Song development in birds: the role of early experience and its potential effect on rehabilitation success

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Abstract

Environmental conditions during the early life stages of birds can have significant effects on the quality of sexual signals in adulthood, especially song, and these ultimately have consequences for breeding success and fitness. This has wide-ranging implications for the rehabilitation protocols undertaken in wildlife hospitals which aim to return captive-reared animals to their natural habitat. Here we review the current literature on bird song development and learning in order to determine the potential impact that the rearing of juvenile songbirds in captivity can have on rehabilitation success. We quantify the effects of reduced learning on song structure and relate this to the possible effects on an individual's ability to defend a territory or attract a mate. We show the importance of providing a conspecific auditory model for birds to learn from in the early stages post-fledging, either via live- or tape-tutoring and provide suggestions for tutoring regimes. We also highlight the historical focus on learning in a few model species that has left an information gap in our knowledge for most species reared at wildlife hospitals.

Keywords: *animal welfare, fitness, rehabilitation, songbirds, song development, tutoring*

Introduction

Song in many birds, notably the oscine passerines, is a learned behaviour (Thorpe 1954, 1958; Marler 1981, 2004), and many studies have shown that there are distinct phases to song development (Bottjer & Johnson 1997; Marler 1997). Recent work has provided a wealth of information on species-specific song development strategies (Marler 1970; Kroodsma & Miller 1983; Catchpole & Slater 1995; Bottjer 2002; Beecher & Brenowitz 2005) as well as revealing the underlying neural circuitry (Nottebohm *et al* 1976; Konishi 1994; Alvarez-Buylla & Kirn 1997; Brainard & Doupe 2001). As songbirds learn their songs in the first few months of life, while the song control nuclei are still developing (Kroodsma & Pickert 1980; Nottebohm 1993; Catchpole & Slater 1995; Mooney 1999), early rearing conditions can have a significant effect on an individual's ability to learn their song (Nowicki *et al* 1998, 2000, 2002; Buchanan *et al* 2003; Spencer *et al* 2003, 2004) and hence have significant deleterious effects on survival, pairing success and fitness.

Wildlife hospitals receive large numbers of nestling/fledgling songbirds to rear and release back to the wild. While there have been considerable advances in veterinary treatment of wildlife, eg Stocker (2005), hitherto little attention has been paid to the impact of husbandry practices on chances of survival post-release. Since the main aim of any rehabilitation protocol is to return an animal to its natural habitat quickly while maximising its chances of surviving and reproducing, effective rehabilitation protocols should ensure normal song development in captive juvenile birds. This is primarily a welfare issue, since the successful rehabilitation of songbirds is unlikely to have a significant impact on most bird populations, although it may have implications for local population dynamics at release sites. However, the contribution of wildlife rehabilitation to conservation is increasingly being recognised (see review by Aitken 2004). Furthermore, developing good rehabilitation protocols with common species enables these techniques to be applied to the captive rearing/breeding and restocking of rare species (Butchart *et al* 2006).

Here we consider the possible effects of reduced song quality on the survival and reproductive potential of released songbirds. We review the current literature on songbird song learning and development and describe the importance of tutoring for normal song development, with a focus on the best practice for tutoring regimes. We then review the developmental stages at which tutoring should occur and briefly discuss other factors that can affect an individual's ability to learn songs.

Why is song development important?

Song in males typically serves two main functions: to acquire and defend a territory and to attract a mate. However, it also enables conspecifics to recognise their own species, which underlies these two main functions

Table 1   Effects of rearing juvenile birds in isloation on song parameters.

Species	Reduction in repertoire size or phrase complexity?	Reduction in syllable structure – complexity?	Reduction in song duration?	Increase in syllable duration?	Increase in inter-syllable interval?	Increase in maximum frequency?	Species recognition?	References
American robin (*Turdus migratorius*)	Yes *	Yes	-	Shorter	Yes	Yes (deafened)	-	Konishi 1965
Arizona junco (*Junco phaeonotus*)	Yes *	Yes	-	-	-	Narrower frequency range	-	Marler 1967
Cardinal (*Cardinalis cardinalis*)	-	Yes	-	-	-	-	-	Dittus & Lemon 1969
Chaffinch (*Fringellas coelebs*)	Yes	-	No	Yes (in some studies)	Yes	Less frequency modulation	Lack of terminal flourish affects female choice	Thorpe 1954, 1958, 1961; Riebel & Slater 1998; Nottebohm & Nottebohm 1978
Coal tit (*Parus ater*)	Yes *	Yes	No	-	-	-	Lack of conspecific to isolated males	Thieckle 1973
European starling (*Sturnus vulgaris*)	Yes	-	Yes	-	-	-	Reduction in responses from conspecific males	Chaiken *et al* 1993, 1997
Greenfinch (*Carduelis chloris*) (reared with heterospecifics)	-	Unstable structure	-	-	-	-	-	Guttinger 1979
Indigo bunting (*Passerina cyanea*)	-	Yes	-	-	-	Narrower frequency range	-	Rice & Thompson 1968
Oregon junco (*Junco hyemalis*)	No increase, reduction after deaf	Yes but increase in some studies	Yes	-	Yes	Yes	-	Marler *et al* 1962; Konishi 1964; Marler 1967
Pine grosbeak (*Pinicola enucleator*)	No	Yes	-	-	Yes but shorter in others	No	-	Konishi 1965
Red-winged blackbird (*Agelaius phoeniceus*)	Yes	-	-	-	-	Frequency direction changes	-	Marler *et al* 1972
Rufous-sided towhee (*Pipilo erythrophthalmus*)	No	Yes	Increase	Yes	-	Similar	-	Ewert 1979
Song sparrow (*Melospiza melodia*)	Yes	Yes	Yes	Yes	-	In some	-	Marler 1967; Kroodsma 1977 (but see Mulligan 1966)
Swamp sparrow (*Melospiza georgiana*)	-	Yes	-	-	-	-	-	Marler & Peters 1977
White-crowned sparrow (*Zonotrichia leucphrys*)	Yes	-	Longer (in subsong)	Yes (in some birds)	-	Narrower frequency range	-	Marler & Tamura 1964; Konishi 1965

In the majority of cases birds were reaered in acoustic isolation from conspecifics; where birds were deafened or raised with heterospecifics this is noted. Dashes denote status unknown due to lack of experiments or authors not stating effects.
* Determined from figures alone in original reference, small sample sizes and no statistical analysis.

Table 2   Effects of large repertoire sizes on individual reproductive success and fitness.

| Species	Early pairing or breeding?	Increased territory quality or size?	Increased extra-pair copulations?	Increased copulation solicitation displays?	Increased mating or reproductive success?	References
Canary (*Serinus canaria*)	-	-	-	-	Yes	Kroodsma 1976
European starling (*Sturnus vulgaris*)	Yes	-	-	-	Yes	Eens *et al* 1991; Mountjoy & Lemon 1995
Great reed warbler (*Acrocephalus arundinaceus*)	-	Yes	Yes	Yes	Yes	Catchpole 1986; Catchpole *et al* 1986; Hasselquist *et al* 1996
Great tit (*Parus major*)	No	Yes	-	Yes	Yes	McGregor *et al* 1981; Baker *et al* 1986; Lambrechts & Dhont 1986
Northern mocking bird (*Mimus ployglottos*)	Yes	Yes	-	-	-	Howard 1974
Pied flycatcher (*Ficedula hypoleuca*)	-	-	-	-	Yes	Eriksson 1991
Red-winged blackbird (*Agelaius phoeniceus*)	-	Yes	-	Yes	-	Yasukawa 1980; Searcy 1988
Sedge warbler (*Acrocephalus schoenobaenus*)	Yes	-	-	Yes	-	Catchpole 1980; Catchpole *et al* 1984
Song sparrow (*Melospiza melodia*)	-	Yes	-	Yes	Yes	Searcy & Marler 1981; Searcy 1984; Hiebert *et al* 1989
Yellowhammer (*Emberiza citrinella*)	-	-	-	Yes	-	Baker *et al* 1987
Zebra finch (*Taeniopygia guttata*)	-	-	-	Yes	-	Clayton & Prove 1989

(Kroodsma & Miller 1983; Catchpole & Slater 1995). Thus, both male and female birds need to be able to identify their own species and song plays an important role in species recognition (Bremond 1968, 1976a, b; Becker 1976; Aubin & Bremond 1983; Clayton 1990). Features important in this context include syntax, element structure, temporal organisation and frequency levels (Bremond 1968, 1976b; Becker 1982; Dabelsteen & Pedersen 1993; Dabelsteen *et al* 1996), all of which are affected by rearing songbirds in acoustic isolation from conspecifics (Table 1). However, not all of these characteristics are used for recognition by all species. European robin (*Erithacus rubecula*) songs that do not contain alternating elements of high and low frequency (pitch) result in significantly lower recognition, from 90% of adult males responding to 50% (Bremond 1968), suggesting that syntax is important. In the European blackbird (*Turdus merula*) frequency level, motif duration, song amplitude and syntax were all important in species discrimination by both males and females, although there were differences between the sexes (Dabelsteen & Pedersen 1993). Syntax and number of elements are important in the

black-capped chickadee (*Parus atricapillus*) (Ratcliffe & Weisman 1986).

Territorial defence

Birds sing to acquire and defend a territory; this is often a necessary prerequisite for breeding and can be related to survival. Song repertoire size (number of different syllables or song types a male can sing) is instrumental in deterring rival males from entering a territory (Krebs 1977; Yasukawa 1981). For instance, Krebs (1977) replaced territorial male great tits (*Parus major*) with speakers, playing either no song, song with one type or a repertoire of songs. The territories with one song type were fully occupied by new males within 18 hours, whereas the repertoire territories took 30 hours to be occupied, suggesting that birds with larger song repertoires are better able to keep a territory. The quality (eg size, food abundance) of a male's territory also varies with repertoire size in great reed warblers (*Acrocephalus arundinaceus*) (Catchpole 1983; Catchpole *et al* 1986), red-winged blackbirds (*Agelaius phoeniceus*) (Yasukawa *et al* 1980), northern mocking birds (*Mimus polyglottos*) (Howard 1974) and

Figure 1
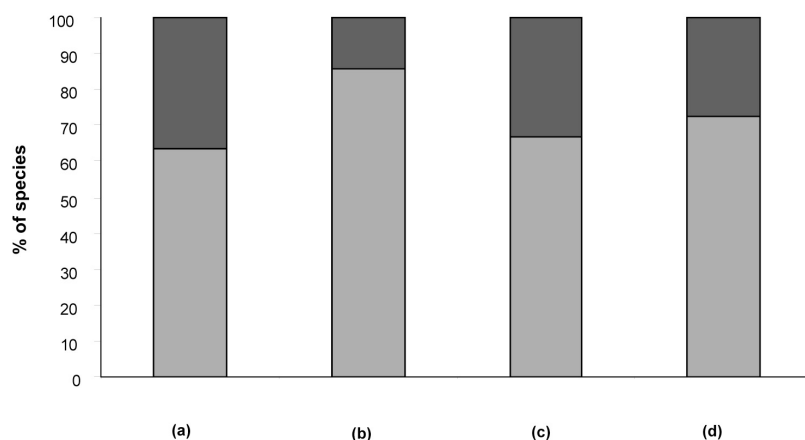
Percentage of species quoted in Table 1 showing abnormal song characteristics when compared to wild conspecifics. Light bars represent species that exhibit abnormalities in the direction of those quoted on the x-axis, dark bars those which show either no abnormalities or differences in the opposite direction of the trait quoted on the x-axis: a) reduction in repertoire size/phrase complexity, b) reduction in syllable complexity eg notes per syllable, c) increase in syllable duration(s), d) abnormal frequency distributions or maximums.

great tits (McGregor *et al* 1981). A large repertoire can also assist in the acquisition of a territory before breeding. Male song sparrows (*Melospiza melodia*) with repertoire sizes between 10-12 song types acquired a territory within 4-7 months of the onset of the territorial season, whereas males with 4-6 song types took 7-15 months (Hiebert *et al* 1989). Males with larger repertoires were also able to hold their territory longer (36-50 months) than males with simpler songs (2-25 months). Repertoire size is therefore an important song characteristic.

Female choice

A reduction in a male's chances of attracting a mate, even if he holds a territory, can have a significant impact on his reproductive success and hence fitness, and several aspects of song have been shown to affect female mate choice (Catchpole & Slater 1995; Searcy & Yasukawa 1996). Across a wide range of species, females prefer males who can sing more often or more complex songs (Catchpole & Slater 1995; Gil & Gahr 2002). Numerous studies have shown that females can discriminate between normal and abnormal forms of their own species' songs (Searcy & Yasukawa 1996). Female song sparrows, for instance, assessed males on the basis of song learning ability (Nowicki *et al* 2002). Females of several species have also been shown to prefer local song dialects when compared to song from another region, eg brown-headed cowbirds (*Molothrus ater*) (King *et al* 1980), white-crowned sparrows (*Zonotrichia leucophrys*) (Baker 1986), yellowhammers (*Emberiza citrinella*) (Baker *et al* 1987), red-winged blackbirds (Searcy 1990) and zebra finches (*Taeniopygia guttata*) (Clayton & Prove 1989).

Several studies have also shown reduced female responses to simple as opposed to complex male song, quantified as the number of song or syllable types in a male's repertoire.

When given a choice of three males with repertoire sizes of 39, 41 and 43 syllables, female European starlings (*Sturnus vulgaris*) were more likely to choose the male with 43 syllables (Eens *et al* 1991), suggesting a highly acute discrimination ability. Thielcke (1970) found that reducing the duration of song phrases in European blackbirds by 50% led to a reduction in female response of almost 80%; increasing duration by 75% also meant that females responded less (60%).

Repertoire size can also influence reproductive success (Table 2), the general consensus being that males with smaller repertoires experience lower breeding success. Eens *et al* (1991) showed that male European starlings with larger repertoires tended to pair with a female earlier in the breeding season. A male with a repertoire size of 35 syllables paired at the start of April whereas one with 67 syllables paired in mid March. There are similar effects on the timing of pairing in the northern mocking bird and the sedge warbler (*Acrocephalus schoenobaenus*) (Table 2). Male great reed warblers with large repertoire sizes (22-24 syllables) produced, on average, three times as many young in a season as those with smaller repertoires (13-14 syllables) (Catchpole 1986).

The effects of isolation on song development

Since juvenile songbirds reared in acoustic isolation from conspecifics tend to develop abnormal song, with reduced song complexity and duration, auditory models are required for a bird to develop normal song. The overwhelming majority of species develop songs that might actually fail to be a signal of species identity when reared in isolation (Figure 1), although very few of these studies tested the quality of the song signal produced. For instance, Thielcke (1973) raised juvenile coal tits (*Parus ater*) in isolation during the post-fledging period. Their adult song showed

Figure 2
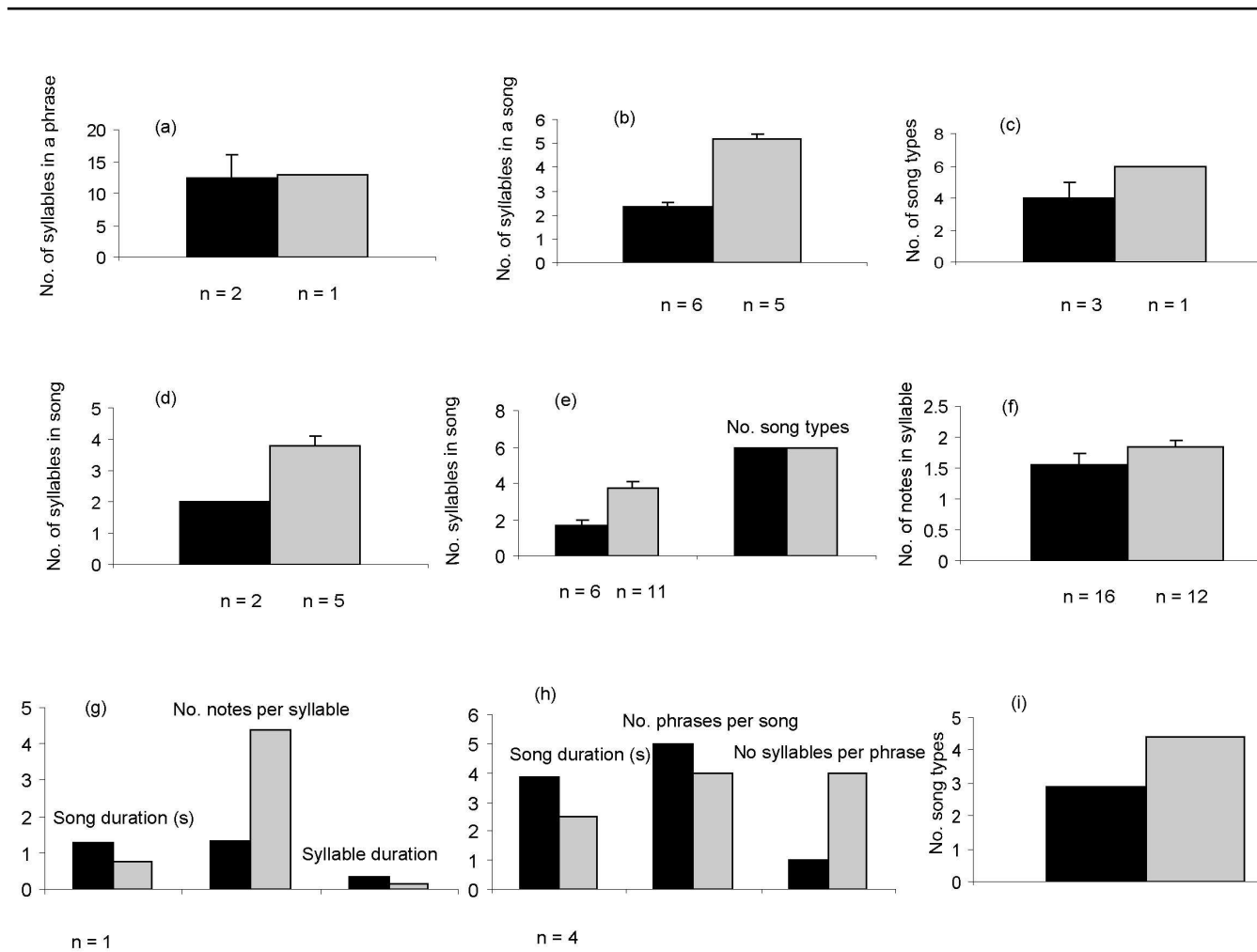
The effects of isolation rearing on different song parameters. Means (± SE) are quoted in all cases apart from (g) where medians are quoted. Where data were provided by authors, sample sizes (number of sonograms) used to determine means are shown on the x-axis. Dark bars denote songs of birds from isloated rearing conditions, light bars wild song. (a) black-headed grosbeak (Konishi 1965); (b) chaffinch (Thorpe 1954; 1958); (c) coal tit (Thielcke 1973); (d) white-crowned sparrow (Marler 1967); (e) Arizona junco (Marler 1967); (f) Oregon junco (Marler 1967); (g) rufous-sided towhee (Ewert 1979); (h) song sparrow (Kroodsma 1977) and (i) red-winged blackbird (Marler *et al* 1972).

reduced complexity in terms of number of song types sung and syllable structure. When Thielcke (1973) played these isolated songs to wild male conspecifics there was no reaction to 5 of the 6 song types used, whereas when exposed to wild-type songs males respond by counter-singing and specific behavioural displays. This and other studies suggest that tutoring is crucial to normal song learning, although species vary in the extent to which their song is abnormal. In some cases isolated birds sing good approximations of their species' song (Leitner *et al* 2002).

Figure 2 summarises the effects of isolation rearing on song structure. Although the data are very variable, and methods and timing of isolation vary between studies, there is a general trend for a significant reduction in song complexity, via a reduction in the number of syllables or song types a

male sings or through reduced syllable complexity, ie the number of sub-elements or notes that make a syllable. There is a significant reduction in song quality, with a 40% mean reduction in song complexity and a 42% reduction in syllable complexity. Thus it is important to provide birds held in captivity with a tutor model from which to learn their species-specific song.

Can birds learn heterospecific songs?

Since many wildlife hospitals do not have space to house each species separately, especially those species admitted in low numbers, it is important to determine the risk of cross-species song learning. The copying of songs between species is normally avoided in natural situations. The song sparrow and swamp sparrow (*Melospiza georgiana*), for

Table 3   Learning deficiencies in songbirds when tutored with tape recordings as opposed to live birds.

Species	Able to learn from tape model?	Reduction in learning ability?	Reduction in repertoire size?	Changes to song syntax?	References
Chaffinch (*Fringilla coelebs*)	Yes	No	No	No	Thorpe 1958, 1961
European starling (*Sturnus vulgaris*)	Yes	Yes	Yes	Yes	Chaiken *et al* 1994, 1997
Indigo bunting (*Passerina cyanea*)	Yes	Yes	-	-	Payne 1981
Nightingale (*Luscinia megarhychos*)	Yes	Yes	-	-	Hultsch *et al* 1999
Red-winged blackbird (*Agelaius phoeniceus*)	Yes	No	No	No	Marler *et al* 1972
Song sparrow (*Melospiza melodia*)	Yes	No	No	No	Marler & Peters 1987
Swamp sparrow (*Melospiza georgiana*)	Yes	No	No	No	Marler & Peters 1988
Treecreeper (*Certhia brachydactyla*)	No	Yes	-	-	Thielcke 1970
White-crowned sparrow (*Zonotrichia leucophrys*)	Yes	-	-	-	Marler 1970; Baptista & Petrinovich 1984
Zebra finch (*Taeniopygia guttata*)	Yes	Yes	-	-	Eales 1989; Adret 1993

Although many studies have used tape recordings, few have compared the song of tape- and live-tutored males with wild birds. Hence the data presented in terms of changes to the structure of adult song come from studies where there was a comparison between tape- and live-tutored or tape-tutored and wild birds.

instance, are closely related species which tend to share breeding habitats. These birds will not learn each other's songs, even when solely tutored with heterospecific song in the laboratory (Marler & Peters 1977). However, captive-rearing can polarise learning by placing young birds in unusually close contact with heterospecifics, when heterospecific song learning can occur. For example juvenile white-crowned sparrows will learn songs from Lincoln sparrows (*Melospiza lincolnii*) with which they are in visual and acoustic contact, even when in acoustic contact with conspecifics (Baptista & Morton 1981; Baptista *et al* 1981; Baptista & Petrinovich 1984; Baptista 1988). European starlings can also mimic conspecific songs, although such mimicry is often added to their song repertoires and not considered 'abnormal' by conspecific males or females (Hindmarsh 1984).

In summary, most bird species will not learn heterospecific song, especially when given a choice between that and conspecific models (Catchpole & Slater 1995). There is a risk of heterospecific learning when species are very closely related or share a song with similar structure or temporal pattern. Little is known about the possibility for heterospecific learning in many British species. However, it appears that the risk of species song crossover is low and that mixed species housing during a tutoring regime is a low risk strategy.

The role of tutoring

Tape recordings versus live birds

While auditory stimuli are required during early growth for normal song development, the mode of such stimuli may also be important. Although training young birds with tape recordings is a widespread solution (reviewed in Kroodsma & Miller 1983; Catchpole & Slater 1995), not all species learn well from a 'tape-tutor' and there has been a great deal of debate about how tape-tutors could affect song learning (Marler 1970; Baptista & Petrinovich 1984, 1986). Species differ in their readiness to learn from tape- and live-tutors in captivity. Swamp sparrows acquire songs from both live- and tape-tutors on the same developmental schedule (Marler & Peters 1988). Chaffinches (*Fringilla coelebs*) (Thorpe 1954, 1958), song sparrows (Mulligan 1966; Marler & Peters 1987) and red-winged blackbirds (Marler *et al* 1972) are able to produce normal species-specific songs from tape-tutors. However, tape-tutoring has proved unsuccessful in the treecreeper (*Certhia brachydactyla*) (Thielcke 1970). Although many species appear to be able to learn from both live- and tape-tutors, tape-tutoring seems to affect adult performance (Table 3). For example, young zebra finches and indigo buntings (*Passerina cyanea*) can learn from tape recordings, but the presence of social interactions with conspecific tutors increases their copying ability (Payne 1981; Adret 1993, 2004; Houx *et al* 2000).

Table 4   Sensitive periods for song learning.

Species	Learning possible in 1st spring?	Sensitive period	References
Barn swallow (*Hirundo rustica*)	Yes	Not tested	Galeotti *et al* 2001
Canary (*Serinus canaria*)	Yes	Lifelong?	Nottebohm 1969; Nottebohm & Nottebohm 1978
Chaffinch (*Fringilla coelebs*)	Yes	Fledgling period and 1st spring only	Thorpe 1954, 1958, 1961; Slater & Ince 1982
Chipping sparrow (*Spizella passerina*)	Yes	Fledgling period and 1st spring	Liu & Kroodsma 1999
Corn bunting (*Emberiza calandra*)	Yes	Learning as adult; song matching	McGregor 1980
Dunnock (*Prunella modularis*)	Yes	Learning as adult	Langmore 1999
European blackbird (*Turdus merula*)	Yes	28-122 days; and 1st spring	Messmer & Messmer 1956; Thielcke-Poltz & Thielcke 1960
European starling (*Sturnus vulgaris*)	Yes	1–18 months, lifelong? Also mimicry	Adret-Hausberger *et al* 1990; Eens *et al* 1992b; Chaiken *et al* 1993; Mountjoy & Lemon 1995; Eens 1997
Field sparrow (*Spizella pusilla*)	Yes	Fledgling period and 1st spring	Lui & Kroodsma 1999
Great tit (*Parus major*)	Yes	Not tested but possible learning as adult	McGregor & Krebs 1982, 1989
Greenfinch (*Carduelis chloris*)	Yes	Not tested but can alter songs after 1st spring	McGregor 1980
Indigo bunting (*Passerina cyanea*)	Yes	Learning as adult	McGregor 1980
Marsh wren (*Cistothorus palustris*)	Yes	15-60 days; learning as adult	McGregor 1980
Nightingale (*Luscinia megarhynchos*)	Yes and improvises	13-70 days; learning as adult	Todt *et al* 1979; Hultsch & Kopp 1989; Hultsch & Todt 1989; Todt & Böhner 1994
Red-winged blackbird (*Agelaius phoeniceus*)	Yes	Up to 70 days; learning as adult	Marler *et al* 1972
Sedge warbler(*Acrocephalus schoenobaenus*)	Improvises on own repertoire from subset of syllables	Not tested	Catchpole 1976, 1980
Song sparrow (*Melospiza melodia*)	No	-	Marler & Peters 1987
Song thrush (*Turdus philomelos*)	Not tested	Sub-song begins at fledging	Heinroth & Heinroth 1924 - 1933; Nice 1943
Swamp sparrow (*Melospiza georgiana*)	No	-	Marler & Peters 1987, 1988
White-crowned sparrow (*Zonotrichia leucophrys*)	Yes, but most learning in first 100 days	13-100 days	Baptista & Petrinovich 1984; Marler 1970; Nelson 1998; Petrinovich & Baptista 1987
Zebra finch (*Taeniopygia guttata*)	No	20-65 days	Zann 1996

It would appear therefore that live-tutors and social interactions could have important influences on all stages of song learning. Much work has been done on the zebra finch; whilst both visual and vocal interactions are important in song learning in males, close social interactions are also important (Eales 1989; Adret 1993). Social interactions with conspecifics have also been linked to song discrimination ability in adulthood in both male and female zebra finches (Sturdy *et al* 2001). Physical two-way interactions between tutor and tutee are required rather than just the presence of an adult male, since 'dummy' birds failed to enhance the ability of juvenile males to copy tape models (Bolhuis *et al* 1999; Houx & ten Cate 1999). Furthermore, the amount of interaction between tutor and tutee has a significant positive effect on song learning (Houx *et al*

2000). However, experiments with nightingales (*Luscinia megarhynchos*) showed that matching an auditory stimulus with a visual one (strobe lighting) enhances song copying ability from tape recordings by increasing the attention paid to the tutor song (Hultsch *et al* 1999).

Another species used to investigate the effects of tape-tutoring on song is the European starling. Chaiken *et al* (1993) raised two groups of juvenile starlings, one given access to live-tutors and the other tape recordings. Birds tutored using tape recordings had approximately half the repertoire size of live-tutored mates. However, when live-tutored males were compared to wild caught individuals, their repertoire size was also approximately halved. While this might suggest that both modes of tutoring are insufficient for song learning, starling repertoire size increases

with age (Eens *et al* 1992a; Eens 1997). So older, wild-caught males exhibit elevated repertoires, and the repertoire sizes Chaiken *et al* (1993) quoted for live-tutored males lay within the normal boundaries of wild first-year males (Eens 1997). Whilst Chaiken *et al* (1993) showed abnormally low song complexity, even for first-year male starlings, they developed a closer approximation of species-specific syntax than untutored isolated males. Chaiken *et al* (1997) extended this work to show that males housed in juvenile pairs, but kept in acoustic isolation from adult conspecifics, could produce a better species representation of their song in adulthood than tape-tutored males.

In summary, social interactions with conspecifics rather than just using a tape-tutor are important during song learning for social reinforcement, and birds reared with conspecifics learn a better approximation of their tutor's song (Adret 2004). It is clear that different species react to tape-tutoring in different ways, and the role of social interactions is still not clearly understood. However, some birds learn well with tape-tutoring and, in wildlife hospitals where birds are to be released soon after independence, the presence of any song model is better than acoustic isolation. We suggest that, where possible, juvenile birds are kept in conspecific groups to allow social interaction and thereby aid song learning. The easiest tutoring scheme in captivity is to play pre-recorded bird song, containing several different species singing in unison, thereby producing a sort of 'dawn chorus' effect. However, since attention may be an important aspect of song learning, any tutoring regime should involve targeted tutoring using several speakers playing a single species' song. The use of a mixed species recording would also make it difficult to control the amount of each species' song to which the birds were exposed.

How often to tutor

Young birds can learn a song after hearing it very few times, even from tape recordings. Nightingales can copy a song without errors after hearing it only 15 times (Hultsch & Kopp 1989; Hultsch & Todt 1992). In European blackbirds 50 presentations of a song is enough for learning (Thielcke-Poltz & Thielcke 1960). However, this ability to learn songs quickly has not been exhaustively investigated and rehabilitation protocols should err on the side of caution. The majority of experimental studies use blocks of tutoring during a 24-hour period, which are usually 2 hours long. This methodology seems to work well for a wide range of species. Live-tutors will inevitably differ in their song outputs; juvenile birds with live-tutors are probably exposed to 2 to 4 hours continuous song per day (estimated from Catchpole & Slater 1995). Where live-tutors are used in a tutoring regime, exposure time to song need not be an issue, but when using tape models the exposure time of juvenile birds to recordings should be at least 2 hours per day to facilitate song learning.

When to tutor

Since hearing is not generally fully formed in nestlings (Catchpole & Slater 1995), tutoring needs to be done once the bird has fledged. However the timing of initial song memorisation differs between species (Table 4). There are two main strategies: age-limited learning and open-ended learning. In age-limited learners song learning is restricted developmentally with early auditory experience determining the acoustic structure of the song. The zebra finch is an age-limited learner; sensory acquisition occurs from day 20 to 65 (Immelmann 1969; Eales 1985; Clayton 1987; Böhner *et al* 1990) and adult song crystallisation occurs by 90-100 days post-hatching (Zann 1996; Brainard & Doupe 2002).

There is no learning of new songs past 65 days of age and hence young birds tend to learn their song repertoires from their fathers.

In contrast, open-ended learners show a high degree of plasticity in song learning sensitivity. Most show learning in the early sub-adult period and their first spring, but they also retain the ability to learn and add new elements to their repertoires in adulthood (Catchpole & Slater 1995). European starlings, great tits and canaries (*Serinus canaria*) can change their repertoires throughout life (Nottebohm *et al* 1976; Nottebohm & Nottebohm 1978; Mundinger 1995; Eens 1997). Extended learning is mainly related to local song dialects and song matching between territorial neighbours (Marler & Tamura 1964; McGregor 1980, 1985; Otter *et al* 2002). In great tits, as in other open-ended learners (Kroodsma 1974; Payne *et al* 1981; Langmore 1999), song is learned from birds on neighbouring territories and birds are able to add new songs to their repertoire throughout adulthood (McGregor & Krebs 1982, 1989). Whilst it is possible that these 'new' song types were learnt as a juvenile and stored in long-term memory (Marler & Peters 1982; Hultsch 1993; Geberzahn & Hultsch 2003; Kipper *et al* 2004), there is good experimental evidence that novel song types can be learnt in open-ended learners (Payne 1978; Mountjoy & Lemon 1995; Eens 1997).

Being able to determine which species brought to wildlife hospitals have a small window of opportunity within which to learn their song is important, since a large portion of this period inevitably overlaps with time at the hospital. However, for many species we know little about the timing of the sensitive period of song memorisation. For 11/21 (53%) of the species in Table 4 there appears to be a sensitive period for learning during the post-fledging period, although several of these species, along with some others, have the ability to learn songs the following spring. Furthermore, the cited sensitive periods for learning are, in many cases, based on experimental exposure to discrete blocks of tutor song. The upper and lower limits of these periods have therefore only been estimated crudely and the real limits may lie at either extreme of these blocks or in a small window within them. In many cases it is difficult to relate these 'windows' of sensitivity to learning in the wild. For example male warblers cease singing after pairing (Catchpole & Slater 1995). Fledgling birds will then potentially be exposed to very little tutor song in the first few months of life, except perhaps from unrelated conspecific males singing nearby. This suggests

that many species may be more flexible in their learning regimes than suggested hitherto.

Table 4 is based upon data for male birds, as they have been the focus of song research. Whilst females of some species also sing, all females need to learn conspecific song so they can discriminate between males when choosing a mate (Catchpole & Slater 1995; Langmore 1999). There is some evidence to suggest that females have a shorter sensitive period for song memorisation. Nelson *et al* (1997) tutored male and female white-crowned sparrows with tape recordings from the age of 15-75 days and then again at 130-150 days. They confirmed that males learnt mainly up to 75 days of age, but could also learn at 130 days. Females seemed to be limited to learning before 35 days of age. Baptista and Morton (1982) also suggested a shorter sensitive period in female white-crowned sparrows. Whilst there is scant evidence that this applies to a range of species, it further complicates rehabilitation protocols.

All species appear to learn their song initially during the fledgling and early sub-adult periods, with others having an additional window during the first spring. So if tutoring in a wildlife hospital cannot occur or is unsuccessful, there is a possibility that young males can compensate in their first season. Because little is known of the ability of many species to learn during the first spring, any rehabilitation guidelines should err on the side of caution and provide live- or tape-tutors during the sub-adult period prior to release.

Other factors affecting the ability to learn

Adverse environmental conditions during crucial stages of development can have a profound effect on several aspects of an individual's phenotype (Metcalfe & Monaghan 2001). A reduction in food availability, predictability or quality during the nestling period can significantly reduce the quality of a male's song in adulthood, even under a live-tutoring regime (Nowicki *et al* 1998, 2000, 2002; Buchanan *et al* 2003; Spencer *et al* 2003, 2004). Adverse conditions can also promote the release of adrenal glucocorticoid hormones; experimental elevation of corticosterone levels during growth significantly reduces song duration and complexity in adulthood (Spencer *et al* 2003). Parasites also reduce repertoire size (Hamilton & Zuk 1982; Buchanan *et al* 1999). Thus any husbandry protocol associated with songbird rehabilitation must provide sufficient nutrition to allow the rapid growth seen in passerine birds, and parasites should be eliminated to maximise the chances of normal song learning.

Animal welfare implications

The impact of husbandry conditions on animal welfare has long been recognised (Young 2003). Since wildlife hospitals in Britain and elsewhere receive a wide range of casualties (Tribe & Brown 2000; Kirkwood 2003), it is clearly important to understand the effects of husbandry techniques on their behaviour post-release. Juvenile birds form a high proportion of wildlife casualties (Best 2003), and their rearing conditions are of paramount importance to ensure the acquisition of normal behaviours (Young 2003). Whilst the preferred strategy is to return a juvenile bird to its natal territory/nest, or to foster it into another nest containing young of the same age, this is often impossible and the bird has to be hand-reared (Best 2003). However, current guidelines for rearing young songbirds focus on feeding and health care and do not consider the importance of song development (Best 2003; Stocker 2005). In this review, we have highlighted the importance of this issue and shown that small changes to song that lie outside the normal range of variation can affect species discrimination, and gross reductions in repertoire size, as seen in isolated birds, can significantly affect territory acquisition, mate attraction, breeding success and hence fitness. Since the overall aim of rehabilitation is to return birds to the wild in a position to survive and reproduce within the limits of the population (Llewellyn 2003), song learning in male and female songbirds should be a key issue for wildlife rehabilitators.

In the absence of field studies into the impact of rearing conditions on the ultimate fitness of rehabilitated songbirds, we have used a review of the literature on song development to make a number of husbandry recommendations for wildlife hospitals. In particular, we show that conspecific tutors are important in maximising the learning ability of young birds. The timing of memorisation of their tutor's song differs across a range of species, but all birds have a sensitive 'window' for learning during the fledgling and early sub-adult periods. Some species have additional periods for learning; although normally restricted to the first spring after dispersal from the natal territory, these can occur throughout life. A second 'window' for learning has important implications for rehabilitation protocols, as it may suggest that some birds could compensate for a bad acoustic start, eg if they could not learn well from a tutor. However, since researchers have concentrated on a few model species, the wider trends across a range of species are mostly unknown.

We have also emphasised the possibility of sex differences in song learning. While females need to learn song to discriminate between potential mates, their flexibility in terms of sensitive periods for song learning is less well known. The limited evidence suggests that they learn earlier and in a shorter period than males; this has implications for tutoring regimes in captivity. Since it is difficult to sex sub-adult birds, any tutoring regime should target tutoring at a period that will benefit both males and females.

The mode of tutoring also influences normal song development in young birds. Whilst using tape recordings can lead to normal adult song in some species, using live birds as tutors seems to be the best way of ensuring good quality song, possibly because social interactions are very important in the learning process. The use of live tutors may be possible in some rehabilitation centres, as in many cases a small number of adult conspecifics may be being held for rehabilitation themselves. In such cases juvenile birds should be housed with these birds, providing they pose no health risks. When no live-tutors are available, tape-tutoring

should be considered the best option. It also seems that social interactions with other juvenile males can ameliorate the negative effects of isolation rearing, and possibly tape-tutoring. This has implications for rehabilitation, since conspecific juveniles can easily been kept in small groups prior to release. Since young birds do not have to be exposed to song on a continual basis in order to learn, this simplifies any tutoring regime. Several other factors, such as food abundance, parasites and stress, can affect song learning and these factors must be considered in any rehabilitation scheme.

Acknowledgements

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