Vocal fighting and flirting: the functions of birdsong

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INTRODUCTION

Birdsong has long been associated in our minds with mating behavior and male aggression. When males are active in defending territories and attracting mates, we think of springtime and breeding seasons. A large body of research on birdsong confirms that its two main functions are repelling rivals and attracting mates.

My aim is to review this evidence and discuss the importance of specific aspects of male song. The aspects of singing behavior that are important for each function vary between species. In a few cases, I will also outline the role that female song may play. One pervasive theme will be how the evolution of song has been driven by the twin selection pressures of female choice and male competition.

EVIDENCE THAT SONG IS IMPORTANT

Is song in fact used in male–male competition and female choice and, if so, which aspects of an individual's song make him more successful when it comes to reproduction? It is possible that individual characteristics are reflected in the song, and individuals who impress with their song may have a greater reproductive success through repelling rivals or attracting females.

So a primary question is whether male song does reflect some aspect of male quality and increases the reproductive success of the singer.

Some simple experiments show that females do respond to male song, and that males can be intimidated by a rival's song. If males are removed from their territories and replaced by loudspeakers broadcasting song, the territories remain unoccupied for longer than silent control territories without broadcast song (Krebs 1976; Falls 1988; Nowicki et al. 1998a). Song evidently does repel rivals from intruding into a territory. Females, on the other hand, are more likely to be attracted to nest boxes where males have been removed and replaced with loudspeakers, rather than to silent nest boxes (Eriksson & Wallin 1986; Mountjoy & Lemon 1996; Johnson & Searcy 1996). Females also respond to song by performing copulation solicitation displays (Searcy 1992a), and tend to approach speakers playing male song in the laboratory (Clayton 1988).

If song is to serve these dual functions, both sexes will use it to assess the male, as a rival or a potential mate. However, the qualities on which males and females should base their assessment are somewhat different. Females need to find a mate who will maximize their reproductive success. We expect that factors such as the male's, age, condition, parental ability, and the quality of his territory will affect his attractiveness as a partner. Where male rivalry is concerned,

competitors need to know the location of a rival male, who he is, how likely he is to attack, and his fighting ability. In some cases, the same song characteristic may give information to both males and females on aspects of the singer to which they will respond. However, in many cases, the information of interest is quite different and we would therefore expect different song parameters to be used.

MALE–MALE COMPETITION: VOCAL FIGHTING

Contests among males may be over mates, a territory, or the resources that attract females, such as a nest or feeding site. So the question is, what kind of song will best prevent a male from trying to take over a rival's nest box, territory, or female? Why should a male pay attention to the song of his rival? Why not fight and let the winner take the spoils? Of course, if a male territory owner can indicate he is such a superior fighter that, in a combat, the rival would lose, then both males may gain from avoiding a fight. Therefore, any song characteristic that suggests, either honestly or by bluffing, that a male is an excellent fighter, should be produced by the male to cause rivals to withdraw.

The outcome of fights is likely to depend on physical strength, fighting skills, and motivation to fight. Factors determining physical strength, such as size, weight, body condition, and energy reserves, become important in the assessment of rivals. Motivation to fight may vary among males, depending on what they have to gain and lose. Males who are more motivated are more willing to escalate a fight and are thus more dangerous opponents (imagine a small dog seeing off a larger one by not giving up, constantly yapping and snapping). Males who have a breeding female on their territory may be more motivated to fight; a male trying to take over a territory may find it easier to move on and try his luck at a new site rather than risk a fight with a highly motivated opponent.

However, what is to prevent a male from singing a song that indicates he is a superior fighter, or highly motivated to fight when in fact he is not? If it is possible for inferior males to signal that they are superior or highly motivated, then an intruder should take account of the possibility of deception. Why retreat when you may in fact be stronger than your rival? This conflict is at the heart of the evolution of the signals that occur between rival males. Territory owners should do all they can to repel rivals, but rivals should only withdraw if they can determine that the signal is a true indicator of superior fighting ability or of willingness to escalate the intensity of a fight.

There are several possible solutions to the signaling problem. Signals that are costly to produce are likely to be honest (Zahavi 1975, 1977) and the cost itself ensures their honesty. We may assume that an inferior male simply cannot produce a signal as costly as the one that a superior male is able to produce. There may be production costs such as the energy needed to utter a particular signal, and males with higher energy reserves may be able to generate a 'stronger' signal than those with lower reserves. This type of cost would lead to a gradual increase in the intensity of a particular song parameter in relation to a male's condition. If body condition affects fighting ability, as is quite likely, then a song reflecting this characteristic will also indicate a competitor's strength.

Alternatively, costs could be imposed by other individuals. A good analogy may be the way humans use aggressive shouting to intimidate rivals. Aggressive shouting will often cause rivals to withdraw, but it also runs the risk that a particularly strong or aggressive individual, rather than being intimidated, will respond physically. If your signal was all bluff you may get injured in the ensuing fight. Therefore, it is better not to signal that you will act aggressively unless you can follow it up if challenged. Replace shouting with singing in a particular manner and you have a good idea of what may happen in territorial disputes in birds. The cost of

cheating, by pretending to be stronger or more aggressive than you are, will be related to the level of probing, or testing, by rivals. Bluffing may occur at some level, and its frequency will be related to the likelihood and cost of being probed.

In this scenario, the signal itself need not be costly to produce, but should indicate the likelihood of attacking, level of aggression, or motivation to fight. This kind of signal is known as a 'conventional signal' (Guilford & Dawkins 1995), so called because the specific form of the signal is arbitrary and a matter of convention. The definition of a conventional signal is that "the signal is more or less arbitrarily related to the message, many signals can carry the same message" – costs are target receiver dependent, so signals can be cheap to produce" (Guilford & Dawkins 1995). As long as everyone understands what different arbitrary signals mean, the system works. With conventional signals there are more likely to be different signal categories rather than gradual increases in the intensity of the same signal, as is likely to be the case for a physically costly signal.

Some signals are affected by physical restrictions and are thus, potentially, indicators of male quality. For example, larger males can produce deeper frequency sounds due to their larger vocal apparatus; a smaller male simply cannot cheat by producing a lower frequency sound. If larger males are better fighters, as is quite likely, then it makes sense to withdraw if you hear a low frequency sound indicating a male is larger than yourself. But this connection is not foolproof. Sometimes physical restrictions can be overcome. In some species the trachea has become elongated so that it is no longer proportional to body size. The frequency of the song, or call, now indicates trachea size and not body size (Fitch 1999). Smaller males can cheat. It would be interesting to see whether the elongated trachea of a large male is still longer that that of a small male. When a cat increases its apparent size by raising its fur on end, a large cat will still look bigger than a small one.

Testing the Role of Song in Male Rivalry

Three main methods have been used to address questions about the role of male song in rivalry. The first is observational. Birds are observed and recorded during aggressive encounters, and their song characteristics are compared to nonaggressive interactions. For example, male barn swallows emphasize rattles in the song during aggressive encounters, indicating that rattles are a relevant component of competitive interactions between males (Galeotti et al. 1997). In another approach, song traits are correlated with measures of male quality that might be important to other males, such as size or age, or with consequences of success in rivalry, such as territory size or quality. In male barn swallows, males who produce lower frequency rattles are in good condition (Galeotti et al. 1997), a useful fact for a rival to know. It seems likely that rattle frequency is important in male rivalry situations.

A second method is territorial song playback. A speaker is placed in the subject male's territory, usually near the edge, and a song is played back to the territory owner. Usually two versions of a song, or two song types, are played sequentially with a pause between the two. The response of the territorial male to each song is measured; indicators of a strong response are an increased singing rate, flying close to the speaker, and increased calling. It is assumed that a male territory owner will respond more strongly to the song that would be more effective in male rivalry situations.

However, there is a problem with this method. You wish to test how the characteristics of the resident male's song function in male rivalry situations, but what you are in fact testing is how songs of intruders or rivals are perceived, recognized and responded to by territorial males (Searcy & Nowicki 2000). The focus is assumed to be on intruder deterrence, but a different question is actually being asked – how worried does a territory owner get in response to different intruder songs? But the important question in

male–male competition is usually – how good are different songs at deterring intruders? In general this may not be a problem, because the same song characteristics may be important to both intruders and resident males. However, you may simulate a very powerful intruder (i.e. a male with a song more typical of a territory owner) and the territory owner who hears that playback may withdraw rather than attempt to fight back. This could result in a situation where very strong stimuli actually *decrease* the territorial response compared to an 'average' strength stimuli (**Fig. 2.1A**). If you were testing the effectiveness of a song as a keep-out signal by playing a territorial male's song to an intruder, then there would be a perfect negative relationship between song stimulus strength and intruder response (**Fig. 2.1B**). Male willow warblers produce a particular syllable type in agonistic encounters (Type A), especially associated with imminent attack (Jarvi et al. 1980). Playback of type A songs to territory owners, simulating a very aggressive intruder, results in withdrawal of the territory holder.

For this reason a third method, the speaker replacement experiment, is perhaps a better way to study how effective different songs are in repelling rivals from a territory. Here a male is removed from his territory or nest box and is replaced by a speaker broadcasting particular song stimuli. We already know that territories broadcasting song remain unoccupied longer than control territories. This type of experiment has been conducted with thrush nightingales, great tits, white-throated sparrows, and song sparrows (Searcy & Nowicki 2000). Unfortunately, this approach is sometimes impractical as intrusions into a territory are infrequent and difficult to observe. In addition, the simulated playback 'singer' is static rather than singing from song posts around the territory. For this reason territorial playback experiments are still the most common method of addressing questions on the functions of territorial song, and how song variants differ in their effectiveness at intimidating rivals. Although care must be taken in the interpretation of the results, it is relatively easy to perform, and does indicate whether males are able to perceive, recognize, and respond to differences between songs. It is thus valuable in identifying the song parameters that are involved in male competition.
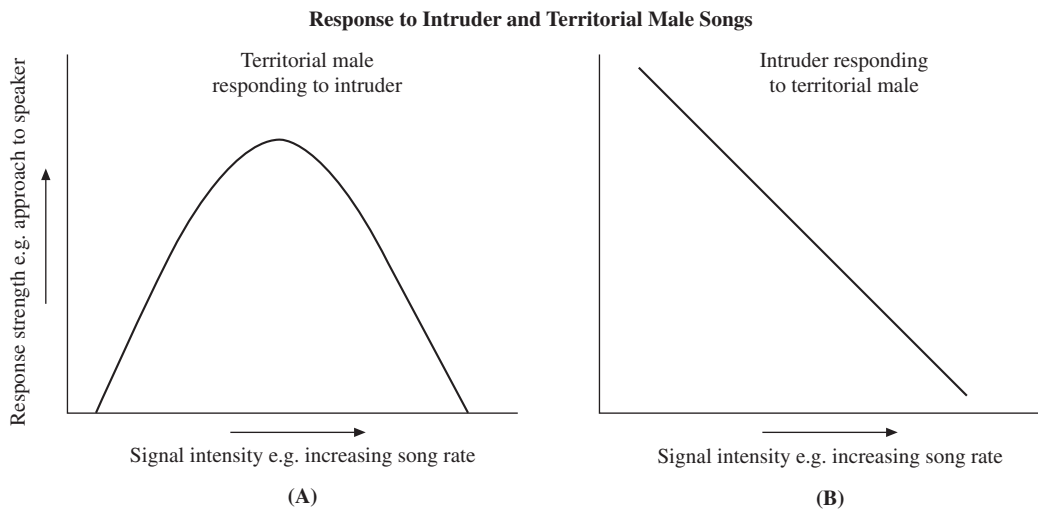

Response to Intruder and Territorial Male Songs

Figure 2.1   The response strength of a male to playback of male songs differing in signal intensity; **(A)** response of a territorial male to intruder song stimuli; **(B)** an intruder responding to territorial male song stimuli. In **A**, the response strength eventually drops with increasing signal intensity.

Simple Changes in Song Characteristics

The simplest way to compare the quality of conspecific individuals is through differences in very basic song characteristics, such as frequency or amplitude changes, song production rate, or the inclusion of particular notes.

One interesting idea is that lower frequency sounds may be indicators of relaxation, because tenseness in the sound production muscles causes an increase in frequency (Zahavi 1982). A male who appears relaxed in the face of danger may be seen as a greater threat; to anthropomorphize, the male appears very confident of winning the fight. However, it is more likely that lower frequencies indicate a larger body size (Beani & Dessi-Fulghieri 1995), although the evidence for this is contradictory. As already mentioned, in some species the relationship between the size of the body and the vocal apparatus may be de-coupled by tracheal elongation (Fitch 1999). Relationships between body size and low frequency have been found across species (Ryan & Brenowitz 1985), but are not always found within a species, although males generally produce lower frequency sounds than females (Ballintijn & ten Cate 1997). In chickadees, playback of male songs with low whistle frequency results in retreating by territory owners (Shackelton & Ratcliffe 1994), suggesting that a low frequency may indicate a more able competitor. The relationship is reversed in roosters; dominant males produce higher frequency sounds (Leonard & Horn 1995). Lambrechts (1996) suggested that high frequency sounds are more energetically expensive to produce than lower frequencies. The reason given is that for most species, including humans, sounds in the bottom quarter of the vocal frequency range are easier to produce than those in the upper frequency range. In summary, although there is evidence that simple changes in the sound frequency of songs may be involved in signaling competitive ability, relationships between frequency and male competitive ability are not always clear.

In the barn swallow (**CD #—**), Galeotti et al. (1997) found that the rattle produced at the end of the song was longer in individuals with higher testosterone levels, a likely indicator of greater aggressiveness (**Fig. 2.2**). In addition, the frequency of the rattle was lower in males in good body condition; also, in competitive situations, the rattles in the song are emphasized by males, suggesting that these signals may be important in male–male competition (**Fig. 2.3**). Differences between individuals in the structure of the rattles can convey important information to the receiver, such as the probability of escalation (longer rattles = more likely to escalate), and the physical quality of the singer (lower frequency rattles = good condition). Rattle characteristics are related to male reproductive success, indicating that the greater competitive ability of males with long, low frequency rattles improves the male's breeding success. The beginning of the song, a complex series of notes, appears to be important in female choice (Møller et al. 1998).

Similarly, a specific song element is important in territory defense in the water pipit (Rehsteiner et al. 1998). Male songs contain the 'snarr' (**Fig. 2.4**), a rasping element with a broad frequency range, very similar to the barn swallow rattle (**CD # —**). Male water pipits with more 'snarr' notes had territories that overlapped less with neighbors, were heavier and were mated more often than males with fewer snarrs. However, breeding success, measured by the number of chicks successfully raised, was not related to the 'snarr' score. The 'snarr' is easily locatable (Dooling 1982a; Wiley & Richards 1982), so a male may be more apparent at his territory boundaries, perhaps with an aversive effect on potential intruders. In addition, the heavier weight of males with higher 'snarr' scores means they are likely to be more formidable opponents. As in the barn swallow a harsh, potentially energetically expensive note is used to signal competitive ability. In both cases differences in the signal are related to differences in male attributes, and this information is potentially useful to rivals selecting their subsequent behavior. We have good reason to believe that harsh loud elements signal male condition, and thus fighting ability, because they are energetically expensive to produce (Obwerger & Goller 2001).
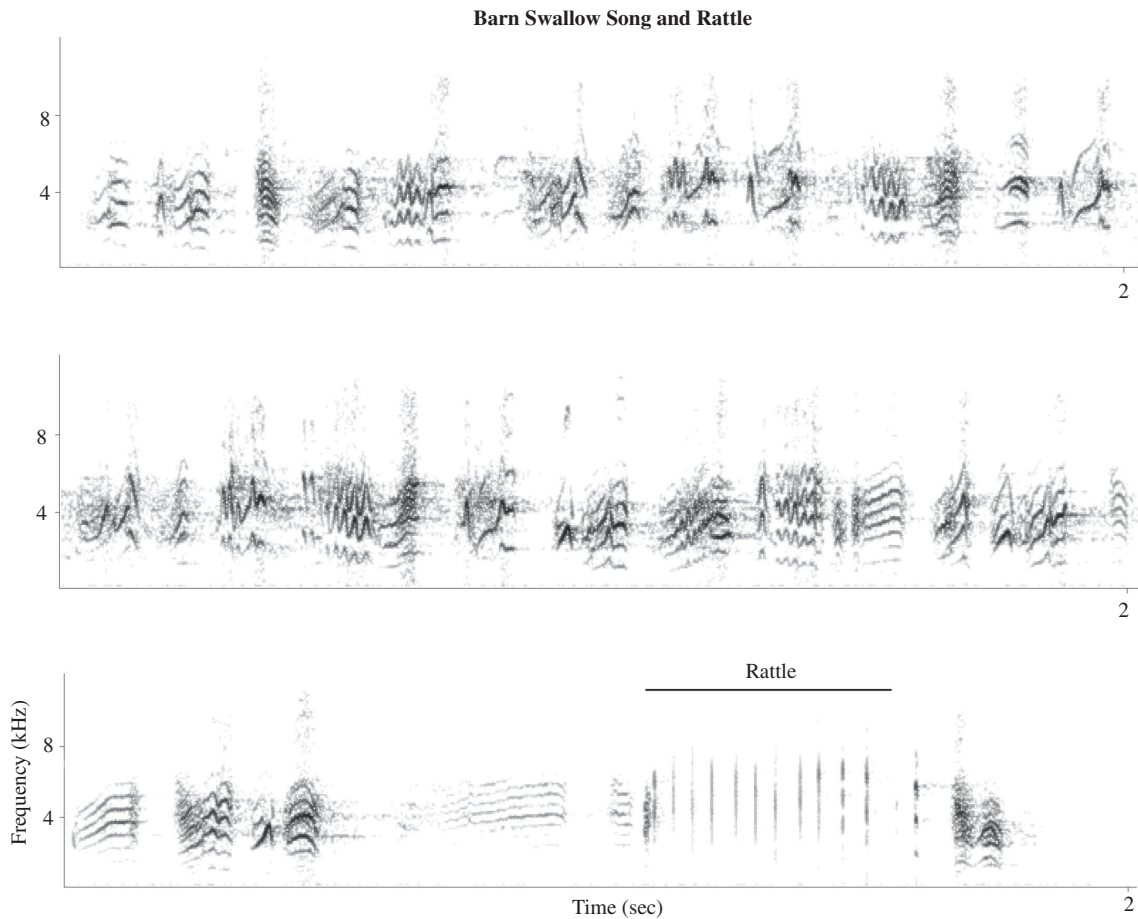
Barn Swallow Song and Rattle

Figure 2.2 Barn swallow males emphasize the rattles in the song during competitive encounters with other males. The rattle is longer in individuals with higher testosterone levels and the frequency of the rattle is lower in males in good body condition. Only one rattle is illustrated.

Increases in song intensity require more energy and thus are readily explained as indicators of male condition (Obwerger & Goller 2001). In blackbirds differences in the potential for aggression are signaled by increasing the intensity of the song, although the structure remains the same (**CD # —**). The low intensity song is slower, has longer motifs, shorter twitters and is often somewhat quieter than high intensity song (Dabelsteen & Pedersen 1990; **Fig. 2.5**). Males change from low intensity to high intensity song when rivals start singing from outside their territories. The change seems to indicate a territory owner's increasing motivation to fight. Males who try to bluff may risk becoming

exhausted and thus disadvantaged in any subsequent fight.

One well-studied species is the collared dove, (ten Cate et al. 2002). Males defend a territory for most of the year and coo from song posts around their territories. An important function of the coo is communication between males. The elements within a coo may consist of a constant frequency or, in adult males, may contain a frequency modulation (a jump in frequency; **Fig. 2.6; CD # —**). Individuals differ in the number of coo elements which are modulated, the percentage of modulated coos overall, and the peak frequency of coo elements are both correlated with weight (heavier males produce
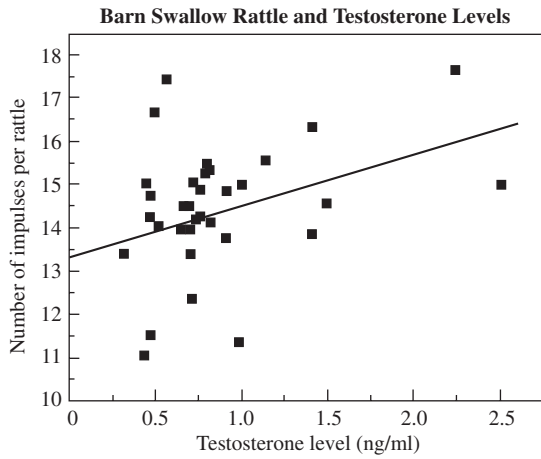
Barn Swallow Rattle and Testosterone Levels

Figure 2.3 The relationship between plasma testosterone levels and the number of impulses per rattle in barn swallow song. From Galeotti et al. 1997.

higher frequency elements, more of which are modulated). Territorial males respond more strongly to playbacks of modulated coos than to nonmodulated coos. The increase in response is due specifically to the modulation, i.e. the *change* in frequency, not the fact that the overall frequency is higher. Ten Cate et al. (2002) suggest that their production by larger males may indicate that modulations are costly; the frequency jump may be difficult to produce except by males in good condition (Lambrechts 1996). An alternative is that there may be a predation cost due to the locatability of signals with simple frequency modulations (Dooling 1982a; Wiley & Richards 1982), especially in open environments. Fitter males that can easily escape from predators, or males willing to take a higher risk may be more likely to modulate their coos.
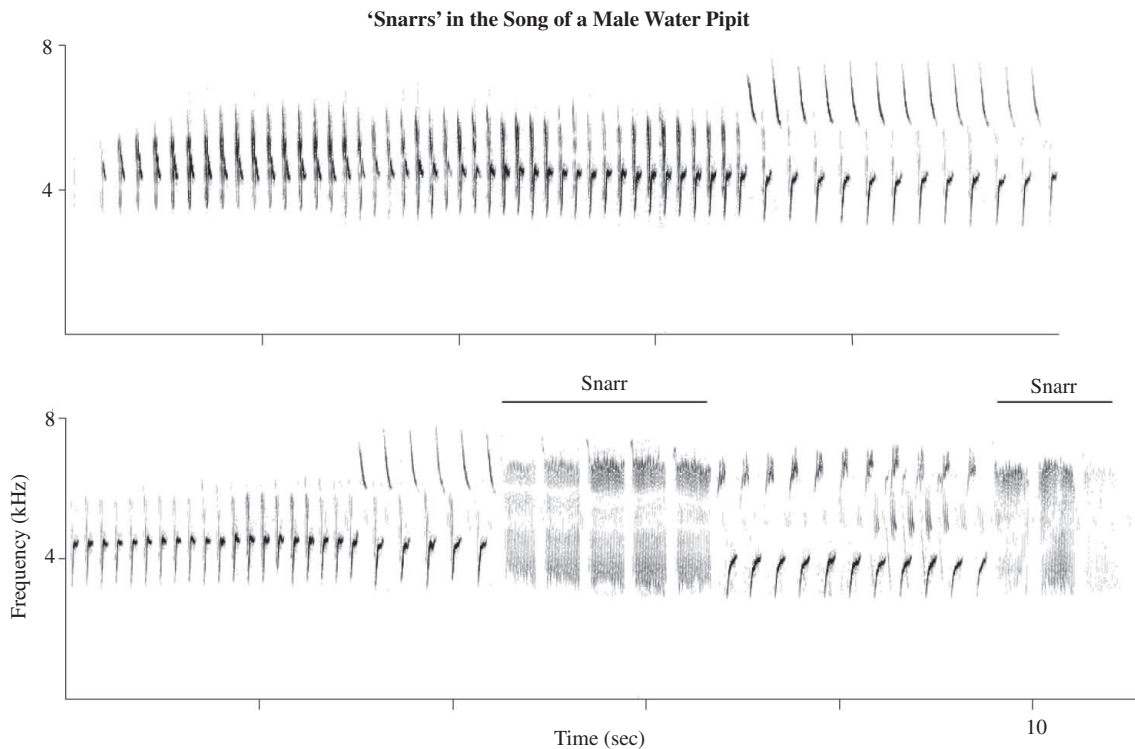
'Snarrs' in the Song of a Male Water Pipit

Figure 2.4 Water pipit songs, the bottom one with a 'snarr' note.

Blackbird Song

High intensity song

(A)

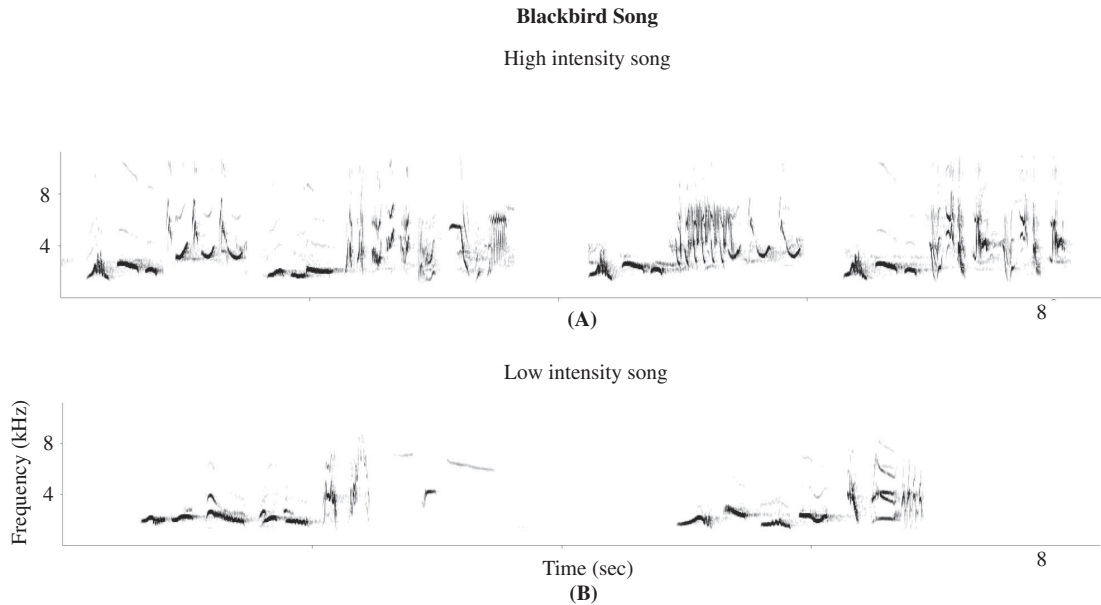Low intensity song

Time (sec)
(B)

Figure 2.5 European blackbird songs. **(A)** High intensity song used in aggressive situations; **(B)** low intensity song, which is slower, has longer motifs, shorter twitters and is often somewhat quieter than high intensity song. From Dabelsteen & Pedersen 1990.
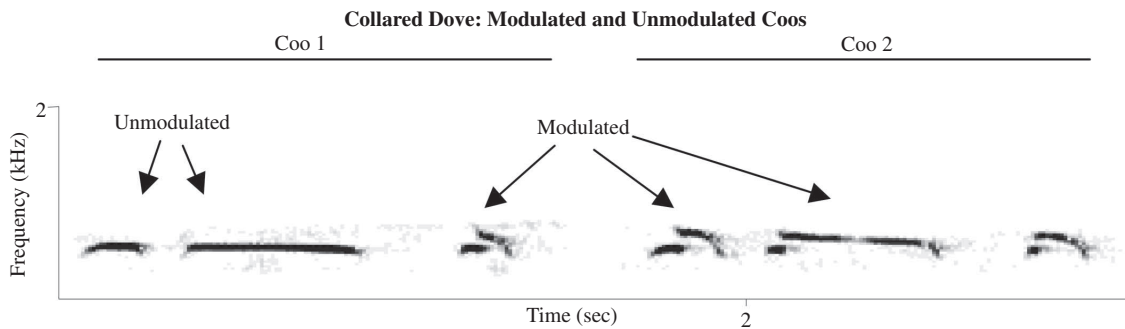
Collared Dove: Modulated and Unmodulated Coos

Coo 1   Coo 2

Time (sec)

Figure 2.6 Male collared doves produce modulated and unmodulated coo elements. The left coo has two unmodulated elements and a third modulated one. The right coo consists of three modulated elements. From Slabbekoorn & ten Cate 1997.

Song Repertoires and Complexity

There are two types of repertoires: (1) a *song repertoire,* where a male sings several different song types but individual song types do not vary much; (2) a *syllable repertoire*, where a number of syllables are recombined to produce different songs (**Fig. 2.7**). In the case of song repertoires a male may produce one version of his song several times before switching to a new type (eventual variation), or he may switch types after every song (immediate variation). Repertoires have often been studied in the context of female choice, but less frequently when it comes to male–male competition. However, in great tits and red-winged blackbirds, speaker replacement experiments show that intruders are less likely to intrude into territories where males have larger repertoires (Krebs et al. 1978; Yasukawa 1981a).
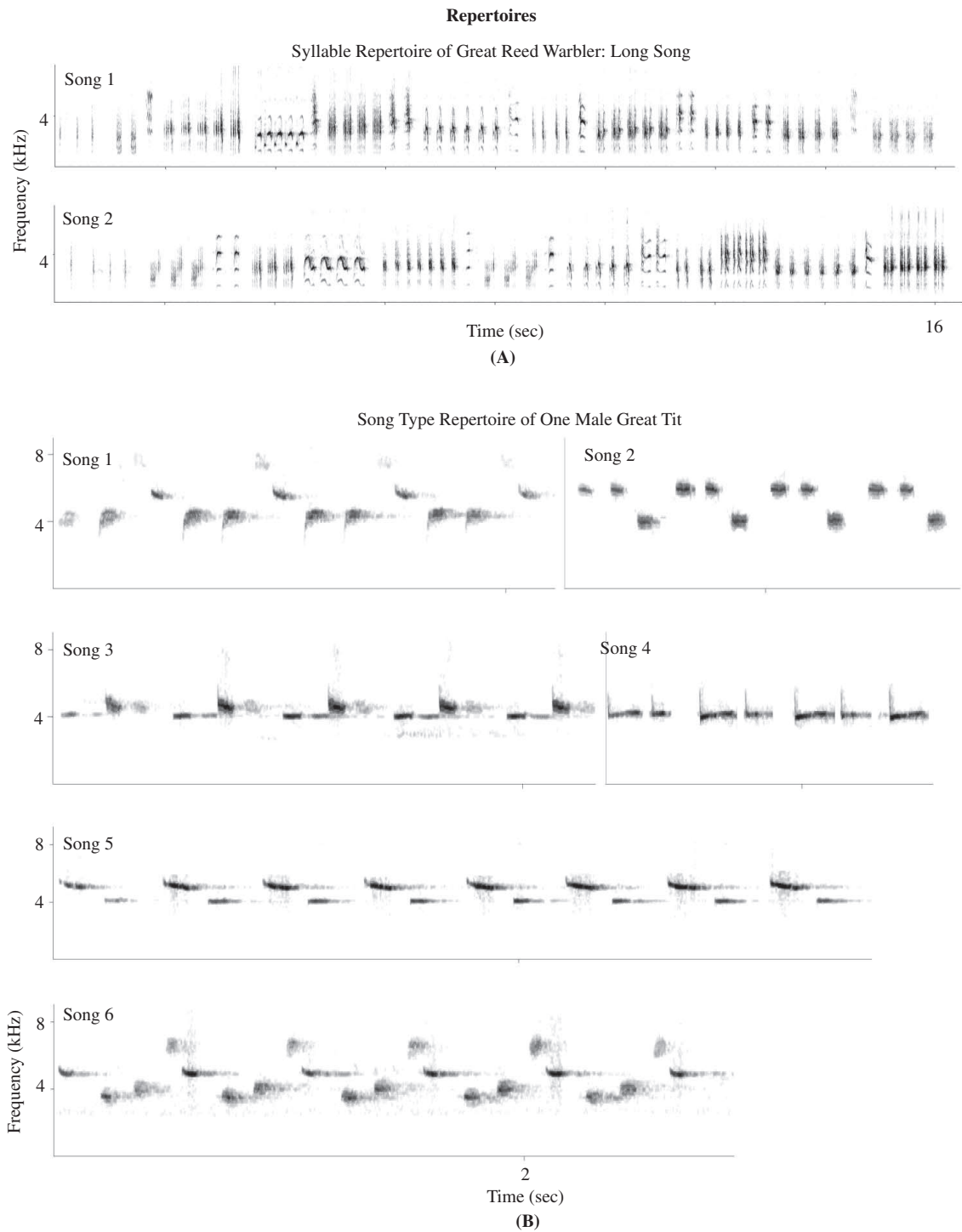
Repertoires

Syllable Repertoire of Great Reed Warbler: Long Song

(A)

Song Type Repertoire of One Male Great Tit

(B)

Figure 2.7 Examples of the two main types of song repertoire, **(A)** a syllable repertoire: a great reed warbler long song; **(B)** a song type repertoire: a great tit.

The success of males with larger song repertoires could occur because intruders habituate to song types (Searcy et al. 1994). If a male switches between songs in his repertoire, the response of the receiver increases in strength after each switch. Thus, a repertoire may be a way of maintaining a response. The magnitude of the recovery of the aggressive response depends upon the similarity of the following song type, and similar song types, even from different individuals, appear to be classed together by the receiver. Interestingly, males treat two different song types from the same individual's repertoire as if they were from different individuals, at least initially. It was suggested that repertoires evolved so that males could fool rivals into believing that there are multiple opponents, although this suggestion was subsequently disproved (Krebs 1977a; Yasukawa 1981a).

In European starlings a complex song, with a large syllable repertoire, is a more effective deterrent to intruders at the nest box (Mountjoy & Lemon 1991), and there is a correlation between repertoire size and the probability of winning encounters (Eens 1997). In a study of song sparrows, song repertoire size correlated with territory tenure and reproductive success (Hiebert et al. 1989). Males with large repertoires acquired a territory more quickly and survived for longer. Why these males with larger repertoires survive longer and are more successful in defending a territory is not known, but the increased survivorship implies that they are in better condition. In some species males learn new songs or syllables every year resulting in an increased repertoire size with age, as in starlings and sedge warblers. It is thus possible that males with larger repertoires are more successful at maintaining territories, not because they have more complex song, but simply because they are older, more experienced, and in better condition, as indicated by their increased survivorship.

Male Louisiana waterthrushes respond to increased aggression from rivals with more complex songs than those used in routine territorial advertisement (Smith & Smith 1996).

However, great reed warblers (**CD # —**), and reed warblers, produce shorter, less complex songs in encounters with other males (Catchpole 1983), as do some other species. Clearly, species differ in whether less or more complex songs are used in aggressive encounters, indicating that the role of repertoire size in male competition is not a simple one.

Although a correlation between repertoire size and reproductive success has been found in several species, this is often due to female choice, not male–male competition. It is more likely that female choice drives the evolution of repertoires, which have then been co-opted in some species, for use in competition between males. The reasons why repertoires may be a good indicator of male fitness will therefore be discussed in more detail later when addressing female choice (see p. **000**).

Song Matching

Song matching occurs when one bird responds to another by singing either the same song (song type matching), or by singing a song that is shared by the two birds but is not being sung at that moment (repertoire matching; **Box 3**, p. 52). Song matching interactions have been studied both by conventional and by interactive playbacks (McGregor et al. 1992), when the experimenter responds to the territory owner with either matching or nonmatching songs. This technique has greatly facilitated the study of dyadic interactions between males, and the effects of both song matching and song overlapping.

It is likely that song matching of both types is a conventional signal (Vehrencamp 2001; see p. **000**). Either matching or nonmatching could indicate a potential aggressive response. Both individuals know their own willingness or ability to fight but, unless they are familiar, not that of their opponent. A cheat would always signal that he is willing to fight so as to scare off rivals. However, some rivals will not be intimidated and these are likely to be the most aggressive. Therefore, the cheat will suffer a cost if his bluff is called by an aggressive opponent. The best strategy is for the signal given to correlate

BOX 3

BROADCAST SONG REPELS MALES AND ATTRACTS FEMALES: REPERTOIRE EFFECTS

The defense of territory is thought to be the principal function of song in communication between males. The most direct test of this function is a 'speaker replacement experiment,' in which males are removed from their territories and replaced with loudspeakers, from which the song of the species under study is broadcast. Intrusion by other males onto speaker-occupied territories is monitored and compared to intrusion onto control territories, either left vacant after the owners have been removed or occupied by loudspeakers playing a control sound such as white noise. This design was pioneered by Göransson et al. (1974) with thrush nightingales, and used subsequently with great tits (Krebs 1977b; Krebs et al. 1978), red-winged blackbirds (Yasukawa 1981a, b), white-throated sparrows (Falls 1988), and song sparrows (Nowicki et al. 1998b). In all cases, intrusion was delayed or less frequent on the territories defended by song than in control territories. Yasukawa's study on red-winged blackbirds is particularly important because he demonstrated not only that song keeps intruders out but that a repertoire of song types is more effective in repelling intruders than is a single song type (see below).

A similar experimental design has been important in demonstrating one of the principal functions of song in male–female communication – the attraction of females to the male and his territory. Here song is broadcast from vacant areas, and visitation rates of females are compared with areas where either no stimulus or a neutral stimulus is broadcast. This design has been applied mainly to hole-nesting species; nestboxes provide convenient focal points for observation of female visits. It was pioneered by Eriksson and Wallin (1986) with pied and collared flycatchers, and then applied to European starlings by Mountjoy and Lemon (1991), to house wrens by Johnson and Searcy (1996), and to hoopoes by Martin-Vivaldi et al. (2000). In all cases, more unmated females were attracted by song playback than by controls, though whether repertoires are more attractive to females has yet to be directly investigated.

William A. Searcy & Stephen Nowicki
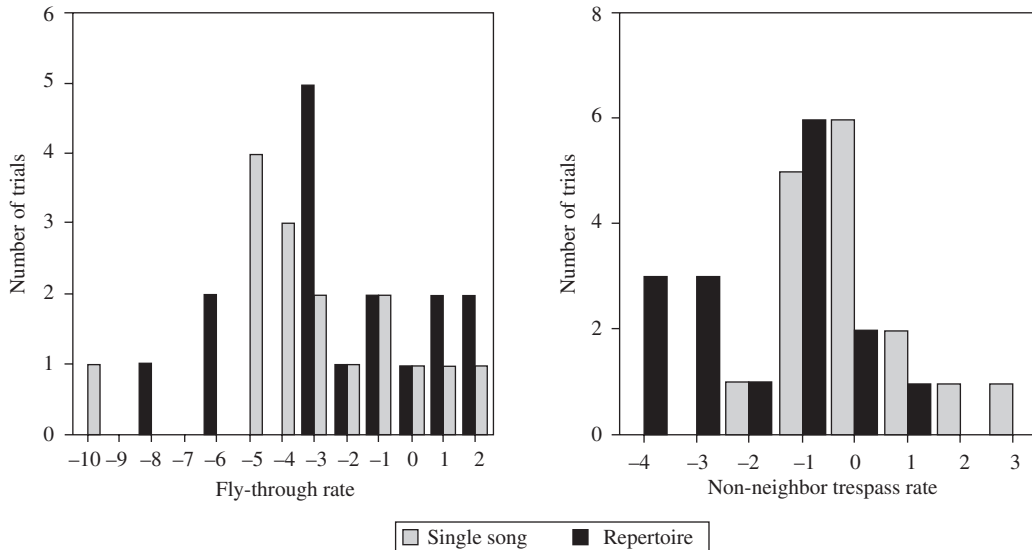
Fly-through rates and non-neighbor trespass rates of red-winged blackbirds were reduced in speaker-occupied territories (Yasukawa 1981a, b). Rates are shown relative to controls (experimental rate minus control rate); negative values indicate a decrease during playback. Playback of both single song types and repertoires of eight song types reduced fly-through rates, whereas only repertoire playbacks reduced non-neighbor trespass rates.

reasonably well with an individual's probability of retaliating. Individuals pay attention to whether rivals match or not, because they gain useful information from the signal. In general, when contestants are equal in ability, fighting is more likely as the outcome cannot be decided by recourse to the signal alone. If conventional signals are indeed arbitrary, there should be species in which both matching and nonmatching is the aggressive signal. So far, only in one out of ten or so studies, on the bobolink, is there evidence that a nonmatching signal is used (Capp & Searcy 1991).

Male song sparrows may respond by repertoire matching in singing interactions with neighbors. It is assumed that repertoire matching indicates to the neighbor that they are recognized, or that the responder is indeed the neighbor (Beecher et al. 1996). It does not appear to be a very aggressive signal, but is more aggressive than singing a nonmatching song. Interestingly, male song sparrows who do not share many songs with a neighbor, and therefore cannot engage in repertoire matching, suffer more aggressive encounters with neighbors (Wilson et al. 2000; Wilson & Vehrencamp 2001). Thus, repertoire sharers are able to communicate more effectively than nonsong sharers who must resort to direct confrontation (Vehrencamp 2001). Song sparrows converge on songs of neighbors after dispersal, perhaps so that they can perform repertoire matching with neighbors (Beecher et al. 1996). Males responded by singing a song shared with the neighbor in 87% of playbacks. To match repertoire the male song sparrow needs to know beforehand what songs they both share. Therefore, in the case of repertoire matching, a shared history is a necessity, but not for song type matching. Neighbors may be responded to in a less threatening way because they are less of a threat than floaters–the 'dear enemy' effect (Falls 1982). Unlike floaters, neighbors already have a territory, although of course some neighbors may be looking to expand. Neighbors are more of a threat at the start of the breeding season when territories are being established.

Song type matching is associated with escalated encounters in early season territory establishment between neighbors, and at all times of the season with intruders, and is associated with subsequent approach in several species including chaffinches (Hinde 1958), great tits (McGregor et al. 1992), cardinals (Lemon 1974), and song sparrows (Nielsen & Vehrencamp 1995). Territorial males tend to match song type in response to unknown individuals and this appears to be a signal of potential escalation (Krebs et al. 1981). The wood thrush avoids matching intruder playback stimuli (Whitney & Miller 1983), perhaps because the stimulus is too strong. Song type matching is clearly a signal of aggressive intention in the song sparrow. Males that match song types follow up with more aggressive responses and they respond more aggressively to signals that match their own song type (Vehrencamp 2001).

Territorial male great tits perform song type matching duels with rivals, and matching indicates that a direct attack may follow (**CD # —**). However, because the degree of similarity of the 'intruder' song to those of the territory owner is important in determining whether a song is type-matched or not, neighbors are song-matched more often than strangers (Falls et al. 1982). This is unexpected, as matching is thought to indicate potential escalation and usually fights are less common between neighbors. However, neighbors are more easily matched by chance as well as by design, and if the effect of overall song similarity is controlled for, strangers are matched more often than neighbors (**Fig. 2.8**). The same was found to be true in corn buntings. However, western meadowlarks match strangers' songs, but not those of neighbors (Falls 1985), without any need to control for similarity (**Fig. 2.9**).

It has been argued that song matching is a conventional signal, and does not reflect male characteristics related to fighting ability or motivation. However, there is a counterargument: matching may actually indicate something about male quality; more specifically, the number of songs you share with your neighbor may indicate
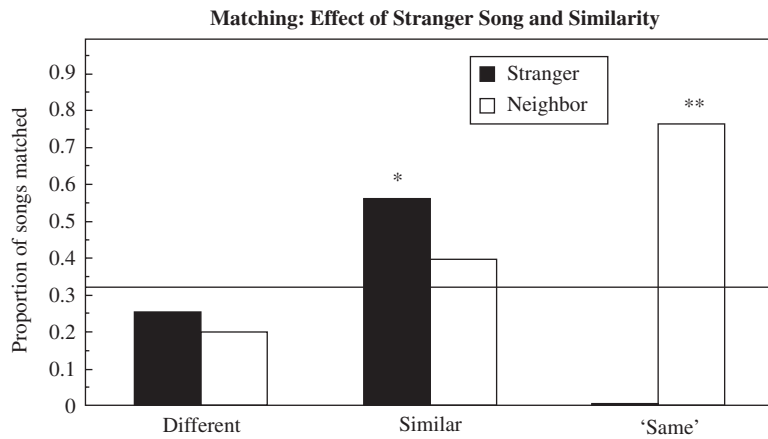
Matching: Effect of Stranger Song and Similarity

Figure 2.8 The proportion of songs matched in response to playback stimuli differing in the degree of similarity and type. Great tits are more likely to match songs to strangers when similarity of song types is taken into account (from Falls et al. 1982). *P < 0.05, **P < 0.01, significance above the line showing the chance level of matching.
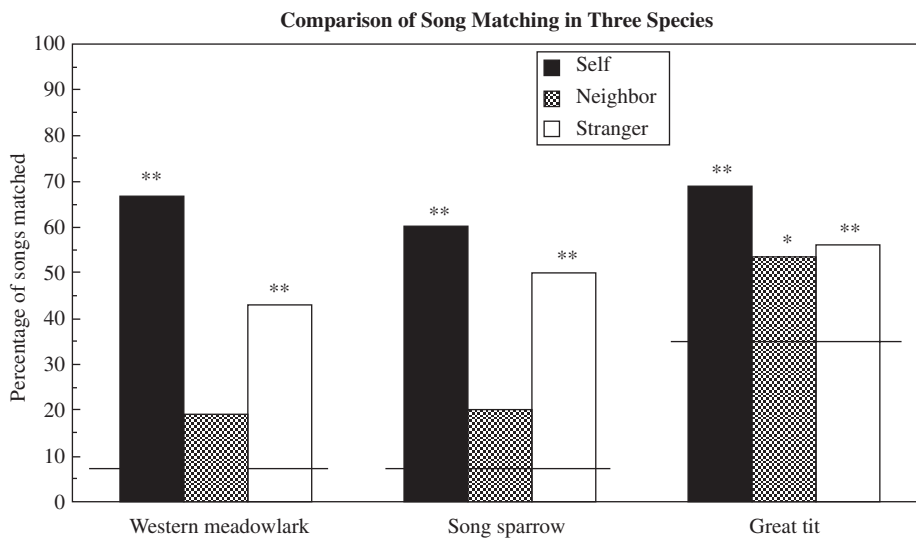
Comparison of Song Matching in Three Species

Figure 2.9 Song matching rates in response to self, neighbor, and stranger songs for three species. The lines represent chance levels of matching. *P < 0.05, **P < 0.01 – significance above chance. The data are for meadowlarks (Falls 1985), song sparrows (Stoddard et al. 1992), and great tits (Falls 1982).

quality. You are more likely to be able to match to neighbors or strangers if you have a larger repertoire. Larger repertoires are associated with increased age, and perhaps condition. Extensive song sharing with neighbors may also indicate you did not disperse far from your song tutor and natal area. Perhaps males who have to travel further to obtain a territory are of lower quality, or are less successful due to their lack of experience in that habitat. By this argument, the degree of song sharing with a neighbor, and thus the ability to song match, is related to dispersal distance and repertoire size. If a male song sparrow does not share many songs with his neighbors he suffers

the consequence of having to fight more often with them (Vehrencamp 2001). In indigo buntings, matching has consequences for reproductive success. Males that match neighbors are more successful breeders, and individuals that match are those that have remained in their natal area (Payne 1982). Thus, whether song matching is a conventional signal or not is not clear.

Overlapping Songs

Birds can time their singing to overlap with that of another bird. Such overlapping appears to be a signal of readiness to escalate contests (Dabelsteen et al. 1996, 1997; Hultsch & Todt 1982). As with song matching, overlapping will depend to some extent on the behavior of both overlapper and the singer being overlapped. Overlapping, extensively studied in nightingales (see Chapter 3), occurs particularly in disputes over territories (Hultsch & Todt 1982); it appears to be aversive as males either avoid posts on which their song is overlapped (Todt 1981) or adjust their singing to avoid being overlapped (Hultsch & Todt 1982).

Nightingales also respond more strongly to an individual they have heard overlapping other males, compared to an individual they have heard being overlapped (**Fig. 2.10**). This implies that eavesdroppers use information gained from listening to dyadic interactions and that overlappers are apparently judged to be a greater threat (Naguib & Todt 1997). Birds also use their own direct experience with an individual to determine their interactive strategy. If a male generally overlaps them, they are more likely to respond strongly even when the individual is not overlapping in that particular bout. Individual nightingales have a consistent tendency to be overlappers or nonoverlappers (Naguib 1999).

Overlapping is also an aggressive signal in great tits (Dabelsteen et al. 1996), European robins (Brindley 1991; Dabelsteen et al. 1997), and blackbirds (Wolfgramm & Todt 1982). Overlapping is likely to be a conventional signal; it is hard to see how overlapping is costly to the overlapper in terms of energy output. However,

an overlapper may reduce the amount of information that the rival can signal, thus reducing its efficiency (see Chapter 3).

Song Switching and Singing Rate

Birds with a song type repertoire often appear to use the rate of change to a new song type as a graded indicator of potential aggressiveness. Switching among song types has been argued to reduce habituation (Falls & D'Agincourt 1982), deceive intruders (Krebs 1977a), or reduce exhaustion of the vocal muscles (Lambrechts & Dhondt 1988). Some species use high switching rate as the default nonaggressive signal and reduce switching in the context of aggressive encounters, whereas in other species males increase their switching rate in aggressive encounters (Vehrencamp 2000). Which behavior occurs probably depends upon its normal, non-aggressive singing style. Species that switch song types relatively often may be more likely to reduce switching rate in territorial encounters. Species that switch less often may be more likely to increase switching rate in aggressive encounters. For example, in the song sparrow an increase in switching rate is associated with subsequent aggressive approaches, and receivers approach a switching stimulus more aggressively (Stoddard et al. 1988). The same is true for cardinals, meadowlarks, and Carolina wrens (Vehrencamp 2000). However, in red-winged blackbirds, banded wrens, and dunnocks the switching rate is decreased in territorial defense situations. In addition, dunnocks increase switching when males interact with females (Langmore 1997; **Fig. 2.11**).

Switching at a high rate does not appear to have a direct cost, although there is a potential cost of retaliation, namely, a stronger approach to individuals that switch at a high rate (Nielsen & Vehrencamp 1995), at least in some species. However, in other species the retaliation cost is in response to a lower switching rate. Thus, there is no consistent rule about whether high or low switching rates are aggressive.

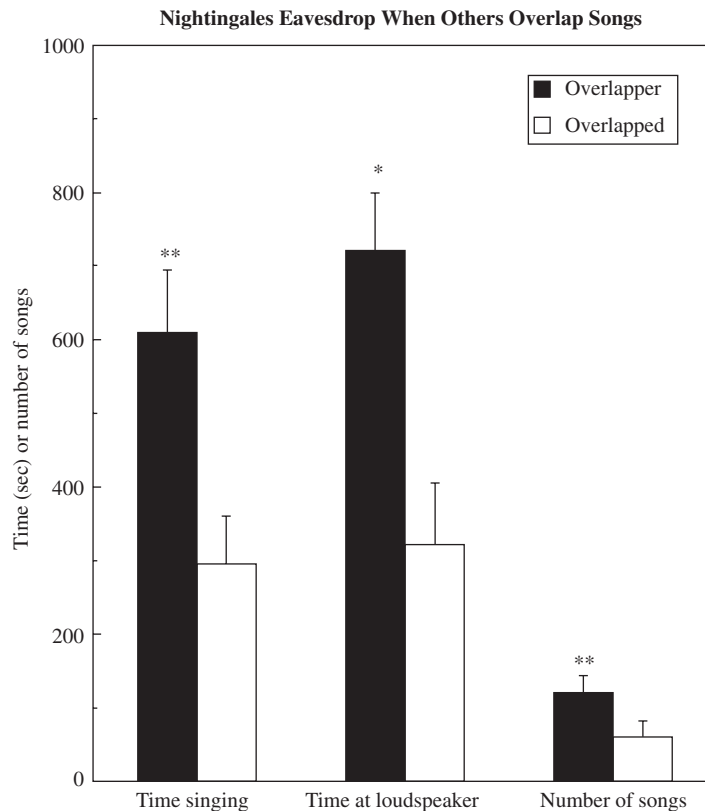An increase in the rate of singing, with more

Nightingales Eavesdrop When Others Overlap Songs

Figure 2.10 Nightingale males respond more strongly to a male they have heard overlapping songs, than to a male they have heard being overlapped. The data show means (+SE) of response measures of males in a two-speaker playback experiment.*P < 0.05, **P < 0.01. From Naguib & Todt 1997.

songs produced or songs produced at a higher rate, is more likely than the rate of switching to be energetically costly, and an increase in song rate is observed in aggressive interactions in some species. In the song sparrow (Kramer et al. 1985) males increase their singing rate in response to playback of intruder stimuli. There are other birds in whom song rate increases in aggressive interactions, such as the great tit (Weary et al. 1988). Song rate changes are most likely to relate to the increase in arousal and aggressive motivation as an intruder approaches. Although song rate increases in the song sparrow during interactions with other males, other work suggests that matching repertoires and switching rate are used by this species for territorial defense. Given that song rate in song sparrows does not appear

to predict the outcome of fights (Bower 1999), it more likely to be a byproduct of increased excitation rather than an important aggressive signal in this species. In general, an increase in song rate appears to be a signal used less by males to assess rivals than by females to assess potential mates.

We thus find that the diversity of the song parameters that are important in territorial interactions is remarkable (**Table 2.1**). In some species song type appears to be important, in others frequency modulations; in yet other species aggressive responses are determined by complex dyadic interactions sometimes involving the use of repertoires. These differences are likely to be due to ecological and social differences between species. In species with repertoires where there
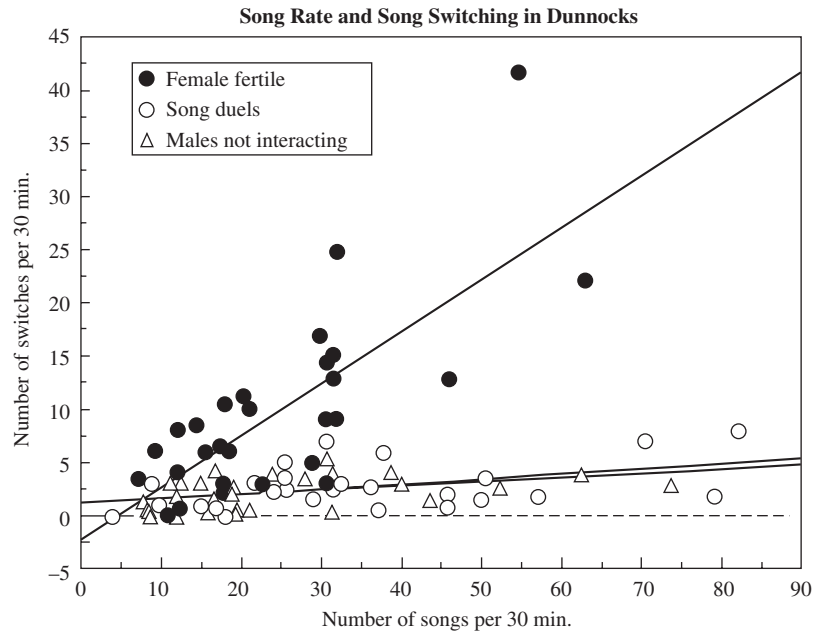
Figure 2.11   The numbers of songs uttered and the rate of song type switching by male dunnocks vary with the situation. ● During the females' fertile period. O When males engage in song duels. Δ When males are not interacting with other males. From Langmore 1997.

Table 2.1   Relationship between song characteristics and male–male competition. ↑ indicates an increase and ↓ indicates a decrease in a song characteristic with increasing male fighting ability, motivation, or attribute that is likely to be related to male fighting ability.

Song characteristic	Relationship between song characteristics and presumed male fighting ability, physical attribute, or motivation
Frequency	partridge ↓; chickadee ↑; barn swallow ↓; rooster ↑; collared dove ↑
Intensity	blackbird ↑; barn swallow ↑
Repertoire	great tit ↑; red-winged blackbird ↑; starling ↑; song sparrow ↑; Louisiana water thrush ↑; great reed warbler ↓; reed warbler ↓
Matching	bobolink ↓; chaffinch ↑; great tit ↑; cardinal ↑; song sparrow ↑; wood thrush ↑; corn bunting ↑; western meadowlark ↑; indigo bunting ↑
Overlapping	nightingale ↑; great tit ↑; robin ↑; blackbird ↑
Switching	song sparrow ↑; cardinal ↑; meadowlark ↑; Carolina wren ↑; yellow warbler ↑; chestnut-sided warbler ↑; redstart ↑; red-winged blackbird ↓; dunnock ↓; banded wren ↓
Song rate	great tit ↑; song sparrow ↑; red-winged blackbird ↑; dunnock↑; banded wren ↓

is song sharing between neighbors you are likely to find repertoire matching. In species with very large repertoires song matching may be difficult, but overlapping or switching is certainly possible. Switching is, of course, only possible if a species possesses a song repertoire. Simple song characteristics such as frequency changes or increases in intensity or rate may be used more often in species that lack repertoires or have simple songs. Birds that can be seen singing from song posts may be subject to different evolutionary pressures than those who sing from cover, and are less subject to predation or retaliation by opponents. However, in the best-

studied species it appears that multiple signals are used in male competition. Male song sparrows use a variety of signals to indicate the likelihood of attack; the same is true for great tits, which appear to use matching repertoires, song rate, and overlapping as signals in aggressive encounters. Whether the same is true for less well-studied species remains to be seen.

Different species may use different song parameters in male–male interactions, and the same parameter may mean different things. In some species, males produce simpler songs in territorial interactions while others increase song complexity (Smith & Smith 1996; Catchpole 1983). Clearly, the meaning of song complexity and song repertoire size vary with the species and under different circumstances. So, although we think we can make sensible predictions about which parameters indicate competitive ability or aggressive potential in males, the fact that species differ in the combination of signals used to interact with rivals suggest that our predictions are not always correct. These are among the many fascinating challenges that confront us in functional studies of birdsong.

MATE CHOICE: VOCAL FLIRTING

In many birds females choose mates on the basis of differences in song (Searcy 1992a). What are the benefits a female might obtain from choosing a particular male over another? If the choice is active rather than random, the time spent assessing and energy used traveling between potential mates will impose some cost. The usual assumption is that females should choose to mate with a male that allows her to have more surviving offspring, by providing 'direct' benefits. For example, a male in good condition may feed young at a higher rate, increasing the female's reproductive success. Females who are mated to a male on a territory with good food resources are likely to have heavier, healthier offspring. However, the idea that females may choose a male, when receiving nothing more than sperm from him, was controversial for many years. It

was accepted that some males could be more fertile than others, in which case a female should choose the most fertile mate, with a potential direct benefit of higher fecundity for her. But why should females choose between males if none of them will provide care for the offspring, a territory from which she can obtain food for the offspring, or a well-hidden nest site?

The answer is that a female can gain 'indirect' benefits from mating with certain males; although she gains no material benefit from them, her offspring may do so. Some males may have 'good genes' which are passed on to the offspring who are then more likely to survive and reproduce. For example, good genes could increase resistance to common parasites (Hamilton & Zuk 1982). Another potential indirect benefit first spelled out in Fisher's runaway hypothesis is sometimes known as the 'sexy son' theory (Fisher 1930). If a female is attracted to a particular male, perhaps because he has an especially attractive color patch, then her daughters may inherit her preference bias and her sons may have brighter patches. Having the preferred coloration, they are more likely to be chosen. A female choosing a preferred male has sons who are also preferred, and daughters who will have preferred sons. Choosy females have sexier sons, and so more grandchildren. The idea that a female may have a bias towards a male with a particular ornament, because of a bias in her perceptual or recognition system, is known as 'sensory bias' (Ryan & Rand 1993). In the case of song we can imagine that a male with a song that is close in frequency to an alarm call, or a male whose song contains a note in the most sensitive part of the hearing range may be more stimulating and thus preferred over other males. A 'sensory bias' may initiate the Fisher runaway process. In the case of sensory bias and the Fisher runaway process, there may be no difference in the fitness, condition, or quality of preferred and non-preferred males. When favored males pass on either good genes or direct benefits, we expect to be able to measure some difference, such as body mass, parasite load or territory quality, between preferred and nonpreferred males.

The division between direct and indirect benefits is not always so simple; for example, a male that is free of parasites will not infect the female (direct benefit), but he may also have superior resistance genes that are passed on to the offspring (indirect benefit). A high quality territory is a direct benefit, but males with 'good genes' may be more likely to obtain such a territory through defeating rivals. The fact that the male has a good territory indicates that he is likely to have more food and will also be in better condition. So, in addition to access to more resources on the territory, the female will also have a high quality mate in good condition. Song may also indicate more subtle differences in a male's suitability as a mate. For example, are the male and female genetically compatible, within the same species and population? Here, both the male and female benefit from mating with the right species so there is no conflict in male and female strategies. We shall see how some of these factors may play a role in making decisions regarding mate choice.

How can different song characteristics indicate that a male is of high quality in terms of providing direct or indirect benefits to the female; which song parameters might females use to choose among males differing in the benefits they may provide? It is clear that females sometimes choose males on the basis of differences in plumage characteristics that reflect mate quality. For example, female widow birds prefer males with longer tails, and female house finches prefer males with a deeper red coloration (Andersson 1989; Hill 1990, 1991). Females often appear to prefer males with more exaggerated ornaments; could the same be true for song? We can presume that degree of exaggeration is a useful choice criterion, because enhanced ornaments tend to be more expensive to produce. Therefore, males who are in good condition, of a higher quality, or have good territories are able to 'afford' larger or more conspicuous ornaments (Zahavi 1975; Grafen 1991).

There are song characteristics that can serve as costly ornaments, serving to differentiate between males of differing quality. Females will be selected to ignore, or devalue, any signal where

a low quality male could fake the signal of a high quality male; a costly signal is one way of ensuring that males are honest. Costly signals are likely to occur when females are choosing for direct benefits or good genes. Lower costs are likely to be found in the case of choice for compatible males, or preferences due to sensory biases. Conventional signals are less likely to be important for female choice. This is not to say that a female may not choose a male whose dominance is maintained through the use of conventional signaling. The male may even be chosen on the basis of the conventional signal. The difference is that the female herself does not impose the receiver-dependent costs, but simply observes the outcome of his competitive interactions with other males (West et al. 1981).

Studies on female preference involve a number of techniques, generally quite different from those applied to the study of male responses to song (Searcy 1992a). In the field or in aviaries, different songs may be played from nest boxes to influence which is occupied first by females. Females may be implanted with estradiol, which makes them more sexually receptive. They are then played songs from different males or different song types, and the number of copulation solicitation displays to each is counted as a measure of preference for that song. Field observations can reveal which males are mated first, provided that there is control for the effects of other variables such as territory quality (Searcy 1992a). Finally, a few studies have used operant conditioning techniques; females press a button or sit on a particular perch to hear a song, and the song she chooses to hear more often is taken as a measure of preference (Collins 1999; Riebel & Slater 1998a). All preference studies strive to relate differences in song to variation in male characteristics. For example, if females prefer males with high song rates, do they then obtain a male with a good territory, with good genes, or both?

Specific Song Structure

An interesting study on female song preferences in canaries showed that males can possess what are

called 'sexy syllables'(**Box 4,** p. 61; **CD #**—). Female domestic canaries prefer songs that they had been exposed to when young but, in one particular strain, songs of a certain type were preferred whether they had been heard earlier or not; even isolated females preferred these 'sexy' song types (Vallet & Kreutzer 1995; Kreutzer et al. 1996; Nagle & Kreutzer 1997). The essential components are notes with abrupt frequency falls and short inter-note intervals. The preference may be due to a sensory bias (Ryan & Rand 1993); perhaps that note fits precisely the acoustic sensitivity of females. However, this note also requires very precise coordination of both the left and right syrinx for production, and could be an indicator of male quality (see Chapter 9). On the other hand, the female preference could be a carry-over from the wild ancestors. Canary song has been highly modified during domestication. New note types have undoubtedly been added by selective breeding and tutoring, and females may not have evolved responsiveness to them. An obvious question is: are 'sexy syllables' part of the original note repertoire of wild canaries, perhaps becoming less frequent after domestication and selective breeding for song quality? 'Sexy syllables' are not all that melodious to the ears of canary fanciers (Box 39, p. 302).

Preference for high quality singing skills has been found recently in the swamp sparrow, in whom females favor certain kinds of trilled notes (Ballentine et al. 2004). There is a trade-off between the rate of a trill and the frequency range of the component notes. Males that produce fast trills are constrained to a narrow frequency bandwidth, so that broad frequency trills are produced at a low rate. However, some males are nearer the performance limits than others, indicating a high quality vocal performance ability. Females give more copulation solicitation displays to such a song. This shows that females use a vocal performance indicator, relating to the trill–bandwidth trade-off, as a choice criterion; whether this indicates differences in male quality is not yet clear.

Female brown-headed cowbirds display a preference for a specific song structure that reflects male dominance, and they prefer the song produced by isolated males (West et al. 1981). It appears that differences in song are determined by the outcome of male interactions. Only dominant males are able to maintain production of potent songs, because males punish rivals producing potent songs, which have a different frequency pattern from nonpotent songs. The fact that isolated males have potent songs is thus easily explained; isolated males are never attacked. This song type is, therefore, a good indicator of the number of fights lost and won, and females may be using it to choose a dominant male. This species is a brood parasite, and the male only provides his genes to the female, but a female may benefit from mating with a male with higher quality genes. A dominant male will not help protect the chicks directly, but dominance may be related to genetic quality, inherited in turn by the offspring. Or perhaps offspring of dominant males are more likely to become dominant themselves and are thus preferred by females because they will have sexy potent songs.

Although it is not yet clear what benefits, if any, females obtain from choosing males with specific note types, this relatively new area of study brings together studies on sound production and mate choice, and is likely to generate more exciting findings in the near future.

Song Repertoires

Measures of song repertoire size are based on the number of different syllables that constitute a song, or the number of different song types. Either way, there are many indications that females prefer to mate with males who have larger repertoires, or more complex songs (e.g. great tits, McGregor et al. 1981; Lambrechts & Dhondt 1986; great reed warbler, Catchpole 1986; song sparrow, Hiebert et al. 1989; aquatic warblers, Catchpole & Leisler 1996), although direct experimental proof is still lacking (see Chapter 4, p. **000**). Furthermore, what benefits females obtain is unclear. The most common correlate of repertoire size is male age. Males of some species make yearly additions to their

BOX 4

FEMALE CANARIES ARE ESPECIALLY RESPONSIVE TO 'SEXY' SONGS

In most songbirds it is unusual to find a song phrase composed of a string of repeated syllables that have both a high repetition rate and a wide frequency range (Podos 1996). It may be that motor constraints on the syrinx and its neural controls impose limits, because producing such a song phrase requires unusual abilities or more energy (Suthers 1999a; see Chapter 9). Depending on the strain, male domestic canaries mostly use their left syrinx during song, but they use their right syrinx to expand the range into higher frequencies. These aspects of song production are controlled by the nervous system, and the lateralization of production of the different song parameters to the right and left sides extends from the periphery up into the brain (Hallé et al. 2003). The repertoire size of male common domestic canaries varies greatly, some singing less than ten different syllables and others more than thirty. Thus, some males can be regarded as virtuosos.

Experiments show that females prefer song with a structure that challenges the motor constraints on rate and frequency range; they favor song syllables with a high repetition rate and a wide frequency bandwidth (Vallet & Kreutzer 1995). The song structures are potent in evoking responses in the brain (Del Negro et al. 2000), and the actual mating preferences do not arise through learning (Nagle & Kreutzer 1997). Both trill rate and frequency bandwidth add to the higher response strength, and supernormal, artificially created combinations of the two characteristics beyond what naturally occurs, lead to the highest copulation solicitation display rates (Draganoiu et al. 2002). Further study is needed to distinguish whether the 'sexy' song phrases elicit more interest from the female because they are an honest fitness signal, or because they exploit a female sensory bias.

Although there is an innate component, the preferences of female canaries are also influenced by the songs that a female experiences when she is young (Nagle & Kreutzer 1997; Depraz et al. 2000); songs are effective in inducing copulation solicitation displays, but they do not stimulate other reproductive activities such as nest building or egg laying (Leboucher et al. 1998). For activities such as these, Kroodsma (1976) demonstrated that song diversity is more important than monotony. Also, female canaries are able to associate the male who is their mate with his particular song and do not confuse it with the song of another familiar male (Béguin et al. 1998). Thus, a female uses the different parameters of male song in various ways, depending on the phase of her reproductive cycle and her prior song experience, both as a young bird, and as an adult.

Michel Kreutzer

A Canary Song with a 'Sexy Phrase'

The 'Sexy Phrase'

Frequency (kHz)

Time (sec)
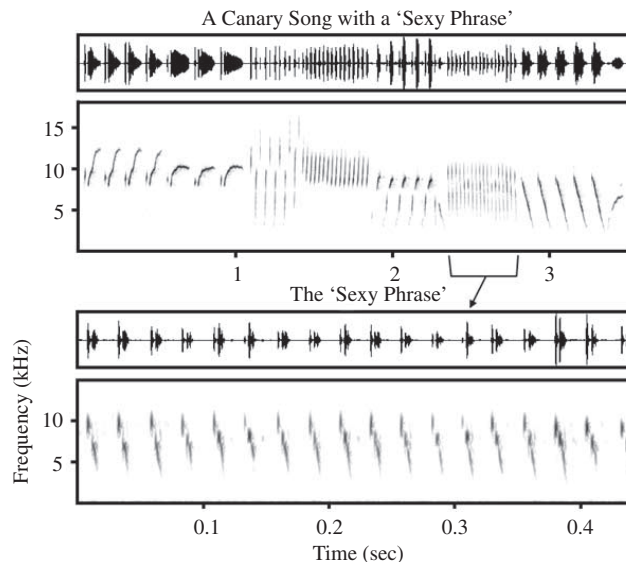
repertoire; therefore, the older the male the more songs he has learned. In the song sparrow, older males have larger repertoires (Hiebert et al. 1989), but the correlation is produced not by adult learning but by the attrition of males with smaller repertoires, who are more likely to die. A similar situation has been found in the willow warbler (Gil et al. 2001). In these cases repertoire size indicates the probability of a male surviving.

Older male pied flycatchers are in better condition and have more complex songs (Lampe & Espmark 1994). However, males with larger repertoires are less likely to survive than males with smaller repertoires from a particular year. There is still a correlation of repertoire size with age, because males learn new songs between breeding seasons but, within an age cohort, males with larger repertoires are less likely to survive. This reduced survivorship is in contrast to great tits (McGregor et al. 1981; Lambrechts & Dhondt 1986) and song sparrows (Hiebert et al. 1989), as already mentioned, where males with larger repertoires are more likely to survive. Lampe & Espmark speculate that testosterone may drive the increase in repertoire size across years. If this is so, males with larger repertoires may suffer the immune cost of increased levels of testosterone (Møller et al. 2000). Female pied flycatchers still prefer males with larger repertoires (Lampe & Sætre 1995). In aviary experiments, females preferred to build nests with males with more complex songs. Sætre et al. (1995) have shown that older males feed the young better than younger, less experienced males. So, female pied flycatchers choosing a male with a large repertoire obtain a male in good condition with greater breeding experience, but with a reduced probability of survival to the next year.

Older male starlings also have larger repertoires (**Fig. 2.12**), and males with larger repertoires are preferred as mates both in the field and in aviary experiments (Eens et al. 1991; **CD #—**). Other than a nest hole, male starlings do not defend a territory, so females gain no food resources. Exploring the role of repertoire size, Mountjoy and Lemon (1991) found that more complex songs deterred male starlings from

entering nest boxes, and that females were attracted to nest boxes defended by males with large repertoires (Mountjoy & Lemon 1996). Eens (1997) found that females prefer larger repertoires. Is repertoire size a signal to males or to females? Eens et al. (1993) found that males sang more songs and included more song types when presented with a female than with a male. Thus it appears that, in starlings, repertoire size functions as an attractor for females, but is also important in male competition.

Female great tits prefer males with three to five song types, rather than those with only one or two (**Figs. 2.7B & 2.13,** Baker et al. 1986). Great tits with larger repertoires survive better and, in general, are more successful breeders. This may be because they have better territories, but assessment of song is probably quicker and easier than a comprehensive assessment of territory quality. Why male great tits with larger repertoires obtain better territories is unclear, although speaker replacement experiments suggest that males with larger repertoires are better able to defend territories (Krebs 1977a). Here again, male competition and female choice are not easily separated. Indeed, in some species the correlation between repertoire size and male mating success disappears when territory quality is taken into account, as in red-winged blackbirds (Yasukawa et al. 1980). In this species, females appear to be assessing territory quality and choosing better territories directly, even though males on these territories do indeed have larger repertoires. However, female great tits do seem to base their choice on repertoire size, which may indicate both male and territory quality, rather than territory quality alone.

The sedge warbler is particularly well studied. In a field study, Catchpole (1980) showed that males with larger syllable repertoires attracted females earlier in the breeding season; also females display more to recordings of larger repertoires (Catchpole et al. 1984). Buchanan and Catchpole (1997) found that repertoire size is one of several cues used in mate choice, and that variability in the trait is important. Repertoire size varied from year to year and was always correlated with mating
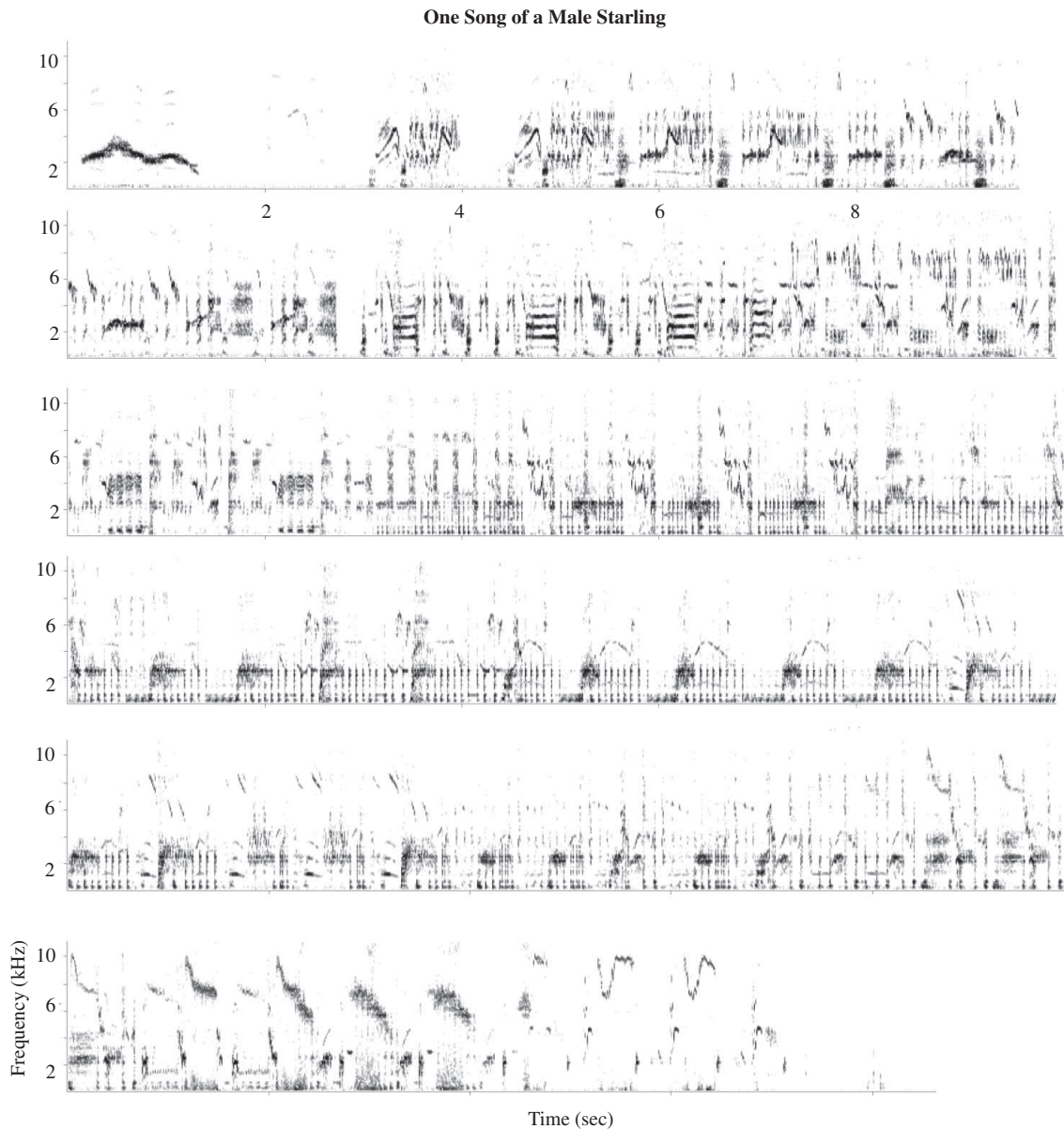
One Song of a Male Starling

Figure 2.12 A male starling song containing all of the basic syllable types and some heterospecific imitations. The male was singing in a nest box, while a prospecting female was in the vicinity (Eens 1997).

success, even when controlling for territory quality. As in other species, older males have larger repertoires. The most striking finding is that males infected with parasites have smaller repertoires (Buchanan et al. 1999). Therefore, females obtain parasite-free, older males by choosing males with larger repertoires. In a related species, the great reed warbler, repertoire size was correlated with the number of extra pair copulations. Female great reed warblers appear to base their choice of mate on repertoire size *and* territory quality. However, females who are
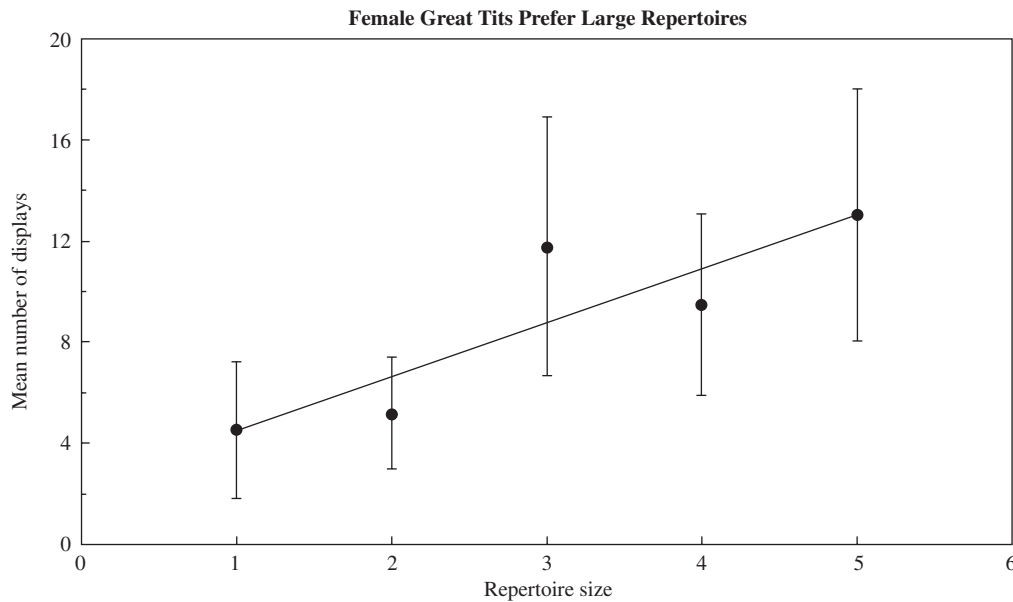
Figure 2.13   Mean number of copulation solicitation displays given by 11 female great tits as a function of male song repertoire size. One to two song types elicited a significantly smaller response than repertoires of three to five song types. From Baker et al. 1986.

paired choose to have extra pair copulations with males whose repertoires are larger than those of their partner (Hasselquist et al. 1996). The relative post-fledging survival of the young is correlated with the genetic father's repertoire size rather than the foster father's (**Figs. 2.14 & 2.7A**). Females thus obtain some kind of indirect genetic benefit from choosing to mate with males with larger repertoires (Hasselquist et al. 1996).

So far, it appears that males with larger repertoires are generally older, have fewer parasites, survive better, and have offspring that survive better. Thus, repertoire size does seem to indicate male quality, but how can it do this? It is not obvious why singing many different songs should be costly. However, if a male is parasitized or in poor condition he sings fewer songs, consistent with the idea that there is a cost. The larger repertoires of older males is usually assumed to reflect the time it takes to learn more songs. But in some species the number of songs a male sings is fixed in the first year or so; they do not learn more songs as they age, but males with smaller song repertoires die, thus

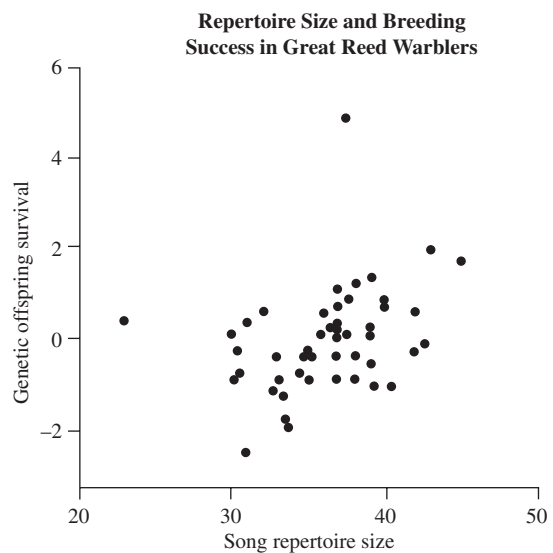producing the observed correlation between age and repertoire size.

Figure 2.14   Relative post-fledging survival of genetic offspring correlates with the standardized male song repertoire size in great reed warblers. From Hasselquist et al. 1996.

It has been suggested that there is a cost to learning a large number of songs in terms of the brain space needed to store them. The assumption is that males with larger repertoires have a larger area in the brain dedicated to song learning (the higher vocal center – HVC). Thus, repertoire size indicates a male's ability to bear the 'space costs' of having a large HVC. However, does repertoire size depend on HVC size and is it really costly? In general, species with larger repertoires have larger song system nuclei in their brain; and, in some species, individuals with more complex songs have larger song nuclei (see Chapter 8). Sedge warbler males with larger repertoires and more complex, longer songs have larger HVCs (Airey et al. 2000). However, although females appear to prefer males with larger repertoires (Buchanan & Catchpole 1997), as mentioned above, there is no difference between paired and unpaired males in their HVC size (Airey et al. 2000); thus female choice for repertoires is not selecting males with larger HVCs. Possibly there is a cost to maintenance of the song center (Gil & Gahr 2002). In the canary, some song system nuclei shrink outside the breeding season (see Chapter 8), suggesting that there may be a cost to its maintenance when not needed. However, it is hard to see why maintaining this area of the brain would increase energetic costs compared to all other active areas. An alternative explanation is that the cost may be developmental (Nowicki et al. 1998a). Birds who suffer early nutritional stress develop smaller song repertoires perhaps because they are deficient in the resources required to develop the song area of the brain, lack the energy to practice singing, or are too weak to pay attention to their song tutors. A nutritionally stressed bird would learn fewer songs as a youngster and, in those species where there is a fixed learning period, the male would have fewer songs for the rest of his life. It is known that defects in early nutrition can affect adult survival (Birkhead et al. 1999), so females should avoid males who have suffered physically when young. Nowicki et al. (2002a) recently tested whether females discriminate against males who learn their songs poorly, as is likely to happen if they have been exposed to nutritional stress. Experienced females preferred males who include a relatively high proportion of learned versus improvised material in their songs, and who copy the learned notes accurately, i.e. are good learners. This demonstrates that variation in learning abilities among males matters to females when choosing a mate. Females could use learning ability as an indicator of quality, assuming it indicates a history of developmental stress (Nowicki et al. 2002a; **Box 5,** p. 66).

Another possibility is that the cost is not energetic but a result of decreased immunocompetence. As mentioned for pied flycatchers (Lampe & Epsmark 1994), repertoires may be controlled to some extent by the male hormone testosterone. Testosterone has a suppressing effect on the immune system, so that a bird with higher levels has a less efficient immune system (Møller et al. 2000). That may be why, in the sedge warbler, males who are parasitized have smaller repertoires. Male testosterone levels decrease as the immune response necessary to fight off the parasites gets under way. The cost of a larger repertoire may thus lie in the hormones needed to develop it, not in learning or singing. Males will differ in their fitness, in the form of disease resistance, and in energy reserves, and thus in the immune system depression that they can bear (Gil & Gahr 2002). A fit male will have higher testosterone levels and still laugh off an infection, whereas a male in poor condition will need to put more of his energy into fighting it off. In either case testosterone levels, and also repertoires, are likely to decrease when a male is infected, but by a smaller degree in fitter males. The early nutrition and the immunosupressant hypotheses both presume that males with a larger repertoire are fitter and thus indicate the benefit a female receives from mating with males with larger repertoires. Males with a large repertoire have been healthy during development and are better able to bear the immunosupressant costs of testosterone. As yet, these ideas are still speculative, but are being addressed by current work (**Box 6,** p. 67).

BOX 5

THE QUALITY OF SONG LEARNING AFFECTS FEMALE PREFERENCES

It is well known that male song influences mating preferences in female songbirds, and many aspects of song are learned by imitation from other males of the same species. Females are more responsive to normal, learned songs than to those developed by a male in social isolation, and are completely unresponsive to the very abnormal songs of deaf males (Searcy et al. 1985; Searcy & Marler 1987; **B**). But the differences between the songs of wild birds, isolates, and deaf birds are gross, involving many different features. What about the finer details of songs that all qualify as normal for the species, and yet vary greatly from bird to bird? Do they influence female responsiveness? In the case of the learned details of song dialects, we know that females base their preferences on those same traits that are affected by learning (Baker et al. 1987b; Balaban 1988). Therefore, we speculated that how well a male learns his songs ought to affect female preferences; in other words females should prefer well learned over poorly learned songs. In the first direct test of this proposition, song sparrows were taken soon after hatching from a population in Hartstown, Pennsylvania, raised in the laboratory, and tape-tutored with songs recorded from the same population (Nowicki et al. 2002). Songs of the hand-reared males recorded at one year were divided into well-learned and poorly learned categories, based on quantitative comparisons with their tutor songs, drawn from the local population (**A**). We then presented these songs to adult female song sparrows from the same population, and measured the numbers of copulation solicitation displays they performed. First, we compared female responses to a set of 10 songs that had both a high proportion of copied notes (mean = 98%), and high note copying accuracy (mean spectrogram cross-correlation [SCC] = 0.69), and another set with a low proportion of copied notes (mean = 29%), and low note copy accuracy (mean SCC = 0.54). The females showed a strong, preferential response to the songs with high proportions of well-copied notes. Then we took a pool of songs, all with a high proportion of copied notes, and chose two subsets, one with high note copy accuracy (mean SCC = 0.71), and the other with low note copy accuracy (mean SCC = 0.59). Females responded more strongly to the songs with the more accurately copied notes, though the preference was weaker than in the first experiment. Evidently, as predicted, female song sparrows prefer well-learned to poorly learned songs.

William Searcy & Stephen Nowicki

Song Sparrow Songs
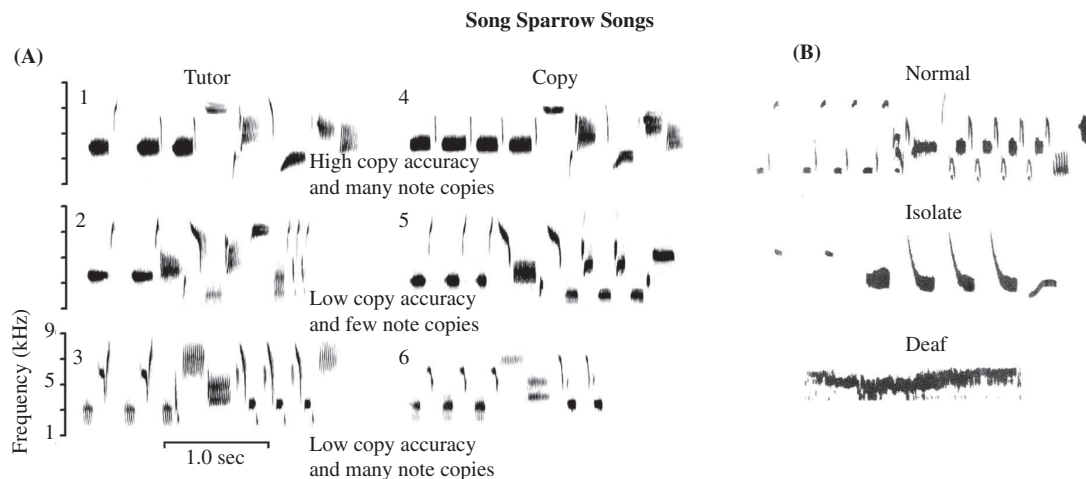
BOX 6

THE HOOTING OF TAWNY OWLS: STRUCTURE AND FUNCTION

The nocturnal tawny owl is highly vocal, giving a variety of calls, the most distinctive of which is the 'to-woo' hoot used to announce ownership of their territory. Tawny owls have individually distinctive hoots (**A**) and, with the aid of a computer, hoots of different birds can be distinguished, using the length of different call components with an accuracy of 99% (Galeotti & Pavan 1991; Appleby & Redpath 1997a). Moreover, their calls are consistent from year to year, so it is possible to monitor owl populations by comparing sonograms between years (Appleby 1995). The structure of owl calls was found to differ between populations (Appleby & Redpath 1997a), but neighbors had dissimilar calls, suggesting that they do not learn from each other. Owl calls did not appear to vary in relation to habitat (Appleby & Redpath 1997b) but, in an Italian study, owls living in woodland seemed to have lower pitched hoots than those living in farmland (Galeotti 1998). Playbacks showed that tawny owls recognize the calls of their neighbors, and exhibit a swifter and more aggressive response to stranger calls than to local territory holders, presumably because strangers represent more of a threat to their territory (Galleoti & Pavan 1993). Males and females often cooperate in defending a territory against an intruder. In playback experiments, females were more likely to respond to female than male calls in their territories, while males showed no distinction, except that they were more likely to respond aggressively to female calls if they had already bred successfully with their mate (Appleby et al. 1999). So, in addition to the territory, males seem to defend a reproductively valuable partner. There is also some evidence that hoots contain other information that may be useful to mates and competitors. Larger males were found to have lower frequency hoots (Appleby & Redpath 1997b). Furthermore, owls with more blood parasites responded more slowly to a challenge and they gave calls in which the highest frequency was lower, and the range of frequencies was smaller (Redpath et al. 2001; **B**). Thus, there is potential for individual owls to assess male parasite load from the speed of response and the structure of the call.

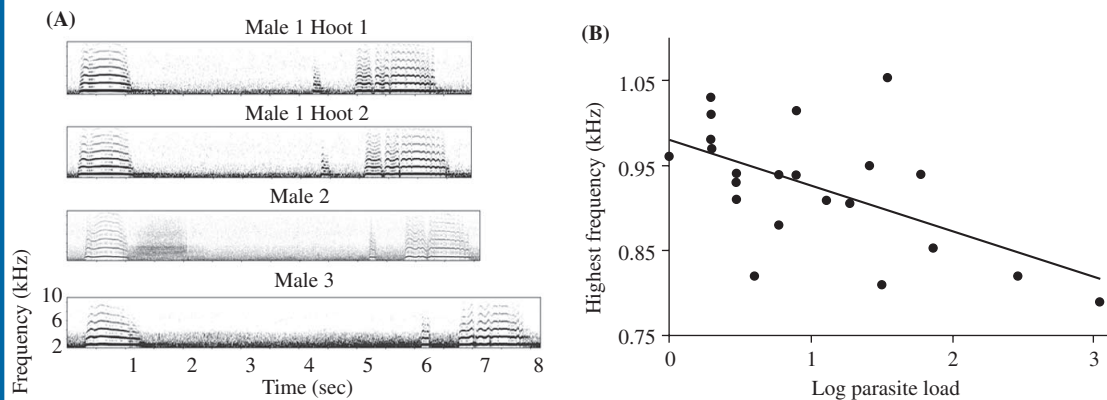**Steve Redpath & Bridget Appleby**

Plate II

Wood thrush
Elliott

Crested lark
Rossum

Song sparrow
Elliott

Hedge accentor
Wothe

As a final point, there is always the possibility that repertoires are preferred by females as a result of sensory bias (Ryan & Rand 1993), and that the benefits they obtain are an incidental byproduct. Searcy et al. (1994) showed that male response to song increases when the song switches to another type in red-winged blackbirds. He hypothesized that the new song type results in dishabituation. Females show the same effect (Searcy 1988); thus female habituation to a stereotyped song may set the stage for the evolution of song repertoires. Females do not habituate so quickly to males who have more song types or a more complex song. Therefore, an apparent preference for the complexity of larger repertoires is observed. To test for a general bias across all species for decreased habituation to repertoires, we must show female preference for repertoires in a species where there are no repertoires. The evidence so far is somewhat contradictory (Searcy & Marler 1984). The results using species with song repertoires supported the dishabituation hypothesis. Female field sparrows and white-throated sparrows showed no preference for an artificially constructed repertoire, something neither species possesses naturally (Searcy & Marler 1981). Female common grackles do show a preference for a combined song of four males (a repertoire) over a single male (Searcy 1992b). However, in this species the preference may be an ancestral trait, rather than evidence of a general bias, as males in all other closely related species have repertoires (Gray & Hagelin 1996).

Zebra finches have no close relatives with repertoires and, although there is some variation in syllable structure within a male zebra finch song, they do not have a true repertoire (Helekar et al. 2000). In a preference experiment females were trained to press buttons to receive a song (Collins 1999; **CD #—**). One button resulted in the playing of an artificial 'repertoire' and one a stereotyped song (**Fig. 2.15A**). All showed a preference for the repertoire (**Fig. 2.15B**). Thus, in a species where males do not possess a repertoire, nevertheless, females show a preference for multiple song types. Repertoires may have

evolved to prevent habituation and, through the cost of learning a repertoire, high quality males may incidentally have larger repertoires. Of course, the question then remains – why do some species lack repertoires and why are some females not biased towards them (Gray & Hagelin 1996)? Perhaps individual identification is more important in some species, or the relative cost of developing a repertoire varies. A short lifespan, a short breeding season, or high predation risks may also affect whether repertoires are favored.

Song Familiarity

In a few species it appears that female choice for song is affected by familiarity. The function of the preference could be mate recognition. Female song sparrows prefer a neighbor's song more than a stranger's songs (**Fig. 2.16**), and give the strongest response to the song of their mates (O'Loghlen & Beecher 1999). In general, females tend to respond more to any song that is similar to that of their mate, but this is obviously not the same mechanism that leads them to a particular mate in the first instance. Preference for familiarity, in songs that are not those of the mate, has also been observed in previously unmated females, indicating that preference for a familiar song is not just due to mate recognition. Female zebra finches prefer songs that are similar to those of their father (Clayton 1990a), or that they heard frequently when young (Riebel 2000; **Box 7,** p. 70). Female brown-headed cowbirds prefer the song of males from a culture to which they have been exposed extensively (Freeberg et al. 1999). So, familiarity can influence female preference for a mate, but the benefits to the female and the function of the preference are not always clear. The most plausible explanation is that the preference for familiarity is a consequence of the way that females imprint on species' song characteristics. Females use song to choose a male of their own species, and they learn some species' song characteristics by imprinting on songs heard when they were young. Songs more similar to those heard when young fit the species-specific template better than
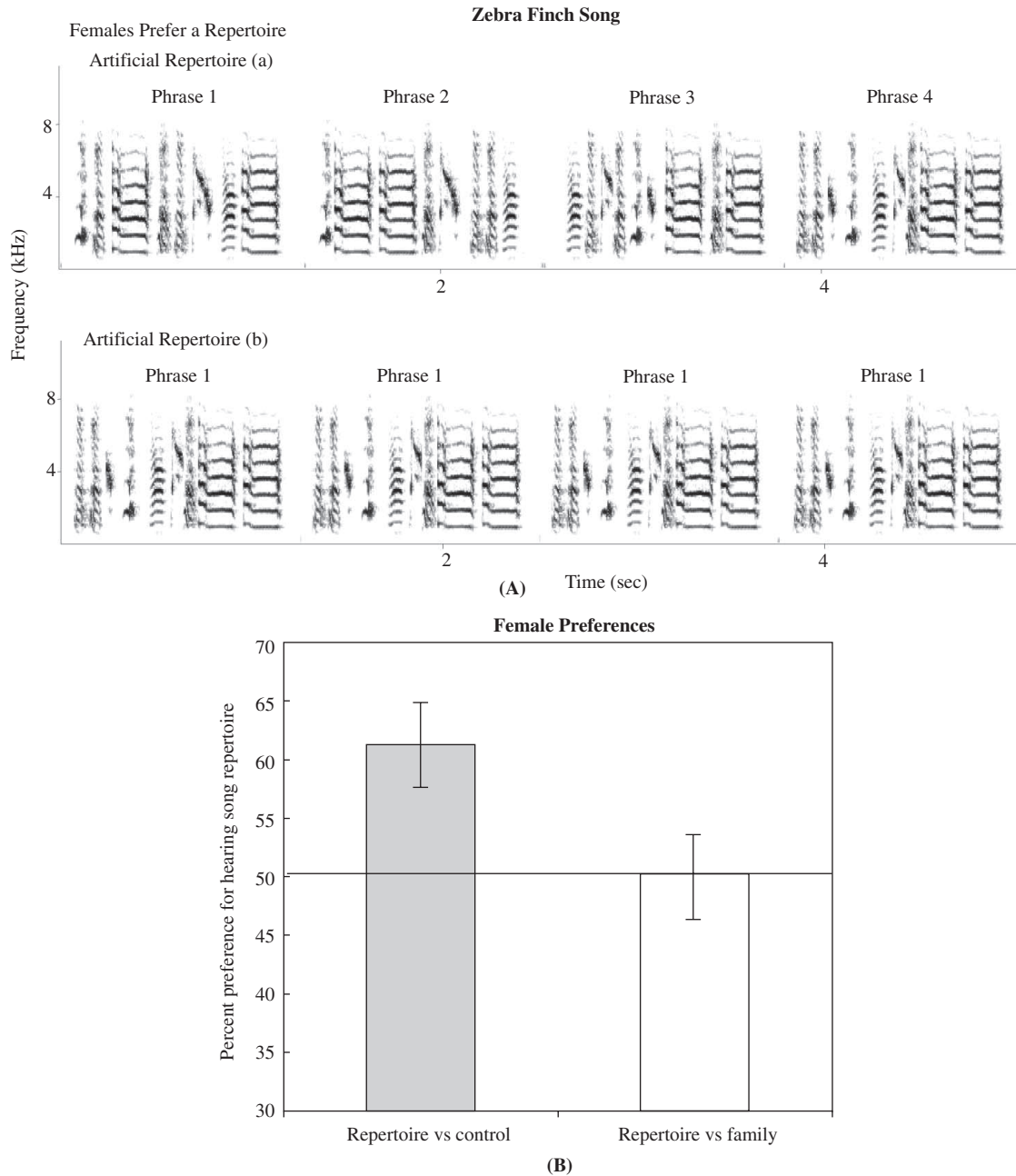
Zebra Finch Song

Females Prefer a Repertoire

Artificial Repertoire (a)

Artificial Repertoire (b)

(A)

Female Preferences

(B)

Figure 2.15 **(A)** Two sets of song stimuli given to female zebra finches – an artificial, varied repertoire (a) and a repeated, stereotyped song (b), as a control. Females preferred listening to the repertoire stimulus. **(B)** In a repertoire versus family experiment, the 'family' stimulus consisted of four very similar songs from different individuals within a family. Here, there was no preference. From Collins 1999.

BOX 7

LEARNING TO SING, LEARNING TO LISTEN: DEVELOPMENT OF SONG PERCEPTION

Given the importance of learned song in mate attraction and stimulation, it would be surprising if potential receivers did not engage in some perceptual learning, with so much of the fine detail of adult song culturally rather than genetically inherited. After cross-fostering between subspecies, female zebra finches preferred the songs of their foster parents, not their genetic fathers (Clayton 1990a). Focusing in on within-population variation of zebra finch song, and sidestepping the effects of social interaction with the singer (Riebel 2000), I limited young females' song exposure to tape tutoring between days 35–65 post-hatching, within the sensitive phase for male song learning. After sexual maturity at 3–4 months of age, song preference was tested by teaching them to peck red buttons for song playback. In three tests (see figure, solid symbols), they consistently chose the taped song they heard early in life over an unfamiliar song, strongly suggesting that preferences for within-population variants of song are culturally inherited. In striking contrast, females raised without any exposure to adult male song (see figure, open symbols) behaved inconsistently, changing preferences between repeated tests. Early exposure to song might turn out to be as crucial for the development of perceptual competence in the receiver as it is in vocal production by the sender. Interestingly, when we tested males and females in the same context with the same songs, preferences for tutor songs were equally strong, although of course only males learned to sing them (Riebel et al. 2002). This supports the idea that early perceptual learning is independent of learning for production: only some learn to sing, but all are likely to learn to listen.

Katharina Riebel
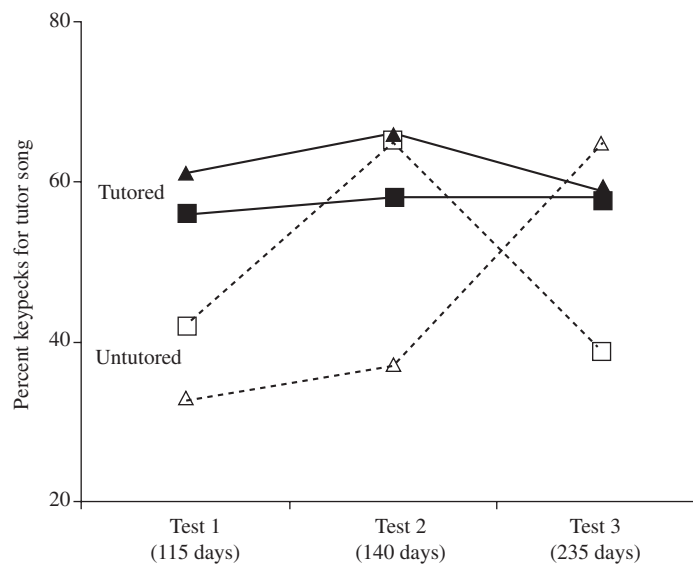
After tutoring, two females consistently preferred the tutor song over an unfamiliar song in three tests at different ages (solid symbols). Two untutored females showed no consistent preference (open symbols). The tutored females had each heard a different song and were given the other's tutor song as an unfamiliar song. The same song combinations were used with the untutored females. Data from Riebel 2000.
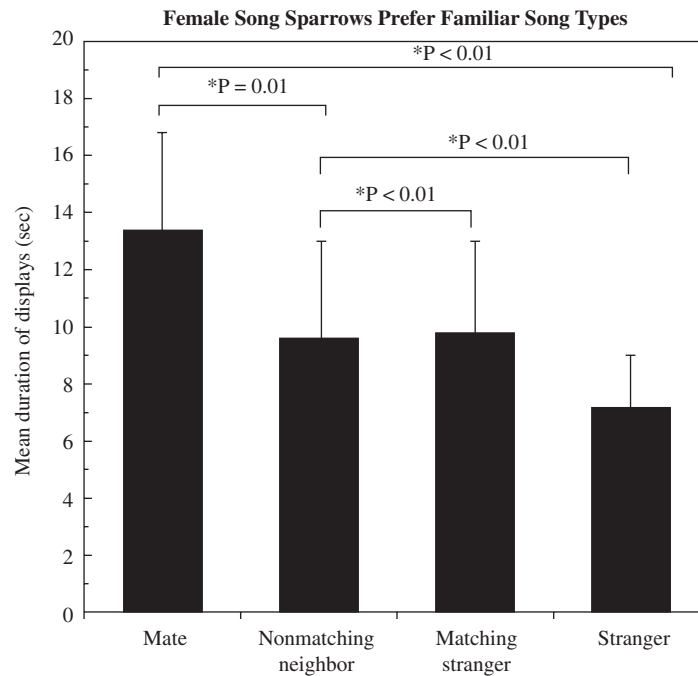
Female Song Sparrows Prefer Familiar Song Types

Figure 2.16   Song preferences of female song sparrows. The figure shows the mean duration of solicitation displays (+SE) during playback of 8 repetitions of a song in one of four categories; mate, nonmatching neighbor, matching stranger, and stranger. *Wilcoxon signed ranks test. From O'Loghlen & Beecher 1999.

unfamiliar songs (ten Cate & Vos 1999). Another explanation is that preference for familiar, or local song results from females using similarity to local songs as a measure of the learning ability of the male (Searcy et al. 2002). As already mentioned, song learning ability may reflect the degree of developmental stress experienced and thus, potentially, male quality (Nowicki et al.1998a).

A preference for a familiar song is known to be vital to breeding success in the village indigobird, which is a brood parasite. Male indigobirds learn their song in part from the host (Payne 1973a; Payne & Payne 1994) and therefore have a similar song (**Box 41**, p. 319). Females prefer male indigobirds who sing the same song as their foster parent species. There are some differences between the host and parasite songs, however, and female indigobirds appear to prefer songs of males of their own species rather than the actual host's song. Given that indigobirds have a number of specializations

that are specific to a particular host species, it is important for a female to find a male from a lineage that has the same host preference.

Local dialects are the most widely discussed aspect of female preference for familiar song types. Some bird species have the equivalent of regional accents and if females preferred familiar song they would tend to mate with males that had the same dialect as the one where they spent their youth (Cunningham & Baker 1983). Balaban (1988) showed a preference for local males in swamp sparrows, and Searcy et al. (1997, 2002) found a preference for local males in song sparrows. Female great tits prefer local males (Baker et al. 1987a). It has been proposed that, because of local genetic differences between dialect populations, it is advantageous to mate with males from the same population. Therefore, females should prefer males with a dialect resembling that of their own population to be sure of obtaining the best male. The outcome would be subpopulations of locally adapted birds.

Whether there are locally adapted populations maintained by females' song preferences has been an area of intense discussion, with sometimes conflicting results being found by different researchers (Petrinovich & Baptista 1984; Baptista 1985; Baker & Cunningham 1985; Chilton & Lein 1996). The most extensive studies are on *Zonotrichia* sparrows (see Chapter 3; **Box 12**, p. 93). As they disperse, female white-crowned sparrows will encounter males both from their own population and from the neighboring population with a different dialect. If females prefer to mate with males from their own population they should choose to mate with males from the same dialect population as their natal one, using song as a cue. Work by Cunningham and Baker (1985) suggests that females do prefer males that sing the dialect of their natal population. However, it appears that females learn some of their song preferences after dispersal and, if they disperse to the area where the neighboring dialect is more prevalent, may prefer males of a different dialect to that of their natal population. In addition, some studies have suggested that males also learn or modify their song after dispersion, in which case the dialect would not necessarily reflect the characteristics of the natal population (Baptista & Morton 1988). However, this is evidence against the local adaptation hypothesis, not against a preference for local song.

Another approach is to induce a female to sing by implanting her with testosterone, the assumption being that the song she sings is that of her natal population. The local adaptation hypothesis predicts that the dialects of the male and female in a pair should generally be the same (Tomback & Baker 1984; Baptista & Morton 1982). Tomback & Baker (1984) found an association between the dialects of mates, but Baptista & Morton (1982), and Petrinovich & Baptista (1984) found that captive females sang songs unlike those of their mates. Preferences can also be studied in the laboratory, by implanting females with oestradiol and playing back songs from different dialects. Baker et al. (1981, 1987b) found that natal dialect songs were preferred, and received more copulation solicitation displays. But Chilton et al. (1990) found no preference for natal dialects. Chilton & Lein (1996) suggested that, in another subspecies, female white-crowned sparrows did not base their choice on dialectical variation in male song, and that it is unlikely that mate choice decisions promote genetic isolation. They did find an association between the songs of mates, but they suggest that females learn the song of their first mate. Females did not respond more strongly in the laboratory to playback of songs of the local type, suggesting that song type was not important although, given that the females were paired, perhaps they were less likely to respond to male song. It should be noted that Chilton and Lein were working with a migratory subspecies, and Baker with a subspecies that is resident the year round and has differently structured song dialects, perhaps an important distinction (**Box 12**, p. 93). Data of Bensch et al. (1998) suggest that female great reed warblers choosing local males would obtain a more fit male, in better condition. This could be because lower quality males are forced to disperse further, philopatric males may be locally adapted, or may have better local experience. Similar arguments were advanced in the discussion of song sharing; local variants of song may be important in both female choice and male competition for similar reasons.

To summarize, female preference for familiar song is often observed, and may be a byproduct of the mate or species' recognition mechanisms (Nelson 1989a), or a way of finding high quality males (Searcy et al. 2002; Bensch et al. 1998), or it may be due to preference for locally adapted mates (Baker & Cunningham 1985).

The Rate of Singing

Song rate, usually defined by the overall time spent singing, or singing within a defined time period, rather than by the speed of note production, is an obvious candidate for a costly signal. The evidence regarding the energy costs of singing is somewhat contradictory. In the

Carolina wren (Gaunt 1987) and the sage grouse, oxygen consumption has been shown to increase with increased song rate. In sage grouse, vigorous males expend twice as much energy per day as males that do not display (Vehrencamp et al. 1989). However, a recent study has shown that metabolic rates increase by only a multiple of 1.05–1.38 during singing (Obwerger & Goller 2001), suggesting that singing for longer is not costly. However, there are other indications that singing may be costly. Males sing more when provided with extra food (Alatalo et al. 1990) and when the temperature is higher (Gottlander 1987; **Fig. 2.17**). Male barn swallows decrease their song rate when they have a high ectoparasite load (Møller 1991). The song rate of pied flycatchers is correlated with food availability and temperature. This suggests that when males have more energy to spare they sing more, so it is possible that birds in better condition will sing more. Of course, some of the cost of singing may result from the incompatibility of singing and feeding, and from singing taking up time and energy that could be spent in other activities.

In one of the first studies to show that singing rate might be important for reproductive success, Payne & Payne (1977) showed in village indigobirds that males with higher song rates had a higher reproductive success. Because this bird is a brood parasite, there are no benefits associated with a territory, from the mate or parental care. The increased reproductive success is likely to be due to the higher genetic quality of males with a higher song rate. Female indigobirds obtain only indirect benefits from males, but song rate can also indicate that a male can provide direct benefits. In stonechats, song rate was correlated with participation in parental care, in terms of feeding nestlings and defending them from predators, indicating that song can indicate behavioral differences between males (Greig-Smith 1982a). Although no mate choice study was conducted, it appears that song rate would be an efficient parameter for female stonechats to use. Other studies have shown not only that song rate correlates with reproductive success or behavior, but that females prefer males who sing at a higher rate, in willow warblers (Rædesater et al. 1987), white-crowned sparrows (Wasserman & Cigliano 1991), and starlings (Eens et al. 1991). Females have good reason to prefer males with a high song rate, which can indicate territory quality (Gottlander 1987), male condition or ability (Houtman 1990; Beani &
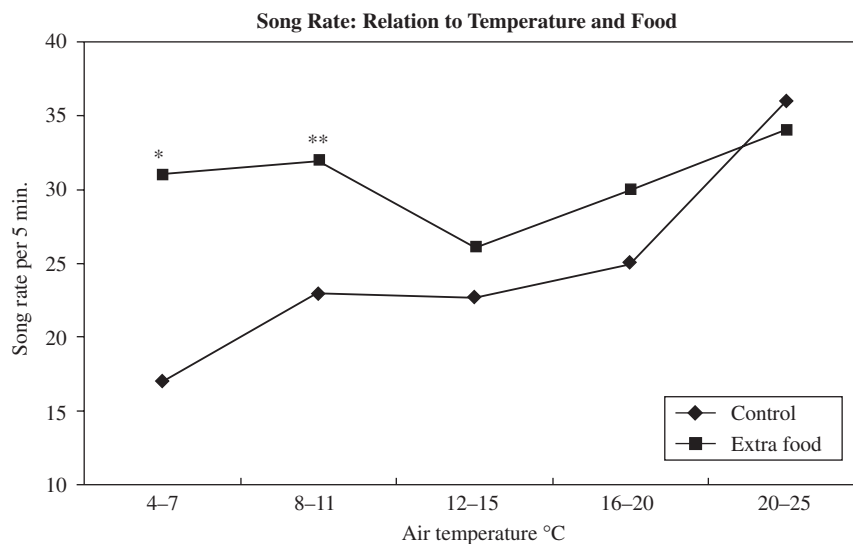

Figure 2.17   The song rate of male pied flycatchers varies with food and temperature. Some differences between the groups are significant *P < 0.05, **P < 0.001. From Gottlander 1987.

Dessi-Fulghieri 1995), or male genetic quality (Houtman 1990; Møller et al. 1998).

Female pied flycatchers prefer males with a high song rate and thus obtain a mate with a good territory (Gottlander 1987; Alatalo et al. 1990). Song rate was not correlated with male physical characteristics in pied flycatchers (Gottlander 1987), which suggests that song rate is not related to intrinsic male characteristics but to territory quality. The assumption is that in better territories a male will generally be well fed, or able to find food more easily, and thus can sing at a higher rate. Zebra finch males provide parental care but no territory. In laboratory experiments, males with higher song rates were preferred by females (Collins et al. 1994) and these males had heavier offspring, indicating a higher genetic quality; song rate is also heritable (Houtman 1990). All males had *ad libitum* food so differences in song rate are unlikely to be food related; female zebra finches probably obtain mates with good genes and in good condition, by using song rate to differentiate between males. Sons of females preferring males with high song rates actually get double benefits; not only are they heavier, and thus presumably more likely to survive, but they also inherit their father's high song rate. If they have a high song rate they are more likely to be chosen by females, i.e. they are 'sexy' (Fisher 1930).

A study on a nonsong bird, the partridge, showed that females prefer males that produced the 'rusty gate' call at a high rate (Beani & Dessi-Fulghieri 1995). This call is affected by the levels of testosterone (Fusani et al. 1994), and increased vigilance postures are observed in these males. Presumably, more vigilant males will protect the young and female more effectively. Male display rate is also important in the sage grouse. The probability that a visiting female will mate with a male is related to his display rate (Gibson 1996). Males display in aggregations called 'leks', which females attend over several days before choosing a mate, so they can determine long-term display rate differences between males (**Fig. 2.18**). Presumably, these males have increased energy reserves or a higher genetic quality. Barn swallow

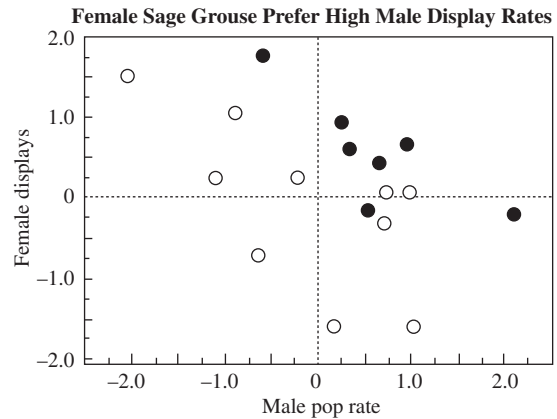**Female Sage Grouse Prefer High Male Display Rates**

Figure 2.18 Female sage grouse prefer males with a high display rate and a short inter-pop interval. ● chosen; O not chosen. From Gibson 1996.

females choose males with high song rates for extra pair copulations (Møller et al. 1998). Again, they only obtain sperm from the male, so are presumably choosing for intrinsic male qualities.

An important question is the reliability of song rate as a measure of male quality. The song rate of male Ipswich sparrows is affected by food provisioning and by temperature, as in other species. Therefore, in warmer weather and in mild years, the song rate provides less useful information as all males can sing at a high rate. In colder, harsher years, only males who are in good condition can sing at a high rate, so song rate becomes a good choice criterion. Indeed, females seem to rely on song rate only in harsher years (Reid & Weatherhead 1990).

In all species studied, if females show a preference at all, they favor males with a higher song rate. It is easy to see why females should use this parameter to choose between males. Males singing more are likely to have greater energy reserves, which indicates to the female that she will obtain a male with a better territory, in good condition, with good genes, who will be a good parent, or some combination of these qualities.

So we find that the role of song in female choice is better understood than its role in male competition. In general, there are fewer contradictions, as can be seen in **Table 2.2**.

Table 2.2   Relationship between song characteristics and female choice. ↑ indicates that an increase in the song characteristic in question is preferred by females and ↓ indicates that a decrease is preferred.

Song characteristic	Relationship to female choice or physical attribute
Frequency	partridge ↓
Performance	occurs in canaries, swamp sparrows, and brown-headed cowbirds
Repertoire	great tit ↑; red-winged blackbird ↑; European starling ↑; song sparrow ↑; aquatic warbler ↑; great reed warbler ↑; willow warbler ↑; pied flycatcher ↑; sedge warbler ↑
Familiar dialect	white-crowned sparrow ↑; zebra finch ↑; brown-headed cowbird ↑; village indigobird ↑; swamp sparrow ↑; great reed warbler ↑; great tit ↑; song sparrows ↑
Song rate	Carolina wren ↑; barn swallow ↑; sage grouse ↑; pied flycatcher ↑; village indigobird ↑; stonechat ↑; willow warbler ↑; white-crowned sparrow ↑; zebra finch ↑; Ipswich sparrow ↑; partridge ↑ (of one note only)

All species where females choose on the basis of male repertoire size prefer males with larger repertoires. Also, all females that pay attention to song rate prefer males that sing at a higher rate. When it comes to female preference for particular note types, too few species have been studied to draw any general conclusions. Female preference for song types has generated some controversy, especially in the white-crowned sparrow. However, the controversy is perhaps over the importance of dialects for promoting population isolation and local adaptation, rather than over the question of whether there is preference for local song types. Preference for local songs has been found in a number of species; in others, no preference has been found but, so far, no preference for foreign dialects has ever been shown. Perhaps preference for local dialects depends upon processes such as the habitat characteristics that facilitate transmission of different song frequencies, or adult movement patterns (Slabbekoorn & Smith 2002b).

There are still unanswered questions about preference for repertoires, and whether repertoires indicate individual male fitness. Although age is a known predictor of repertoire size in many species, it is not the case for all. Repertoire size, as a way for females to choose older males, is a factor only in some species. Studies showing that parasite load correlates with repertoire size are an important step towards answering this question. Male song rate, perhaps the best understood song parameter with respect to female choice, is almost certainly a signal of adequate energy reserves. It indicates individual condition or territory quality, or both, and females have a good reason to prefer males who sing more.

ONE SINGER: MULTIPLE FUNCTIONS

A song typically repels rivals and attracts females. There are three ways for a song to perform both functions.

(1) The same song characteristics could be used to indicate the singer's ability to perform both functions; for example, a high song rate could attract females and repel rivals. In great tits, red-winged blackbirds, and starlings repertoire size appears to be used by both males and females to assess singers. As shown in **Tables 2.1** and **2.2**, in a few species males and females use the same song characteristics for assessment.

(2) Different aspects of singing behavior could be effective in interactions with males and females, even when the same song types are sung to both sexes. Yellow warblers, chestnut-sided warblers, and American redstarts repeat one song type when signaling to potential mates, and sing a series of song types, including that sung to females, when signaling to potential rivals (Spector 1992; Kroodsma et al. 1989; Weary et al. 1994). Great tit males match rivals to deter competitors, while the females use song repertoire size to choose a mate. The songs sung in each

case are the same, but different parameters are used as the response criterion.

(3) Either (i) different song types, or (ii) different parts of the same song are effective in interactions with males and females (see p.**000**).

The challenge posed by the dual function of song can be addressed in several ways, depending on the combination of evolutionary pressures to which a particular species is exposed, acting sometimes in concert and sometimes in conflict (**Box 8**, p. 77).

Song Types

The use of different song types, or different song parts, for interactions with males or females is perhaps the most interesting solution to the dual function challenge. Given that male rivals and potential mates are interested in different qualities of the singer, it is not difficult to understand why this has occurred. In some cases songs sung to males and females differ in complexity as well as type. The great reed warbler uses long songs for mate attraction and short songs for territory defense (Catchpole 1983). The aquatic warbler produces complex songs (known as C songs) to attract females, and shorter songs of one or two phrases to interact with rival males (Catchpole & Leisler 1996). Male dusky warblers sing an individually specific stereotyped song (S song), or an extremely complex, variable song (V song); the S song is used to guard the territory and interact with neighbors, and is produced frequently when the female is fertile, presumably to guard against potential extra-pair copulations (Forstmeier & Balsby 2002). Females choose a mate based on the V song and prefer those that are more complex.

In a few species different parts of the same song may perform different functions. In chaffinch song, the end flourish seems to be more important in mate attraction (Riebel & Slater 1998a), and the trill in male–male competition (Leitao & Riebel in press). Females prefer relatively longer flourishes and males respond more strongly to relatively long trills.

The song of the blackcap (**CD #—**) also consists of two parts, an initial warble and a terminal whistle (**Fig. 2.19**). There are indications from unpublished work of mine that the whistle is important in territorial conflicts and the warble in interactions with females. The whistle is louder and easily locatable; the warble is complex, quieter, hard to locate, and inaudible at a distance, and becomes shorter as the breeding season progresses, when there is no longer a need to attract a female. Thus the warble and whistle may perform different functions. In water pipits and barn swallows certain notes address a particular function. The 'snarr' in water pipits and the rattle in barn swallows both appear to have competitive functions (see p. **000**). The rest of the song of both species is involved in attracting females. These examples give a flavor of the various ways in which males find efficient solutions to solve the problem of the dual functions of song.

Evolution Through Sexual Selection

Sexual selection has affected the evolution of song characteristics in all species. It has driven the evolution of some very complex patterns of singing behavior, such as interactive singing, in which the details provide information about the singer. This is thus a level above a simple sing–receive–react sequence of behaviors. Song learning itself may have evolved to allow males to sing different song types that are more stimulating to females and more intimidating to rivals. Sexual selection may also have affected processes of speciation; female preference for particular song types may have driven speciation in groups such as the indigobirds.

The same set of evolutionary pressures, attracting a mate and repelling a rival, result in different outcomes from species to species. For example, in the appraisal of individual differences by zebra finches, song rate has evolved as the main intraspecific song parameter used in female mate choice, whereas in the great reed warbler repertoire size is the most important choice
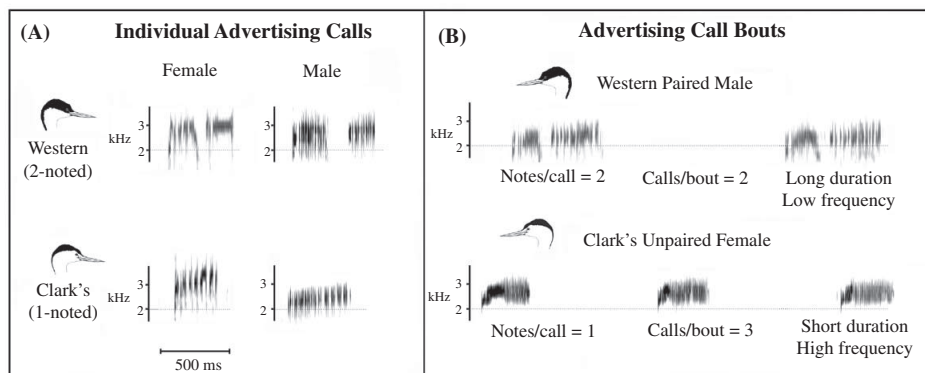
BOX 8

SPECIES AND MATE RECOGNITION AMONG CALLING GREBES

Western grebes and Clark's grebes are sibling species that often breed in mixed colonies. They both use special advertising calls to attract potential mates as the first step in pair formation. This is followed by an elaborate courtship sequence that includes the striking 'rushing-on-water' and 'weed dance' displays. Displays of the two species are nearly identical, and male western grebes often engage male Clark's grebes in joint 'rushing' or 'barge-trilling' displays to attract the attention of females. In fact, until the mid-1980s, Clark's grebe was considered a color-phase of the western grebe. Storer (1965), however, reported strong assortative mating within the two types. In addition, spectrograms revealed that the advertising calls of Clark's grebes lack the distinctive 10–20 ms gap in calls of western grebes (Nuechterlein 1981; **A**). These calls are clearly involved in choosing mates rather than territorial defense, since birds court and form pairs outside the nesting colonies. Playbacks from floating blinds to actively courting birds revealed that males of mixed species populations readily distinguish the two call types based on whether a gap in the call is present. Early in the season, courting males of both types only answer and approach female calls of their own type. However, when an artificial 10–15 ms gap was spliced into the same Clark's female calls that they had been ignoring, western grebe males began answering and approaching as to western grebe female calls. Hybridization between the two species does occur, and follow-up experiments suggest an explanation. As the courting season progresses, late-courting western grebe males are much more likely to answer and approach playback calls from Clark's grebe females than earlier in the season. Hybrid pairings are most common late in the season, and are unlikely to be the result of mistaken species identity. Rather, individuals of both sexes may become less choosy as the pool of available mates decreases (Nuechterlein & Buitron 1998).

Although grebe advertising calls are not complex, they convey a wealth of additional information (**B**). Advertising calls of females are higher and longer than the calls of males, and playbacks show that unpaired males easily distinguish this difference. Playbacks to males that are courting in a crowded area demonstrated that they are able to instantly use the individual characteristics of an unpaired female's advertising call to answer her selectively and repeatedly while approaching from a distance. After pair formation, both sexes use the individual characteristics of their mate's advertising call to locate each other when separated. Paired birds are less vocal, and usually only answer playback calls from their own mate. Calls are given in bouts of 1–7 similar calls. When communicating with their mates, grebes tend to use shorter call-bouts (1–2 calls) than unpaired birds (3–7 calls). In playbacks with varying bout lengths, courting males were less likely to answer a given female call when it was presented to them in short rather than long bouts. Thus, variations in the structure of their rather simple advertising calls enable grebes to identify the species, sex, pairing status, and individual identity of courting birds. This may allow grebes to reserve their more spectacular and energetically demanding displays for demonstrating other qualities such as health and vigor.

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(A) Individual Advertising Calls — Western (2-noted): Female, Male; Clark's (1-noted): Female, Male. 500 ms. (B) Advertising Call Bouts — Western Paired Male: Notes/call = 2, Calls/bout = 2, Long duration, Low frequency. Clark's Unpaired Female: Notes/call = 1, Calls/bout = 3, Short duration, High frequency.
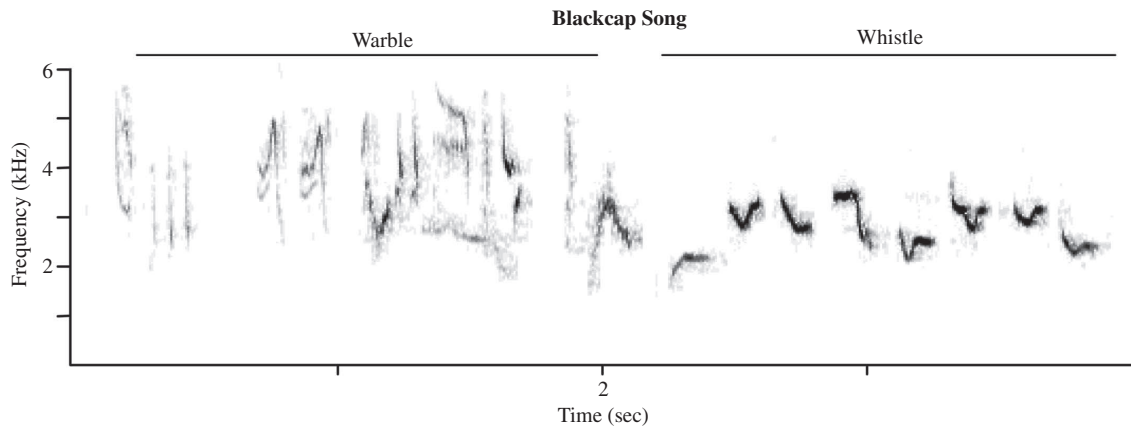
Figure 2.19   A song of a male blackcap showing the whistle and warble sections. The warble is quiet, whereas the whistle is loud and easy to locate.

criterion. The structure, complexity, and temporal arrangement of songs is also affected by other aspects of behavior and ecology (Slabbekoorn & Smith 2002b). For example, species in which males can attract more than one mate tend to have more complex syllable repertoires (Read & Weary 1992). The great disparity between the most successful and least successful males in polygamous species adds to the pressure to attract females by performing virtuoso songs; the selection pressure for complexity is stronger than in monogamous species, in which, because the male is involved in rearing the chicks, females are more likely to base mate choice on signals indicating that the male will be a good parent (Catchpole 2000). Interestingly, song type repertoires (as opposed to syllable repertoires) are larger in species where males provide more parental care (Read & Weary 1992). Whether a species is migratory or not is another important factor. Catchpole (1980) suggested that migratory species have more elaborate songs because they are under pressure to pair early, defend a territory forcefully, and breed successfully in a short time, so that sexual selection is more intense. We need to study more species before we can determine more accurately just how selection pressures affect song patterns across species (Read & Weary 1992).

FEMALE SONG AND DUETTING

Generally speaking, males sing and females do not, because it is usually a male responsibility to attract a female rather than vice versa. Also, males are generally the sex that holds territories and competes with rivals for access to females. Of course, this assumes that the only functions of song are to defend territories or attract mates. However, in a number of birds females sing songs much like males (Langmore 2000). Female song has been found in at least 40 species; it is thought to be more common in tropical species, which are less well studied, so the true number of species in which there are female singers may be much higher. Females are generally harder to observe singing and, in a number of sexually monomorphic species, singing birds assumed to be male were subsequently found to be female. There are singing females in superb fairy wrens (Cooney & Cockburn 1995; **CD #—**), white-crowned sparrows (Baptista et al. 1993), blue-breasted waxbills (Collins pers. obs.), European robins (Lack 1965), long-tailed manakins (Trainer et al. 2002), dusky antbirds, and starlings, to name but a few. Langmore (1998, 2000) has outlined the situations in which females have been found to sing.

Functions of Female Song

Female song may have several possible functions. It may attract a partner or a male for extra-pair copulation, induce copulation with a mate, or aid in retaining a mate by maintaining the pair bond. Alternatively, females often have as strong a reason as males to defend their territory from intruders, who may compete with her for food for herself and her offspring, try to take over nest sites, or engage in extra-pair copulations with her mate. The potential functions of female defense differ from those of males only in that a territory is not obtained specifically to attract a mate.

One of the best known examples of a female singer is the European robin; females sing in the winter and defend their own territories. The song functions just as male songs usually do in other species (Lack 1965), to defend a territory in order to have sole access to the resources. Superb fairy-wren females sing to defend their territory, perhaps because males are always sneaking off for extra-pair copulations (Cooney & Cockburn 1995). However, the song of the female fairy-wren may encourage other males to visit her territory so she can engage in extra-pair copulations herself (**Fig. 2.20**). Female song

functions in territory defense in several other species where males are frequently absent from the territory, as in fairy-wrens, or where food resources are scarce in the winter and females defend winter territories, as in robins and mockingbirds (Lack 1965). Female Australian magpies in communal groups sing to defend a territory against threats from other colonies (Brown & Farabaugh 1991). Interestingly, in this species, the syllables of the female's song are more complex than those of the male.

In several polygynous species, female song is used in aggressive interactions between females as a form of mate defense. Red-winged blackbird females produce simple 'teer' songs in the context of female–female aggression (Yasukawa & Searcy 1982). The more females a male obtains in his 'harem' the fewer resources there will be for each, so it pays females to repel rivals.

The females of all three species of cordon-bleu finch sing occasionally (Goodwin 1982; Gahr & Guttinger 1986; Collins personal observation; **CD #—**). Males and females defend a small area around the nest site. The song appears to be less complex than that of the male (Collins personal observation; **Fig. 2.21**). The females seem to sing mostly before egg laying in the breeding season, but can sing at other times of
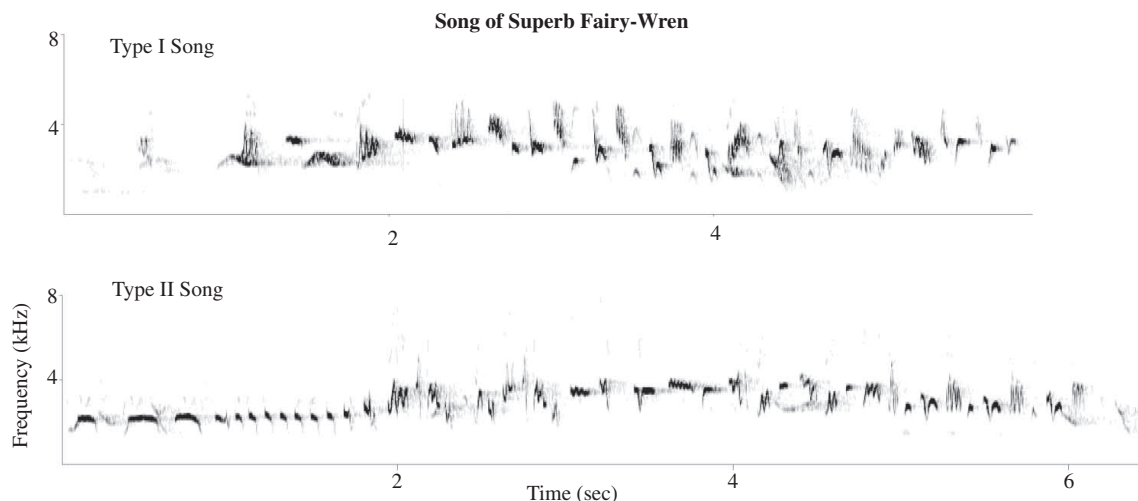

Figure 2.20 Superb fairy-wren territorial songs. Type I song uttered by both males and females; type II song used only by males.

Male and Female Cordon-bleu Songs

Red-cheeked Cordon-bleu
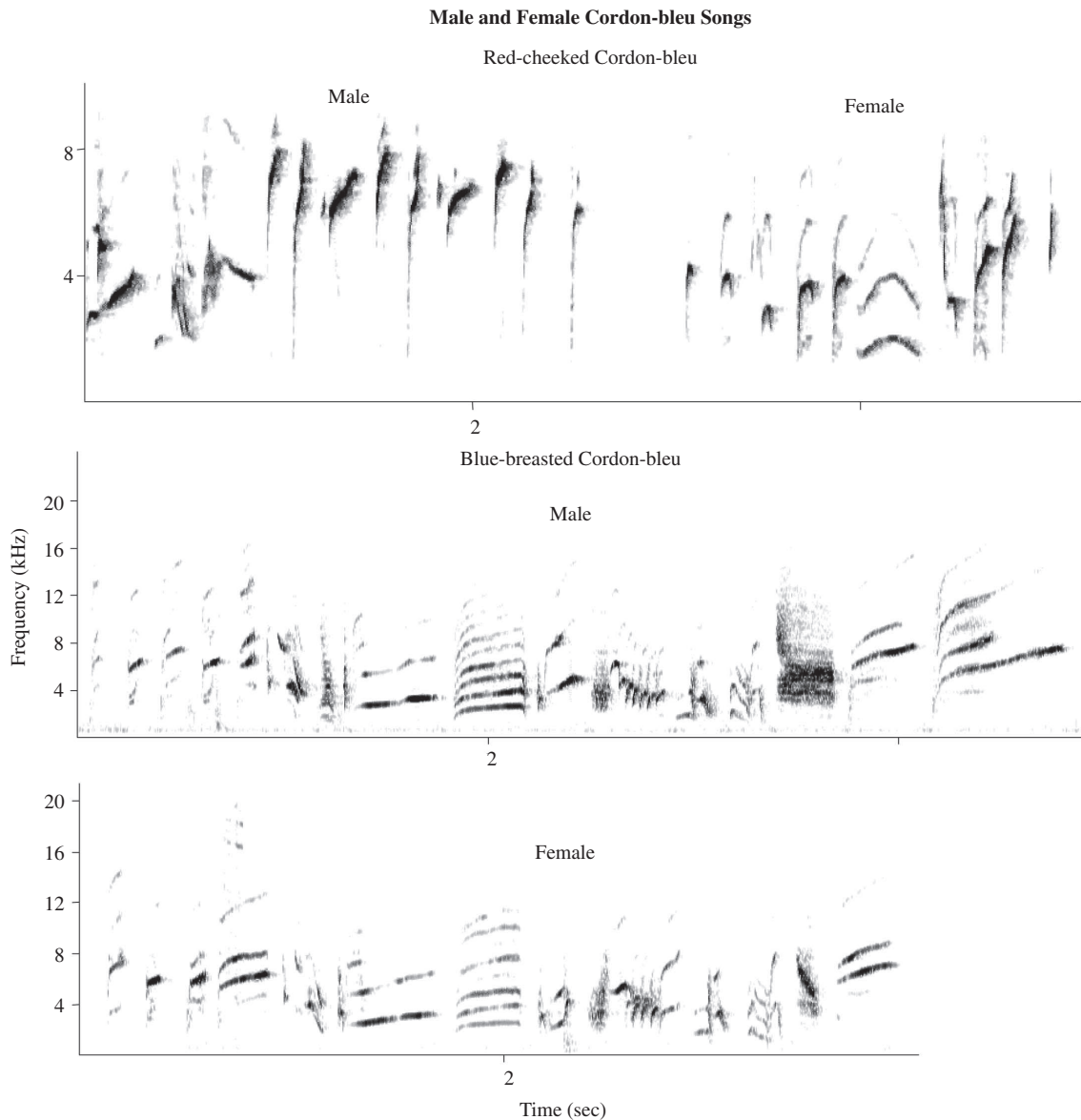
Blue-breasted Cordon-bleu

Time (sec)

Figure 2.21 Male and female songs from the red-cheeked and the blue-breasted cordon-bleu.

the year. The function is probably to maintain the pair bond or synchronize breeding (Gahr & Guttinger 1986). In slate-colored boubous (Sonnenschein & Reyer 1983) female song has been shown to synchronize breeding.

The only species for which there is evidence that female song functions in mate attraction is the alpine accentor (Langmore et al. 1996). Accentors breed in groups of up to four males and four females. Males feed the chicks of females they have mated with, so it is to a female's advantage to mate with all males in the group. When females are fertile there is intense competition through song to attract a male for

copulation; playback of female song attracts males. The same is possibly true for the dusky antbird, in which females sing after losing a mate (Morton 1996a). Langmore (2000) suggests that this function of female song may be important in tropical species with a territory that is defended the year round; widowed females may need to attract a new mate without undue risk of losing their territory.

Duetting – Song in Synchrony

So far, I have described cases where males and females sing in bursts, or bouts, independently of each other. The song is directed at intruders, rivals, mates or potential mates, but is, essentially, done alone. There is another style, involving duetting, in which the songs of partners are interdependent.

Duetting occurs "when members of a mated pair sing in combination with one another, either synchronously or alternately" (Langmore 1998). The duet may function in territorial defense. It may be more effective than solitary defense, perhaps because each member of the pair can defend against intrusion by a same-sex intruder, as in dusky antbirds (Morton 1996a), or the Polynesian megapode (Goth et al. 1999). In other species, such as bay wrens, the duet may function in mate guarding (Levin 1996 a, b), but with different roles for male and female song. Levin found that the female part of the duet functioned to repel female intruders and the male part to guard his mate from extra-pair copulations.

There is one case of duetting involving two males. In the long-tailed manakin, pairs of males duet to attract a female, usually with a lead male and a follower. Male pairs may stay together for years and, over time, come to match each other's song in terms of frequency (Trainer et al. 2002). Eventually, the subordinate male may take over as the lead male.

More work is needed on female song and duetting. The function of female song has been studied in only a few cases. Duetting has received more attention, but again the function is not always clear. Generally female song and duetting appear to function similarly to male song; repelling rivals, defending resources, and attracting a mate. There could be a contrast between female and male song in the synchronization of breeding. We do not know what kind of female songs are more successful at attracting mates or repelling rivals. As for males, songs that are more complex, more energetically expensive, and more salient may be the most effective. As yet there has been little work on song learning by females. Do females learn from males, females, or their mate? Slate-colored boubou females learned their song from females and males learned from males (Wickler & Sonnenschein 1989), but whether this pattern recurs is not known. In general, the same kind of selection pressures appear to be acting on female song as upon male song.

CONCLUSIONS

The study of the functions of birdsong is one of the most active areas of research in behavioral ecology. Song is clearly important for both competition and attracting a mate. The need to advertise your quality in such a way as to convince receivers that they should mate with you or leave you alone has driven the evolution of song in a number of ways. Individuals within a species differ in the types of song they sing, and potential rivals and mates pay attention to those differences and act accordingly. The differences between individuals in song relate to differences in aggressiveness, male quality, and the resources made available. By using song to judge individual rivals and mates, birds avoid fights they would lose and obtain better mates. The specific parameters that signal quality differ between species, and song types and singing behavior may differ depending upon whether the song is addressed primarily to rivals or mates.

One common outcome of the need for singers to advertise is that songs become more complicated and versatile, and perhaps more costly to produce and thus more cheat-proof as signals. This will be true for interactions with

males and females. However, there is still argument about why song repertoires appear to be most important to females for choosing a mate in one species whereas, in another, song rate is more significant.

To achieve a deeper understanding of the patterns and processes involved in the evolution of song, we need to integrate the study of sexual selection with the neurobiology of song learning, mechanisms of sound production, and the use of comparative studies to reconstruct the evolutionary history of song. I predict that some of the most exciting research to come will focus on female preferences for specific note types, and on the physiological and morphological factors affecting repertoire size. We have far to go before we fully understand all the nuances of birdsong as a way of flirting and fighting.