, because it may not always be clear what are the important environmental variables. These are general approaches that we have used in this thesis, particularly with respect to the presence of conspecifics and food availability as environmental variables subject to manipulation.

MOTIVATION AND RATIONALE

In this thesis we attempt to unravel some of the evolutionary processes behind a range of reproductive strategies of two species of songbirds. We do this by observing the reproductive behaviour of individuals, with knowledge and manipulations of their environmental conditions (in this case food availability and social circumstances). Specifically, we used two main approaches to manipulate the environment of the birds to study the effects on different conditions on reproductive strategies: (1) manipulation of the social environment by simulating the presence of conspecifics (usually intruding competitors), and (2) supplementary feeding to manipulate the territory quality (food availability). The general aim is to examine how the behavioural patterns that emerge relate to evolutionary and individual optimization theory.

The specific model systems used are two common species of songbirds: the winter wren (*Troglodytes troglodytes*) and the Australian reed warbler (*Acrocephalus australis*) (see Box 1.2). Common features of the songbird group include the use of complex acoustic signals by one or both sexes in reproduction, almost universal parental care, and the widespread occurrence of extra-pair paternity. All songbirds make multiple investments in the course of reproduction, in territories, in gametes, and in offspring care, and correspondingly we have attempted to consider the interplay between these modes whenever possible. The broad reproductive strategies studied in this thesis are territory defence, mate attraction and parental care (incubation and feeding offspring). In many songbirds,

sexual signalling is most prominent in males, and some of the aspects of reproductive behaviour under consideration (e.g. territorial behaviour) are primarily the domain of males. Therefore, in most cases we have studied traits from a largely male perspective.

OUTLINE OF THE THESIS

This thesis is organized into five parts, comprising this introductory chapter, eight empirical chapters (chapters 2 to 9) which deal in turn with the three main behavioural components of reproduction in songbirds (parts II-IV), and a concluding discussion in part V (chapter 10).

Part I. Introduction

Part I contains a general introduction to the issues that we consider throughout this thesis (**this chapter**), followed by a chapter about the development of molecular tools that are used in the study of mating systems and other aspects of molecular ecology (**chapter 2**, with Marco van der Velde and Jan Komdeur).

Part II. Territory defence

The first stage in reproduction for most songbirds, as for many other animal taxa, is the establishment of a stable territory or breeding position where reproduction can take place. Territories are a crucial step in reproduction for many species, because they ensure access to resources that are essential for successful reproduction (Stamps 1994). While the role of sexual selection in driving the evolution of many sexual signals is well known and most secondary sex traits³ studied have a dual function (Berglund *et al.* 1996), most research to date has been focussed on inter-sexual processes (reviews in Andersson 1994; Berglund *et al.* 1996). In part II, we discuss signal evolution (the song of winter wrens) primarily in terms of territory defence. In many territorial systems, sexual signals can be considered as quality signals or signals of individual identity (Dale *et al.* 2001). How a sexually selected signal (song) is used in the territorial strategies of male winter wrens is the topic of part II. We use playback experiments as the primary methodology in this section. In the first place, **chapter 3** (with Sanne Boessenkool, Margreet Drijfhout and Jan Komdeur) deals with the need to recognize competitors individually in a territorial system (the wren), and in particular competitors representing different levels of threat, such as familiar neighbours and unfamiliar intruders. Furthermore, we examine how this issue might act on the elaboration of song complexity in wrens. In the second place, **chapter 4** (with Jan Komdeur) also deals with the evolution of song as a sexual signal, but viewed primarily in the context of a quality signal. We consider how male performance during intra-sexual competitions may be used by females as a mate choice cue, and how males may consequently adjust their defensive strategies to enhance their mating success.

³ Physical and behavioural sexual characteristics in mature organisms that are not directly connected with the act of reproduction (Darwin 1871).

Part III. Mate attraction

The role of mate attraction has been one of the most intensively studied aspects of sexual selection over the last three decades. Andersson's (1982) classic study on tail length and female choice in a widowbird (*Euplectes progne*) instigated a surge in empirical studies on the topic, while Zahavi's (1975, 1977) landmark papers on the handicap principle provided a theoretical framework for the evolution of secondary sexual traits through honest signalling. In contrast to territory defence, sexual signalling for mate attraction is usually considered in terms of quality advertisement only. In part III, we discuss signal evolution (male song and nest building in Australian reed warblers) primarily in terms of mate attraction. We adopted this emphasis on mate attraction because these signals have been hypothesised to be largely driven by female choice in this and similar species (e.g. Catchpole 1973; Courtney-Haines 1991; Hasselquist *et al.* 1996), and because we were also looking for variation in pairing success in these studies. In **chapter 5** (with Nienke Beintema, Justin Welbergen and Jan Komdeur) we use a supplementary feeding experiment to examine the role of food availability on song production in the Australian reed warbler. One essential but often overlooked component of the handicap principle is flexibility in the signal in the face of variation in the 'condition' of the signaller (Zahavi 1975; 1977; Nur & Hasson 1984). We address this issue by examining the flexibility in song production within individuals in response to frequently changing environmental conditions. In **chapter 6** (with Nienke Beintema, Justin Welbergen and Jan Komdeur) we continue our experimental study of the role of food availability in sexual signalling. In this chapter, we consider a unique 'non-bodily' signal, the display nests of Australian reed warblers. We also report the outcomes of variation in this signal for mate attraction.

After investigating the settlement patterns of female winter wrens in one of the only other recent detailed studies of the breeding biology of this species, Burn (1996) concluded that this species displays 'neutral mate choice' (i.e. females settle at random). However, genetic mating patterns may reveal a different pattern. It is now known that in many species of birds, females copulate with males other than their social mate, resulting in extra-pair fertilizations (see Box 1.1). Molecular techniques have opened up the possibility to measure paternity in wild populations with great accuracy. In **chapter 7** (with Marco van der Velde and Jan Komdeur) we study the occurrence of extra-pair paternity (see Box 1.1) in wrens using the panel of five microsatellite markers described in chapter 2. We report the rate of extra-pair paternity in two populations of this species. In addition, we relate the occurrence of extra-pair paternity to the genetic quality of the social father, revealing that the genetic diversity of males is strongly related to the presence of extra-pair offspring in their nests.

Part IV. Parental care

If an individual has successfully obtained a breeding territory and acquired a mate, it then has to decide when and how much to care for its offspring. Parental care is ubiquitous in songbirds (e.g. Lack 1968; Clutton-Brock 1991), and most species display biparental care to some extent. This care may take several forms, but the most commonly encountered forms in birds are incubating the eggs and providing food to the offspring. **Chapter 8**

(with Jan Komdeur) incorporates both intra-sexual and inter-sexual processes to examine parental care. We examine the trade-offs faced by Australian reed warblers parents between caring for offspring, defending the breeding area and, in the case of males, pursuing additional mating opportunities. We show that such trade-offs can have a profound affect on the strategies of males, and that the expression of these trade-offs depends on the spatial presence of conspecific individuals. This chapter thus combines male and female perspectives on parental care, and deals with cooperation and conflict between the sexes in reproductive strategies. In **chapter 9** (with Cas Eikenaar and Jan Komdeur) we again use a supplementary feeding experiment, in conjunction with video observations and nest temperature loggers, to examine the role of food availability on incubation strategies in Australian reed warblers. Unlike the previous chapters, this chapter focuses on a female perspective; we show that incubation is an entirely female responsibility in this species. Our data demonstrates that higher food availability on the breeding territory leads to an increase in female incubation attendance, which in turns appears to result in an increase in hatching asynchrony. We discuss the role of energetic constraints on incubation and the adaptive potential for facultative adjustment of hatching asynchrony in altricial birds.

Part V. Synthesis

Finally, in part V (**chapter 10**) I summarize the main findings of the thesis and discuss them in a more general framework. I also discuss some limitations of the project, together with some suggestions for future research.

BOX 1.1. EXTRA-PAIR MATING IN BIRDS

Monogamy is the most common social mating system encountered in birds (Lack 1968; Davies 1991) accounting for around 81% of species (Cockburn 2006). However, it is now known that in many species females copulate with males other than their social mate, resulting in extra-pair fertilizations. Indeed, extra-pair paternity is so common that it must represent an extremely important component of the sexual selection in this group. A meta-analysis by Møller & Ninni (1998) indicated that variance in male mating success, when taking into account extra-pair paternity (based on genetic parentage analyses), was on average increased by a factor of 4.6 over the variance in putative male mating success (based on observations of social pairing). Over the last two decades, new molecular techniques such as DNA fingerprinting have opened up the possibility to measure genetic parentage with great accuracy. Since the revolutionary application of these techniques to the study of extra-pair mating of birds, the effects of sexual selection acting on this kind of sperm competition has been the subject of intense investigation. A recent review on the topic of extra-pair paternity in birds revealed that, in contrast to their social mating systems, genetic monogamy is the exception rather than the rule in passerine birds (Griffith et al. 2002). Extra-pair paternity was found to occur

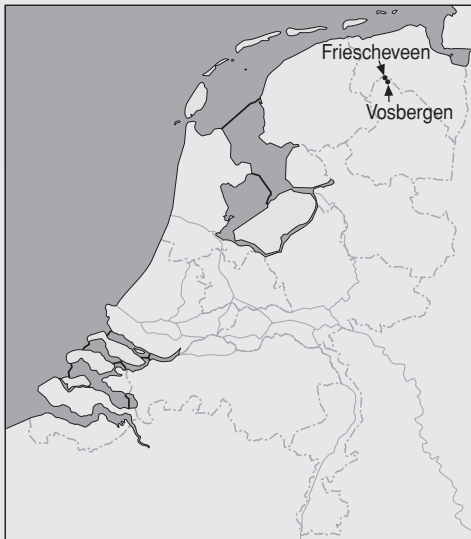
regularly in 86% of species so far studied. On average, 11% of offspring in 19% of broods have been the result of extra-pair fertilizations in these studies. Both winter wrens (chapter 7) and Australian reed warblers (Berg 1998; M. Berg & M. Bleeker, unpubl. data) are known to have a relatively high rate of extra-pair paternity. In most birds, females are thought to have at least some control of whether extra-pair copulations take place (Birkhead & Møller 1992a). However, it is still largely unknown why females seek extra-pair fertilizations. Neither the characteristics revealing male and female quality nor the benefits accruing to females that select attractive males (and their offspring) have been fully identified.

BOX 1.2. THE STUDY SPECIES

For many research questions about the adaptations of animals in the wild, birds offer an excellent research opportunity. This is because they can be individually marked, are easily observable, and a plethora of field experiments are feasible. Furthermore, many general aspects of their behaviour and ecology are already well known

Winter wren (*Troglodytes troglodytes* Linnaeus 1758)

We studied winter wrens from 1999 to 2002 at two nearby field sites in the north of The Netherlands (53° 8' N, 6° 35' E; Fig. 1.1). These two sites comprised *ca.* 60 ha of mostly deciduous woodland, interspersed with some coniferous woodland and open pastures. The winter wren (family Troglodytidae) is a small brown passerine (*ca.* 10g) that inhabits a variety of habitats, including any type of woodland, gardens and farmland. Males



sing a loud and complex song throughout the year, although song production is highest during the breeding season (April to July). Wrens breed in fully enclosed nests, which are usually located low in a shrub, vine or tree stump. Nest predation is common, and most females attempt several broods during the breeding season. Clutch size is usually 4-7 eggs, but decreases as the season progresses. Only the female incubates, and the level of care provided by the male during the nestling period is highly variable. Polygyny is quite common, with up to 50% of males obtaining one to 4 secondary females (reviewed in Burn 1996).

Figure 1.1. Map of field site locations for winter wrens (*Troglodytes troglodytes*).

Incubation takes 14-18 days, and the nestling period is 15-19 days. Most wrens are resident year round, but territoriality may decline outside the breeding season. Males often defend the same territory for more than one year, but most individuals live for only 1-2 years. For further information on the general biology of wrens see Armstrong (1955) and Cramp (1988).

Australian reed warbler (*Acrocephalus australis* Gould 1838)

We studied Australian reed warblers from 1997-2000 at two field sites on the outskirts of Melbourne, Australia (38° 2' S, 145° 7' E; Fig. 1.2). These two sites consisted of ca. 150 ha of predominately of common reed (*Phragmites australis*) surrounding lakes. One of these sites, Edithvale-Seafood Wetlands, was designated a RAMSAR site in August 2001 and represents the last remaining part of the once extensive Carrum Carrum Swamp which was largely drained in the 1860s. The Australian reed warbler (family Sylviidae) is a small brown passerine (ca. 18g) that inhabits vegetation surrounding lakes and water courses, largely common reed, and bulrush or cumbungi (*Typha* spp.). Males sing a loud and complex song throughout the breeding season (September to January). The birds breed in nests constructed between vertical reed stems, and in our study sites produced up to four broods per year. Clutch size is usually 2-4 eggs. Polygyny occurs occasionally, but most pairs are socially monogamous and males usually provide considerable food to offspring (although only the female incubates). Incubation takes 13-14 days, and the nestling period is 9-11 days. Most juveniles disperse from the natal area (only one juvenile was recaptured on the study sites), but adults often return to the same breeding site over several years. The Australian reed warbler is migratory, and arrives on the breeding sites in south-eastern and south-



Figure 1.2. Map of field site locations for Australian reed warblers (*Acrocephalus australis*).

western Australia in spring. The Australian reed warbler is sometimes considered a subspecies of the clamorous reed warbler (*Acrocephalus stentoreus*), which ranges through Asia and the middle-east (Cramp 1992). For further information on the general bio-logy of the Australian reed warbler see Higgins *et al.* (2006), Cramp (1992) and Courtney-Haines (1991).

