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Song copying and cultural transmission in indigo buntings

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Abstract. First-year male indigo buntings, *Passerina cyanea*, copy the song of a neighbouring male during their first breeding season. To determine whether they assess their neighbours and copy selectively the songs of certain males, the following predictions were made from hypotheses of assessment and socially biased learning: (1) first-year males assess a neighbour and copy his song if he meets a minimum standard; (2) first-year males prospectively assess the breeding success and survival of several neighbours, then copy the song of one that has a high breeding success, and (3) first-year males sample their neighbourhood for a common song and conform to it. The 'song model' was identified and the male's breeding success determined in 580 cases of cultural transmission. More males than expected at random had either zero or more than two other males copy their song. One predictor of song transmission by potential 'models' was age (first-year or adult), a trait assessable by plumage colour. Adult males were more likely to transmit their song than were first-year males. In one population the bluer first-year males were more likely to be copied than were the browner first-year males. Also, a male that arrived early in the breeding season was more likely than a later arrival to be copied. The first-year males in a dense neighbourhood were more likely to copy a neighbour's song, but they did not generally conform to the most common song in their area. Although time of arrival and a minimal standard of plumage and behaviour may explain some variation between males in cultural success, much of the variation was unexplained. Many adults were not copied, because of the age structure of the population with more adults than first-year males. Also, many males that had a successful breeding season were not copied, perhaps because their success was unpredictable early in the season when most first-year males acquire a local song.

Cultural transmission is a process of social learning within and across generations (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). Culturally transmitted traits may continue over many generations, often from older individuals to younger ones, and these we refer to as 'traditions' (Payne et al. 1981; Shils 1981). Which individuals are effective 'models' in the transmission of their cultural traits and traditions may be determined by circumstance or by choice. Songbirds are ideal for a study of cultural transmission, as they learn their songs by hearing conspecifics, normal song does not develop without hearing or socially interacting with the 'models' (Kroodsma 1978, 1982; Payne 1981; Petrinovich 1985; Baptista & Morton 1988) and cultural traditions in the form of discrete song types can continue for many generations (Payne et al. 1981; Payne 1985; Thielcke 1992). Here we ask the question, from whom do the birds learn their songs?

In the seasonally migratory indigo buntings, *Passerina cyanea*, song is copied from a neighbouring male in the first breeding season after hatching, when the birds return from the tropics in spring (Payne 1981, 1983b; Payne et al. 1987). Only the male sings. A first-year male may sing one song or several different songs in turn over a few weeks early in the season, then he settles on the one song type that he will sing for the remainder of his life. About 80% of the first-year males copy the song type of a local neighbour. Buntings with matching songs are usually on adjacent territories. First-year males usually copy the song of an individual bunting, rather than combining elements from two or more males (Payne 1981; Payne et al. 1988). The other 20% of the first-year males retain a unique song and do not copy a local song. Some males with individualistic songs in their first year are copied when they return in a later year (Payne et al. 1988). We observed all males

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and recorded their songs and their neighbours' songs as part of a longitudinal study of individually marked birds and their breeding success throughout their lifetimes.

Although song copying is common, the chance that a particular male will transmit his song (be copied) is low because older males outnumber first-year males in a population and because not all first-year males copy a local song (Payne et al. 1988; Payne 1989; Payne & Payne 1990). The surplus of 'models' and the immigration of many first-year males over several years allowed us to compare the circumstance of song transmission in many cases. We observed many different song types in order to compare independent transmission events. In this paper we use the observations from our long-term study of buntings to document the cultural transmission of songs and the breeding biology of individually marked birds, and to test whether first-year males assess their neighbours and select certain ones to copy.

Songs may vary with an individual bird's fitness (Payne & Payne 1977; McGregor et al. 1981; Greig-Smith 1982; Payne 1983a, b, 1985; Lambrechts & Dhondt 1986). Hearing its neighbours' songs might allow a first-year male to assess and select its 'model' for song learning, much as a non-territorial male assesses a territorial male to challenge for its territory (Parker 1974; Arcese 1987; Freeman 1987; Hiebert et al. 1989) and a female chooses a mate or a breeding site (Janetos 1980; Parker 1983; Borgia et al. 1985; Bradbury et al. 1985; West & King 1986; Trail & Adams 1989; Zack & Rabenold 1989; Hill 1990; Beletsky & Orians 1991; Eens et al. 1991). In addition, discussions of social learning in humans (Boyd & Richerson 1985) suggest to us some possible 'rules' or testable hypotheses of song transmission in birds.

To test whether buntings copy certain males, we first looked for variation between the potential 'model' males and between songs being copied, for potential patterns of copying. A null hypothesis implies that a first-year male copies non-selectively or randomly, and predicts that the success of potential 'models' in transmitting their songs is described by a random distribution of the number of males that copy them. A founder effect hypothesis proposes that early-arriving males are more likely to be copied because more first-year males will hear and copy them as the first singing males they encounter, even when arrival date is not associated with their breeding success.

Using our longitudinal field observations of individual buntings within and between seasons, we then asked whether the first-year males assess another male before copying his song. Do they assess the future success of other males? Do they copy the song of certain neighbours, and are those neighbours the males with high breeding success? Do they sample their neighbours for the most common song types and then copy in a frequency-dependent manner?

Three potential means of assessment were tested to determine whether first-year male buntings assess their neighbours and style their own song after one of them. These assessment hypotheses are as follows: (1) Standard fitness hypothesis. The hypothesis offers the idea that the first-year males are biased by one or more simple traits in the 'model' males of higher fitness. Assessable traits include a standard of plumage condition, song quality, song quantity, and territory size or habitat where the 'model' male has a territory. (2) Comparative fitness hypothesis. Rather than copying the first 'model' male that meets a certain standard, a first-year male prospectively assesses several males, then copies the song of the one with a predicted relatively high fitness. In comparing several males, his assessment is finely attuned to fitness differences among them. The effect of preferential assessment may be judged by the variation among the number of first-year males that copy a certain male, and whether the male is copied at all. In this hypothesis the breeding success and survival of males whose songs are copied are greater than in those that are not copied, and the association of their 'cultural success' or song transmission with their breeding success is greater than explained by a simple threshold effect in hypothesis 1. (3) Convention hypothesis. A first-year male selectively copies a song that is given by a certain number of other males. Song traditions are transmitted in conformity, with the trait that is the most common being the one that is selectively copied, as suggested for cultural transmission in humans (Boyd & Richerson 1985). The probability of copying or being copied may vary either with the number of resident males sharing a certain song, or with the number of neighbouring males in a density-dependent or frequency-dependent manner.

METHODS

Field Methods

We observed indigo buntings from 1978 to 1991 in two populations in southern Michigan, one at

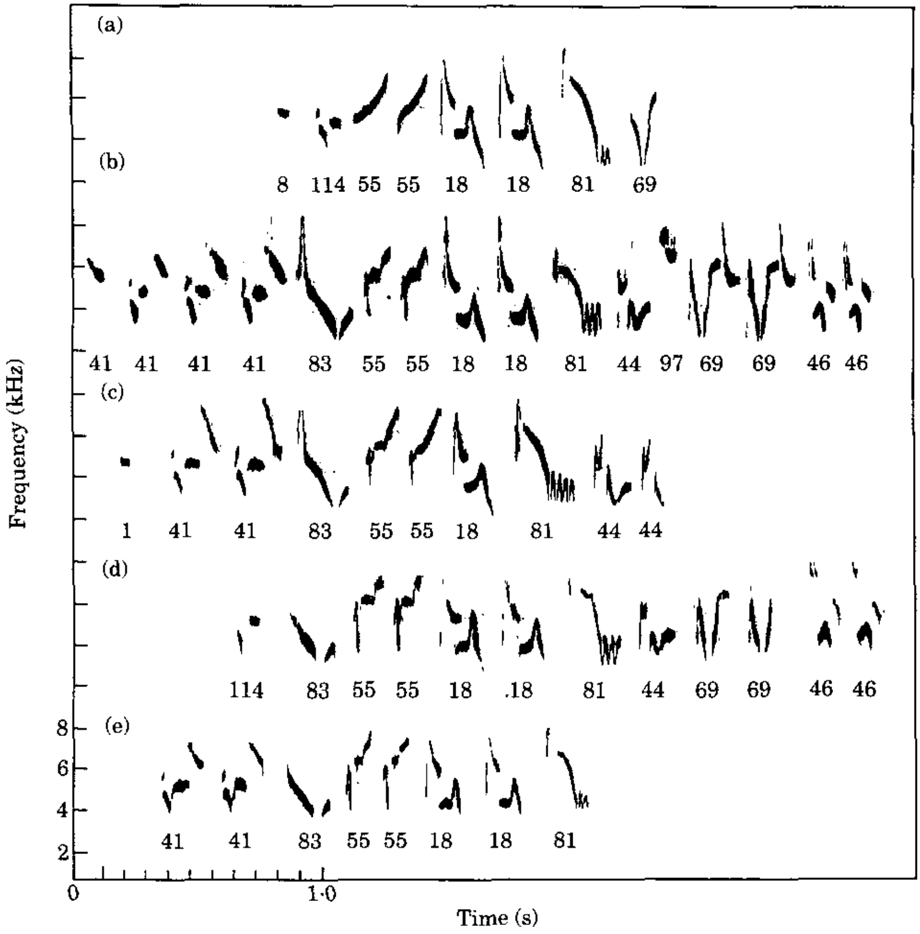

Figure 1. Variation among indigo buntings with matching song types allows determination of the male that a first-year male copied. Males (a)–(d) are adults, and male (e) is a first-year male; all were tape-recorded at Niles in 1983. Numbers 1–98 refer to a catalogue of song figures (Thompson 1970); 114 may be a variant of 41 but we considered it distinct. All five males shared at least three kinds of song figures in the sequence 55–18–81. Compared with male (e), male (a) had introductory figures 8 and 114 (or a variant of 41), lacked 83, and had a variant of 55; male (c) had the same sequence but an unpaired figure 18 and the most complex figure 81 and the bird was 1 km distant; male (b) was similar but had four introductory figures 41, and male (d) had an introductory figure 114 and lacked figure 41. The introductory song figure (1 or 8) was often not very loud and sometimes a bird omitted it. Male (e) probably copied male (d), who had a similar figure 83 and was the only adult with this song within 200 m of male (e).

the George Reserve and adjacent Pinckney State Recreation Area in an area of 12 km^2, the other at Niles in an area of 4 km^2 (Payne 1981, 1983a, b, 1989, 1991, 1992; Payne & Payne 1989, 1990; Payne et al. 1987, 1988). Each male was tape-recorded on his territory and captured in a mist net as he flew to and attacked a dummy mount and a playback of a bunting song. We determined the age by greater primary coverts; first-year males (yearlings, born in the previous year) had one or more brown greater primary coverts, while older adults had all blue coverts. Plumage was scored by the proportion of blue on the body and head; birds were scored in colour intervals (100% blue, 99–80% blue, 79–60% blue, 59–40% blue, 39–20% blue, 19–1% blue, and 0% blue: mixed whitish and brown), separately for the head and body, then scores were summed with the body score weighted three times the score of the head, to give a graded scale that fit our visual impression of overall plumage colour. Nearly all adult males 2 years or older were all blue, and most first-year males had blue plumage mixed with brown. We individually marked the birds with colour bands and a U.S. Fish and Wildlife Service numbered band and then released them. We marked and observed nearly all resident males in the two study areas from 1979 to 1985 (Payne et al. 1988). Male territories and singing positions were plotted on a map taken from an aerial photograph. As the females and nests were located we monitored their success and failure, and we banded their nestlings between 5 and 6 days of age. Nests were checked for fledging and nest locations were plotted on a map. The distance of one male to another was determined from the map.

The breeding season extends from mid-May (the earliest egg dates) to late July for most buntings, although a few eggs are laid in late August (Payne 1992). Beginning in the first week of May, we tape-recorded the first-year males weekly through the breeding season to detect their time of song change; older adults were taped less regularly. We analysed the recorded songs with a Kay Elemetrics Sona-Graph model 7029A. Bunting song consists of a series of paired elements or 'song figures' given in a regular sequence, which is repeated by an individual male hundreds of times without variation except for deletions of terminal song figures from some songs. We scored song figures by visual comparison of the spectrogram with the directory of Thompson (1970) and compared the sequences of song figures with the computer program MATCH, using the number of song figures in the same sequence as the criterion of song matching (Payne et al. 1981). We recognized the songs of any two birds as the same 'song type' if they shared at least three different song figures in sequence (Fig. 1). In practice, if they matched three figures they usually matched a string of five or six figures, which would be the length of a typical indigo bunting song (Thompson 1970; Emlen 1972; Payne et al. 1981). Buntings have about 100 song figures in the species' repertoire (Thompson 1970). Although the song figures are widespread throughout the species' range (Shiovitz & Thompson 1970), males do not share three-figure sequences unless they have learned their songs from each other or a common source (Payne 1981; Payne et al. 1981, 1988). We also recognized two songs as a match when they shared a string of at least three out of four song figures. This allowed us to include songs that were copied from the song 'model' with minor change (substitution, omission, or addition of a song figure) (Payne et al. 1981, 1988). By this three-of-four criterion we included an additional 64 first-year males (for 10·5% of the total of 608 first-year males that matched a song) as copying the song of another male. Within a song type we observed variations among males in shape and number of the song figures in the audiospectrograms, and we used these variants to trace the source of a first-year male's song to the male that he copied, his 'model'.

A few males copied sequences of song figures from more than one 'song model' as judged either in the sequences of song figures within a 'cultural hybrid' song or in a persistent repertoire of two song types rather than one. The 'hybrid' males and males with two persistent songs were uncommon and comprised fewer than 5% of all males (Payne et al. 1988). For males with 'hybrid' songs we used the first sequence of three or more song figures in the song as the definitive song (the later song figures were not always given, as a singing male sometimes truncated a song; Thompson 1970; Payne et al. 1981) and for males with 'bilingual' repertoires we used the song that we recorded most often.

In analyses of song copying and breeding success, we included a male as a potential 'song model' when he met the following criteria: (1) banded and of known age (first-year or older adult), (2) 'resident' on the study area long enough to complete a nesting attempt to the fledging stage (a 'resident' was there for at least 28 days, Payne 1989), (3) observed continuously throughout the breeding season (i.e. was not overlooked early or late in the season), (4) breeding success for the season was determined, (5) survival or failure to return in the following year was known, (6) arrived on the study area by 10 June and (7) observed in one or more years from 1979 to 1985. A male in one year constitutes a 'case', and an adult male provided more than one case when he returned in subsequent years.

We determined the number of first-year males that copied the song of a potential 'song model' by comparing the shared song figures, their variant shapes, their repetition (singlets, doublets and triplets) and their timing within a song (Fig. 1). Occasionally, two or more first-year males shared a song that was unique (i.e. not shared with an adult model). When one first-year male sang it first, he was a potential 'song model' of the others, and when two or more first-year males arrived within 3 days of each other and we did not determine which sang it first, each was a potential 'song model' of the other. When two or more males had similar songs and arrival dates and only one had its territory adjacent to the first-year male, the closest neighbour was credited with the transmission. When two or more males could have been the 'song model' for a first-year male and no differences were apparent in their song, seasonal activity or location, we excluded all males with the song type in that year from the analysis. By these criteria, it was clear to us in 1015 of the 1090 cases (93%) whether the male's song was copied by another male. We were uncertain in the 75 other cases (7%). Each male that met the criteria for residence and for resolution as a 'song model' was counted for as many years as he was observed (387 males were present for 1 year, 200 for 2 years, 228 for 3 years, 124 for 4 years, 45 for 5 years, 24 for 6 years, seven for 7 years). The sample involved a total of 608 banded males (317 at the George Reserve, 291 at Niles). Because some first-year males switched their songs more than once in a season, copying one neighbour then moving to a new site and copying another (Payne 1983b), we took their last song in the season as their definitive song. Each first-year male was counted only once as a song copier. The number of documented first-year males that copied a local 'song model' was 580 (321 at the George Reserve, 259 at Niles), and this is the sample size we used for determining the context of cultural transmission events.

We measured mating success within a season as the number of females nesting on the male's territory (about 15% of the breeding males have more than one female, Carey & Nolan 1979; Payne et al. 1988) and breeding success as the number of young buntings that fledged from nests on his territory. Because of extra-pair copulations and fertilizations (Payne 1983a; Westneat 1987, 1990; Payne & Payne 1989), the number of young fledged may not equal the number that were genetically fathered by a resident male. Nevertheless breeding success as defined here corresponds with the number of young that might be observed by the resident buntings and their neighbours, and is closely correlated with the number actually fathered based on DNA fingerprinting studies (Westneat 1990), so is appropriate for behavioural assessment. A few first-year males copied a neighbour's song only in late summer, although most males copied a local song within a few weeks of arrival. We determined survival of males by observation in the next season (Payne & Payne 1990), and longevity and lifetime success by continuing the observations to 1991.

Statistical Analyses

Univariate chi-squared tests, correlation tests, Student's t-tests, ANOVAs and linear and polynomial regressions were computed for most tests ($\alpha = 0{\cdot}05$). We used logistic regressions (logit) to test whether the breeding success of a male was associated with the transmission of his song to a first-year male. In this analysis, song transmission of the male case was scored as success or failure. Logistic regression allows a test of the effects of independent variables on a two-state dependent variable. It allows a test of effects of independent variables that are graded (such as the number of fledglings produced in a season), binary (such as first-year or adult age), or a combination of these (Finney 1971; Fox & Guire 1982; Aldrich & Nelson 1984). Finally it allows an estimate of the effect of one variable on the dependent variable, by comparison of the log-likelihood G-statistics when other variables are included or excluded from the analysis.

RESULTS

Variation between Males and between Songs

We determined the transmission of song from one potential 'model' male to a first-year male for 317 resident males at the George Reserve and 291 males at Niles. Combining the number of copiers for each potential 'model' in all years that he was resident between 1979 and 1985 (a total of 1015 cases), fewer than half of the resident males were copied. At the George Reserve, 212 (33%) resident males were copied in their lifetime, and at Niles 130 (45%) were copied. The number of first-year males that copied a resident male over his lifetime ranged from zero to six at the George Reserve and from zero to 17 at Niles. Copying by first-year males was common but few 'model' males were copied.

We found no obvious difference in acoustic structure between songs that were matched or not matched by other males. We also found that most songs were locally transmissible, insofar as they were shared by two or more males. Of the resident males whose songs were not copied (potential 'models'), only 8% at the George Reserve and 19% at Niles had locally unique songs. The other resident males either copied a local male or were copied by another male (196 males with 69 distinct song types at the George Reserve, and 130 males

Table I. Biological success and cultural transmission of indigo buntings, 1979–1985

Area	Success	Age	*N*	Min	Max	$\bar{X}$	SE
George Reserve	*N* young fledged*	Adult	355	0	8	2·11	0·104
		First-year	198	0	8	1·43	0·124
	N song copiers†	Adult	332	0	6	0·92	0·069
		First-year	177	0	2	0·09	0·02
Niles	*N* young fledged	Adult	356	0	10	2·43	0·111
		First-year	182	0	8	1·59	0·129
	N song copiers	Adult	341	0	5	0·74	0·054
		First-year	166	0	2	0·04	0·017

*Nestlings that survived from all nests on a male's territory.

†The number of buntings that copied their song from the male.

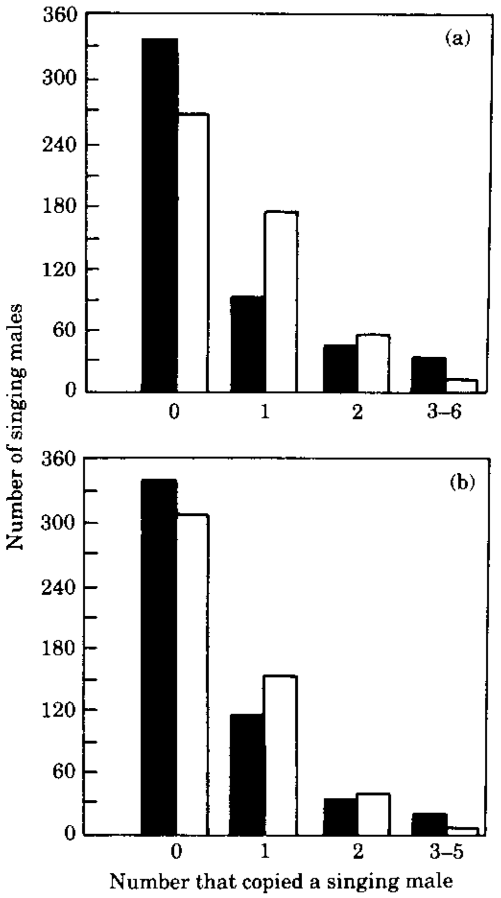

Figure 2. Number of first-year males that copied the song of resident male indigo buntings (both adults and first-year males as potential 'song models') at (a) George Reserve and (b) Niles. ■: Observed and □: expected.

with 44 song types at Niles). Because they shared a song with at least one other male, most males that did not transmit their song nevertheless had a locally transmissible song. In the years before they were adults, we observed most of these same males copying the song of a neighbour during their first-year season, so the adults shared their songs largely as a result of copying in an earlier year. A few males in the first few years of the study were originally banded as adults, but we banded most males as first-year males, and we determined their songs in all years of their lifetime. We also tested whether certain songs were transmitted proportionally more often. We compared the mean number of copiers per male for males that shared the same song type, where an analytic group consisted of the male-year cases with a common song type, and a group had at least six cases (range=6–47). We found no significant difference in the transmissivity of song types (ANOVA, George Reserve, $F_{27,358}=1\cdot22$, NS; Niles, $F_{25,380}=0\cdot74$, NS). The results suggest that variation in song transmission was related to the male singing the song, rather than to certain songs.

Random Cultural Transmission (Null Hypothesis)

A null hypothesis predicts that the number of first-year males that copy the song of a resident male can be described with a random distribution. The number of first-year males copying the songs of each banded resident male in each breeding season was determined from 1979 to 1985. The numbers observed were compared with those expected in a Poisson distribution (Sokal & Rohlf 1981). A

Poisson distribution is an appropriate random model insofar as it assumes that song transmission by a male is infrequent and the copying events are independent of each other. The first assumption is supported by Table I and Fig. 2, and the second is supported by the last section of the Results.

Most males did not transmit their song to another bunting (Fig. 2). The mean number of first-year males that copied an individual male's song at the George Reserve was 0·63 ($N=508$ male cases), and at Niles the mean was 0·51 ($N=507$ male cases), so song transmission was an infrequent event for a 'model' male, due to the occurrence of more singing males available as 'models' than as 'copiers' in the population (Payne *et al.* 1988; Payne & Payne 1990). More males than expected transmitted their song either to no first-year males or to three or more first-year males, and fewer males than expected transmitted a song to one or two first-year males (George Reserve, $\chi^2=53{\cdot}13$, $df=3$, $P<0{\cdot}01$; Niles, $\chi^2=21{\cdot}21$, $df=3$, $P<0{\cdot}01$). Considering only the adult males, the distribution was similar to that of all males; more 'model' males than expected were unsuccessful or had three or more 'copiers' (George Reserve, $N=332$, $\chi^2=48{\cdot}85$, $df=3$, $P<0{\cdot}01$; Niles, $N=341$, $\chi^2=18{\cdot}23$, $df=3$, $P<0{\cdot}01$). Few first-year males were copied (George Reserve, $N=12$; Niles, $N=5$) and the frequency distribution of first-year males that copied them did not differ from random (George Reserve, $N=176$, $\chi^2=4{\cdot}48$, $df=2$, NS; Niles, $N=166$, $\chi^2=1{\cdot}56$, $df=1$, NS). From these results we reject the null hypothesis, that the distribution of the number of males that copy the song of 'model' males is random.

The test involved observations of each male for as many years as he was present, thus to determine whether the cases of a male were reasonably independent, we compared the variance in song transmission (number of copiers in each year) attributable to variance between males, in 'model' males that were present for 3 adult years or longer. The mean number of their 'copiers' varied significantly between 'model' males (ANOVA, George Reserve, $F_{55,142}=1{\cdot}87$, $P<0{\cdot}01$; Niles, $F_{64,165}=2{\cdot}13$, $P<0{\cdot}001$), and only a small proportion of the overall variance was due to the variance between the males (covariance analysis, George Reserve, 19·8%; Niles, 24·3%). We note that the condition of a mate (including his plumage in the breeding season), his age (especially from his first year to his first adult year), his breeding success, his habitat, and the number and identity of his neighbours may all change and provide some independence of cases across years. Previously, we also found no significant correlation from year to year of the breeding success of individual males (Payne 1989). Because we found considerable independence in the cases of a male across years, we include all 1015 cases as potential song models.

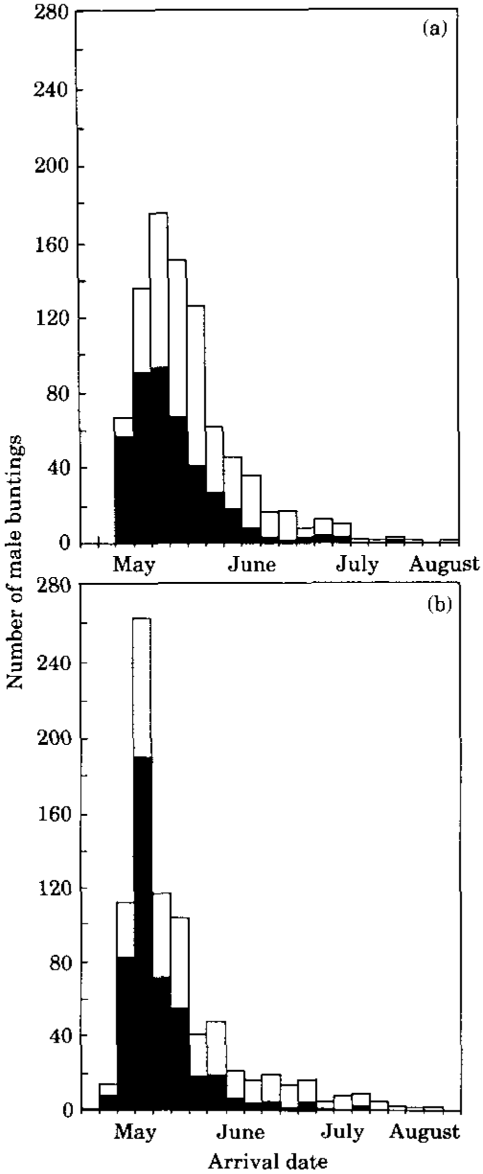

Figure 3. Date of arrival of male buntings at (a) George Reserve and (b) Niles from 1979 to 1985.

Founder Effect (a Neutral Hypothesis)

Song transmission may occur on a first-come, first-copied basis. If the date of arrival of the 'model' males affects their song transmission, the effect is likely to be indirect, as when the early settlers take their territories, and the first-year males are attracted to these areas and copy the songs irrespective of male condition; rather than direct, as though active assessment. First-year males arrive later than adult males on average, but the dates overlap broadly between age groups and many first-year males arrived before the median date of arrival of the adults (Fig. 3). Female buntings begin to arrive about 2 weeks after the earliest males (Carey 1982; Payne 1992). Several first-year males copied their neighbouring males' songs a week before the earliest females arrived, so it is unlikely that females affect song copying at this time of the year.

Most first-year males that copied a local song acquired it within 2 weeks of their arrival, and sometimes within a day or two. The mean date of arrival of male buntings that had a nest was 16–22 days earlier than the mean date of first nest. The mean date of arrival was 21 May and the mean date of first nest was 10 June. Most first-year males that copied the song of a local bunting did so by 8 June; some switched their song after their first nesting attempt (Payne et al. 1988; Payne 1991).

We compared date of arrival with breeding success and song transmission in the 'model' resident males that arrived by 10 June. Breeding success was significantly correlated with date of arrival at the George Reserve between adult males ($N=332$, correlation coefficient $b=-0{\cdot}124$, $P<0{\cdot}05$), although not between first-year males ($N=176$, $b=-0{\cdot}097$, NS). Early males were not significantly more successful in breeding at Niles (adults, $N=341$, $b=0{\cdot}002$, NS; first-year males, $N=166$, $b=0{\cdot}053$, NS). Breeding continues later into summer at Niles, where both second nesting attempts and second broods are more frequent (Payne et al. 1988; Payne 1989). Although breeding success of adult males was significantly associated with their date of arrival at the George Reserve, the date of arrival explained a very small proportion of the variation in success ($r^2=0{\cdot}015$). Early arrival was associated with song transmission for adult males in both areas (George Reserve, adults, $b=-0{\cdot}192$, $P<0{\cdot}01$; Niles, adults, $b=-0{\cdot}166$, $P<0{\cdot}05$). There was no strong or consistent association of date of a male's arrival and his breeding success. Therefore the date of arrival appears to be associated with song transmission through a cultural founder effect (Mayr 1963; Baker & Jenkins 1987), with the song of the early-arriving resident males being copied both by the early and the later first-year males, rather than being a cue which might be used in active assessment.

Resident males that arrive early may have longer seasons of residence, which were as long as 102 days at the George Reserve ($\bar{X}\pm$SD$=64{\cdot}52\pm17{\cdot}25$) and 117 days at Niles ($71{\cdot}67\pm7{\cdot}77$). Arrival date was associated with the total period of residence (George Reserve, adults, $N=332$, $b=-0{\cdot}501$, $P<0{\cdot}001$; Niles, $N=341$, $b=-0{\cdot}326$, $P<0{\cdot}001$). However, the variation in the duration in residence was not associated with song transmission. For resident adults, the length of residence was not significantly correlated with the number of males that copied their songs (George Reserve, $b=0{\cdot}105$, NS; Niles, $b=0{\cdot}039$, NS). The lack of correlation between date of arrival and the number of first-year males that copied a male's song is probably a result of early-season learning of song. A first-year male may hear a song early in the season and sing it later. A few first-year males changed songs to copy a neighbour as late as mid-July, but even they may have heard the songs earlier in the season. In this comparison, the date of arrival is more important than the length of residence in determining the number of males that copy a bunting's song.

Standard Assessment (Adaptive Hypothesis 1)

The hypothesis of standard assessment predicts that first-year males are more likely to copy the song of a 'model' male that meets certain phenotypic criteria associated with fitness (e.g. successful breeding, the production of fledglings), than the song of a male below these minimum standards. The hypothesis predicts an association between the biological success of a 'model' male, and cultural transmission of his song to a first-year male. In a series of logistic regressions, we tested whether the variation among resident males in fitness was associated with their song being copied. First, we tested whether being copied was associated with breeding success of the 'model'. Second, we considered the effect of age and date of arrival on song transmission. Then we tested whether the remaining variance in breeding success accounted for the differences between males in song transmission, and whether the residents that

Table II. Cultural transmission of song in indigo buntings

Variable Area, N	b^* coefficient	SE	z	P
George Reserve, $N=508$				
Partial model, without breeding success†				
Age (first-year, adult)	2·48	0·32	7·72	***
Arrival date	−0·04	0·01	−2·92	*
Full model, with breeding success‡				
N females	0·18	0·27	0·66	NS
N fledglings	0·05	0·06	0·95	NS
Niles, $N=507$				
Partial model, without breeding success§				
Age (first-year, adult)	3·33	0·48	7·12	***
Arrival date	−0·03	0·02	−2·06	*
Full model, with breeding success††				
N females	0·32	0·19	1·73	NS
N fledglings	0·01	0·54	0·16	NS

*$P<0.05$, **$P<0.01$, ***$P<0.001$.

†$G=115.34$, $df=2$, $P<0.001$.

‡$G=117.09$, $df=4$, $P<0.001$; $\chi^2=1.75$, $df=2$, $P>0.05$, NS.

§$G=133.91$, $df=2$, $P<0.001$.

††$G=137.46$, $df=4$, $P<0.001$; $\chi^2=3.55$, $df=2$, $P>0.05$, NS.

were copied were more likely to survive and return in the next breeding season. Finally, we compared song transmission in relation to the plumage of potential 'models' to test the importance of the visual aspect of the first-year males in their cultural success.

'Model' male buntings varied in their success in breeding and in transmitting their song to a first-year male. On average, adults were twice as successful in breeding as the first-year males and were more than 10 times as successful in transmitting their songs (Table I). Nearly all adult males had at least one nest (Payne et al. 1988). If first-year males copy the songs of adult males, then they would nearly always be copying a bird that will nest at least once, so they would do better than copying a singing male at random. The adults that transmitted their songs also all sang and held a territory.

Breeding success

When both age groups of males were considered together, breeding success was associated with whether or not a 'model' male transmitted his song to another male. In the comparison of breeding success and cultural success using the logistic regressions, the number of fledglings produced (the independent variable) was associated with whether a male was copied (George Reserve, $N=508$, $G=8.97$, $P<0.01$; Niles, $N=507$, $G=5.77$, $P<0.05$). When the comparison was limited to adult males, the association was not significant (George Reserve, $N=332$, $G=2.14$, NS; Niles, $N=341$, $G=0.12$, NS). Although the frequency distribution of the number of first-year males that copied an adult 'model' was non-random (Fig. 2), this effect did not appear when the occurrence of song transmission was compared with male breeding success.

To determine whether cultural success is explained when other variables are considered we carried out a series of logistic regressions. First, we compared the cultural success of a male (whether his song was copied by at least one other bunting) with his age and arrival date, which accounted for some variation in song transmission among 'model' males. Then, we compared his cultural success with (1) age, (2) date of arrival of the male (in residents that arrived by 10 June), (3) mating success or number of females and (4) breeding success (the number of buntings fledged), with (3) and (4) being our end-of-season measures of fitness. When all variables were considered together, only age and arrival date were significantly associated with song transmission (Table II). Adults were more likely than first-year males to be copied, and early arrivals were more likely to be copied than later arrivals, as in the earlier analyses.

Mating and fledging success were associated with being copied, although a regression including the number of mates and number of young fledged did not explain significantly more variation between 'model' males in cultural transmission than did a regression with only age and date of arrival in spring (Table II). The difference in the G-statistic in the two regressions approximates χ^2; the value was not significant ($P > 0{\cdot}05$). That is, a correct prediction of breeding success did not significantly increase the likelihood that a male's song would be copied.

The test is conservative since colinearity among variables will affect the relationship of each one to the dependent variable. To show the association between variables, we combined ages and tested the significance of correlations for males of all ages. Mating and breeding success were correlated with date of male arrival at the George Reserve ($N = 508$, mating success: $b = -0{\cdot}092$, $P < 0{\cdot}05$; breeding success: $b = -0{\cdot}146$, $P < 0{\cdot}01$) but not at Niles ($N = 507$, mating success: $b = -0{\cdot}021$, NS; breeding success: $b = -0{\cdot}019$, NS), and date of arrival was correlated with the number of buntings that copied a male's song (George Reserve, $b = -0{\cdot}21$, $P < 0{\cdot}01$; Niles, $b = -0{\cdot}19$, $P < 0{\cdot}01$). Because the association of song transmission and breeding success was conservatively attributed to age and date of arrival, the test may have underestimated the effect of assessment, but there was no significant association between breeding success and song transmission when we limited the analysis to adult males (Table I). Because females settle on a male's territory and breed over a 4-month period, the number of fledglings cannot be determined until the end of summer, and thus a male's breeding success is not obvious early in the season. Even a correct prediction of a male's breeding success is no more than a marginal predictor of his cultural success.

Nesting date

If first-year males observed the nesting activities of other males, they could narrow their range of 'song models' to the more successful males, but then they would delay their own song development.

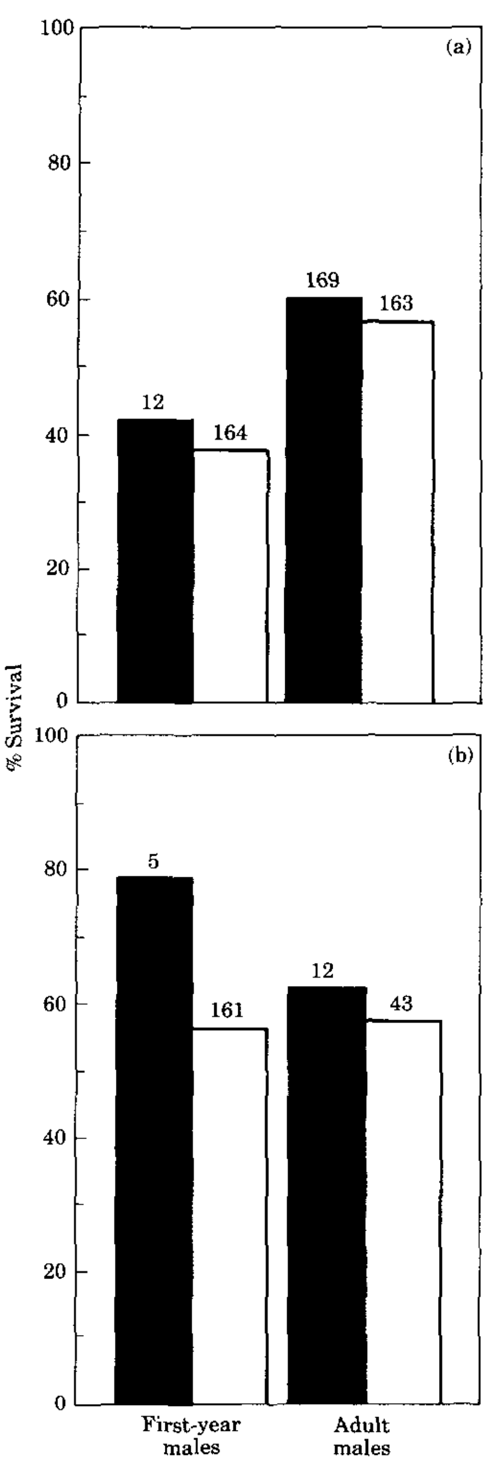

Figure 4. Survival in male buntings at (a) George Reserve and (b) Niles, in relation to their song transmission in the previous year. First year males copying: yes ■, no □; adult males being copied: yes ■, no □. N values are shown above bars.

If the 'models' nested by a certain date, however, they still might be selectively copied. To test the effect of nest date on song transmission, we considered all males that had a nest on their territory. In 957 cases for which a resident male's song transmission and breeding success were known, a female built one or more nests and laid one or more eggs.

We compared the results of a logistic regression of age and arrival date on song transmission with a regression that also included the date when the first egg was laid. At the George Reserve, in the cases where a 'model' male had at least one nest, song transmission was associated with age and date of arrival ($N=471, G=98{\cdot}3, df=2, P<0{\cdot}05$). Including the date of nesting did not significantly increase the association with song transmission ($G=2{\cdot}26, df=1$, NS). At Niles, song transmission was associated with age and date of arrival ($N=486$, $G=125{\cdot}5$, $df=2$, $P<0{\cdot}05$); adding the date of nesting accounted for little more variance in song transmission ($G=2{\cdot}05$, $df=1$, NS). In both areas, the 'model' males that were copied tended to nest earlier but not significantly so. The timing of song copying and nesting were not closely associated with the time of a male's arrival, as many first-year males nested before they copied a local song, and many others copied a local song before any buntings nested (Payne et al. 1988).

Annual survival

If first-year males copy the song of males that will survive, then we expect an association between the probability of a 'model' male's song being copied and the probability that he will return the next year. We compared whether the resident males whose songs were copied were more likely to return. No significant association was observed between survival of the potential 'model' and his cultural success (Fig. 4). At the George Reserve, the resident adult males whose songs were copied were no more likely to return than adults that were not copied (George Reserve, $G=0{\cdot}69$, NS; Niles, $G=0{\cdot}52$, NS). Between the resident first-year males, birds that copied a song were no more likely to return the next year than birds that did not (George Reserve, $G=0{\cdot}76$, $df=1$, NS; Niles, $G=0{\cdot}28$, $df=1$, NS). We conclude that neither copying nor being copied is associated with annual survival.

Plumage

Buntings might assess 'model' males by breeding plumage, which usually is completely blue in adults and partly brown in first-year males. The fitness assessment hypothesis predicts that, within the

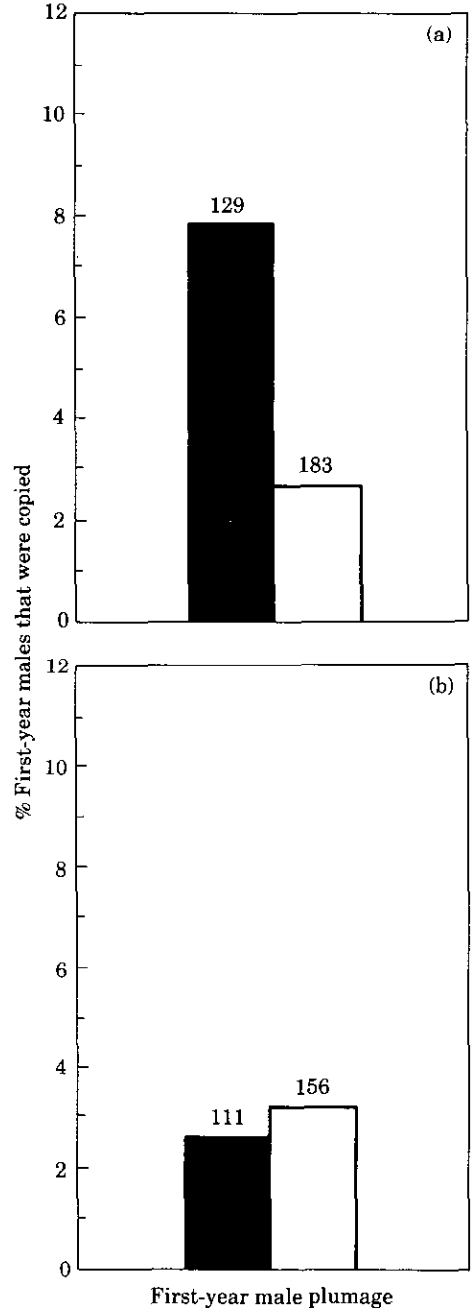

Figure 5. Plumage colour and success in song transmission in first-year male buntings observed in 1979–1985 at (a) George Reserve and (b) Niles. Plumage colour: ■: blue; □: more than 20% brown. N values are shown above bars.

Table III. Regression analysis of the breeding success (number of fledglings) of a male bunting and the number of first-year males that copied his song

Area	Age	N	b	r^2	F	P
George Reserve	Adult	332	0·016	0·001	0·21	NS
	First-year	176	0·004	0·000	0·06	NS
	All	508	0·047	0·007	3·51	0·06
Niles	Adult	300	0·001	0·000	0·05	NS
	First-year	166	0·020	0·026	4·41	*
	All	507	0·040	0·007	3·71	0·05

*$P<0·05$.

first-year males, songs of bluer males are more likely to be copied than songs of browner males, because blue first-year males are similar in plumage to adults, and adults are more successful breeders (Table I; Payne et al. 1988). We compared song transmission between the first-year males, as they varied considerably in plumage colour. We did not compare the older males, as most adults were all blue (Payne 1992), and we usually did not handle them in years after banding to describe plumage in detail.

Does variation in plumage between the resident first-year males explain their variation as 'models' in song transmission? First-year males with bluer plumage were significantly more likely to transmit their song at the George Reserve ($N=176$, $G=5·47$, $df=1$, $P=0·019$), but not at Niles ($N=164$, $G=1·88$, $df=1$, NS), where fewer first-year males were copied. When first-year males were grouped into blue (≥80% blue) and browner (<80% blue) plumage classes, again the blue males were more likely to transmit songs to another first-year male than the browner birds at the George Reserve ($G=4·17$, $df=1$, $P<0·05$), and not at Niles ($G=0·06$, $df=1$, NS) (Fig. 5). The difference between study areas may be related to the lower density and lower breeding success of buntings at the George Reserve (Payne et al. 1988; Payne 1989; Table VII). If the results can be extended to a comparison of first-year males and adults, the plumage differences between age groups may in part explain why the songs of the older adult males are selectively copied.

Comparative Assessment (Adaptive Hypothesis 2)

Comparison may involve a first-year male sampling several males and using cues available to rank them, then copying the one with the higher prospective fitness. Fine-scale assessment might lead to variation between the effective 'song model' males in the number of males that copy their songs. We did not observe the first-year males visiting one neighbouring male after another, but they might compare several singing males simultaneously from their own territory.

Within-season association of song copying and breeding success

To test whether prospective assessment of breeding success might account for the variation between males in transmitting their song, we computed regressions for the number of young fledged on the male's territory and the number of first-year males that copied his song; we transformed variables to arccosines for computation (Table III). For all males of both age groups, breeding success was associated with being copied ($N=1015$, $b=0·04$, $F=6·41$, $P=0·01$), although less than 1% of the variance ($r^2<0·01$) in song copying was explained by breeding success. Within an age and area, the slope b was positive. The males that were successful as breeders tended to have more first-year males copy their songs, but the result was statistically significant in only one of four groups, the first-year males at Niles. The low variance in song transmission explained by breeding success indicates that most of the observed variation in song transmission is not attributable to an accurate assessment of a 'model' male's biological success.

Lifetime breeding success

The comparative assessment hypothesis predicts an association of the lifetime breeding success of a

Table IV. Correlation of the number of males that copied a male bunting's song over his lifetime with his lifetime breeding success

Area	Variable	Partialled variable	N	b	P
George Reserve	Breeding success	None	276	0·468	***
		Longevity	276	0·006	NS
Niles	Breeding success	None	225	0·457	***
		Longevity	225	−0·034	NS

***$P<0.001$.

Table V. Comparison of songs in father and in his first-year offspring

Song	Niles		George Reserve		Totals
	Sons	Daughters	Sons	Daughters	
Different	54	36	6	6	102
Same, observed	4	4	0	0	8
Same, expected*	4·67	3·25	1·15	0·15	9·22

*Expected values $N_e=\Sigma[N_m/N_p]$, where N_m = number of males with father's song type during offspring's first-year season, and N_p = number of breeding males in the sampled area.

bunting and the number of first-year males that copy his song over his lifetime. Lifetime breeding success and song transmission were determined in the 300 males that either (1) appeared as first-year males by 10 June from 1979 to 1984 and remained at least 28 days, or (2) appeared as first-year males and returned in the next year regardless of their first-year period of residence. Breeding success and song transmission were determined to 1991; three males (1%) were still alive in 1991.

Both lifetime song transmission and lifetime number of fledglings were greater on average in males with a longer lifespan. At the George Reserve, 10% of the males accounted for 66% of all transmissions of song, and at Niles, 10% of the males accounted for 47% of all song transmissions. The variance in lifetime breeding success of indigo buntings is determined in large part by the number of years they survive (Payne 1989). When the years survived was included as a partialled variable in the correlation of song transmission and lifetime breeding success, song transmission was not significantly associated with lifetime breeding success (Table IV). Although the number of first-year males that copied a male's song was correlated with his lifetime breeding success, this was due to a cumulative effect: the longer-lived birds had more first-year males copy their songs over the years but they were not copied proportionately more often.

In summary, first-year male buntings copied the songs of successful breeders. When each age class was compared separately, the trends were not significant. Between the adults, not all of the successful breeders were copied, and breeding success accounted for little variance in song transmission. Between the first-year males, birds with blue plumage were more likely to be copied than birds with more brown in their plumage. It is unlikely that a young male bunting assesses other males for quality, except for age which may be signalled by the blue plumage.

Assessment by Convention (Adaptive Hypothesis 3)

The hypothesis of a bias for transmitting a conventional behaviour predicts that whether a song type is copied depends on the density or the frequency of the song type, or both. The common song types may be copied selectively, as suggested for humans (Boyd & Richerson 1985). In contrast a null hypothesis predicts that song types are equally likely to be copied, with a probability set by their

Table VI. Association of the number of first-year males (*N*) with a song type and the number of adult males with the same song type

Area	Order	*N*	*b*	r^2	*F*	*P*
George Reserve	Overall	182	0·34	0·11	11·4	***
	First	182	0·73		16·0	***
	Second	182	−0·05		6·81	**
Niles	Overall	179	0·49	0·24	28·5	***
	First	179	0·66		6·68	***
	Second	179	−0·16		4·26	***

**$P<0·01$, ***$P<0·001$, polynomial regression; *b* indicates the regression slope for each polynomial order of the regression.

frequency in the population. The number of males that a bunting may sample is unknown and presents us with a problem of scale, so we examined both the number of males in a study area and the number of males near a first-year male's territory.

Assessment at the population level

For the largest sample of males that a first-year male might assess, we first considered the number of singing males on the study area. The biological significance of the number on this spatial scale is that it is about equal to the number of males estimated as a random source of songs for the buntings with the same song as their father. When buntings that we banded as nestlings returned to breed, they did not have their father's song, but a few males later acquired their father's song either from their father or from another male with the same song type (Payne et al. 1987). Females usually mated with a male whose song differed from their father's, but they occasionally mated with a male with the same song. We updated through 1991 the values in Payne et al. (1987) for the first-year buntings with the same song as their father's (and, for the females, mated with a male with their father's song type), and allowed for the number of males with the same song that their father sang. The proportion of first-year buntings with a song like their father's was close to the proportion expected if the buntings copied a male at random in a population of about 80 singing males, the number of resident males during early June on each study area (Table V).

We compared the number of adult and first-year males with each song type, considering all males on the study area. Some song types were widespread and birds sang these across more than 1-km distance within the study area (Payne et al. 1988; Payne & Westneat 1988). The number of first-year males that had a particular song type was significantly associated with the number of adults with that song type: song neighbourhoods with many adults had many first-year males as well (Table VI). The first-order regression term was significant. However, the slope of the second-order term was negative, so the common song types were copied less often than expected, rather than more often as predicted by an hypothesis of convention. Also, the regression model accounted for less than 3% of the overall variance. That is, on a large scale we found no frequency-dependent song copying.

Assessment by neighbourhood density and convention

On a more local scale the first-year males may assess their neighbours. A first-year male might assess an area as a place to settle when the local density is high, with singing males providing cues to suitable habitat and visiting females, much as a female or male in a lekking species may be attracted to a site where other females are attracted (Wiley 1991; Gibson 1992). The number of males sampled may be the number singing as heard from a male's territory. An hypothesis of density- or frequency-dependence predicts that a first-year male bunting is likely to copy a song if it is given by two or more neighbours or if it is the most common local song. We asked three questions at the scale of a territory neighbourhood. (1) Was song copying by a first-year male related to the number of territorial males nearby? (2) Was the most common song more likely to be copied? (3) Was a song more likely to be

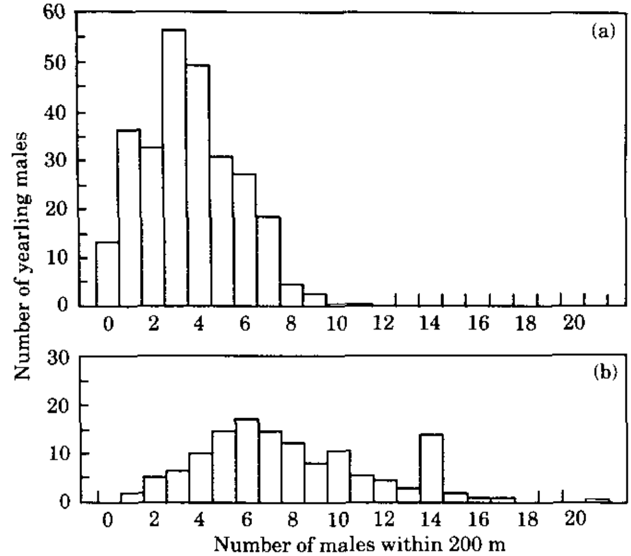

Figure 6. Frequency distribution of the number of neighbouring males of first-year male indigo buntings at (a) George Reserve and (b) Niles.

Table VII. Neighbourhood densities (resident males within 200 m) of first-year male indigo buntings

Variable (*N* first-year males) Area	*N*	Min	Max	$\bar{X}$	SE
George Reserve					
Total number of neighbours	290	0	11	3·67	0·129
Neighbours with same song		0	5	1·18	0·066
Neighbours with other most common song		0	4	1·30	0·049
Neighbours with most common song		0	5	1·78	0·058
Niles					
Total number of neighbours	250	1	21	7·55	0·224
Neighbours with same song		0	10	1·92	0·105
Neighbours with other most common song		0	9	2·49	0·093
Neighbours with most common song		1	10	3·20	0·092

copied if a higher proportion of males shared the song?

From our census data we determined the songs a first-year male could hear during his first 10 days on the study area (or a shorter time, if he did not remain that long) from maps and song spectrograms from 1981 to 1985. We used a distance of 200 m, as we heard songs and saw intrusions of males over that distance; 200 m includes males on adjacent territories and often the males on the next territories as well. First-year males arrived on the area and copied a song as late as August, so we included first-year males arriving at any time in the breeding season. When a male nested, we used his territory as the centre of his neighbourhood. When he did not nest, and when he moved, we used the site where he spent the most time during his first 10 days.

Most first-year males settled near another male bunting (Fig. 6). A few of them had no neighbours within 200 m although they had a local song. Some heard a song in one site, then moved and sang the same song at a second site. Others sang a song unlike any other males in the study area; these first-year males may have heard it elsewhere, then introduced it into the area. Many first-year males

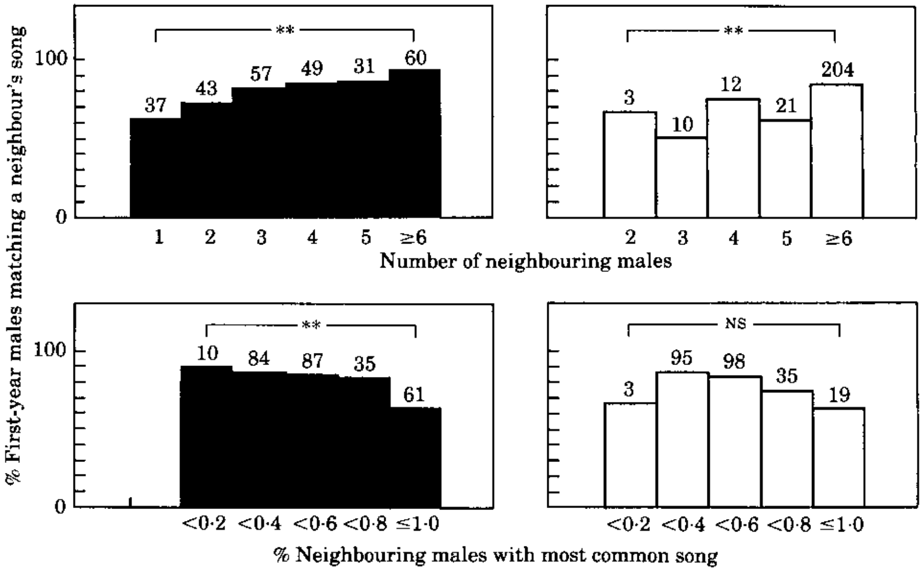

Figure 7. (a) Proportion of first-year males that matched a neighbour's song in neighbourhoods varying in density and (b) the proportion of neighbouring males with the most common song at George Reserve (■) and Niles (□).

Table VIII. Effect of the number of local neighbours on song copying by first-year male indigo buntings: step-wise logistic regression

(Step) Variable Area	*N*	*G*	*P*
George Reserve			
(1) *N* days resident on study area	277	31·24	***
(2) *N* neighbouring males		8·99	**
(3) *N* neighbours with most common song		0·56	NS
Niles			
(1) *N* days resident on study area	250	39·31	***
(2) *N* neighbouring males		14·06	***
(3) *N* neighbours with most common song		0·77	NS

$^{**}P<0·01$, $^{***}P<0·001$. *G* indicates the difference in *G* from the preceding step.

copied a local song during their first 10 days, although some did so weeks later (Payne et al. 1988). Most buntings had several males in their neighbourhood, and more than one male in the neighbourhood had a song they did not copy (Table VII).

If song is copied independently of the density of singing males, then the proportion of first-year males copying a song will not vary with the number of singing males in the area. But if song copying is density-dependent in a positive direction, then the proportion of first-year males that copy a song will increase with the number of singing males. Excluding the 13 males with no neighbours within 200 m (their history was unknown, although five matched a song elsewhere at the George Reserve), song matching was compared between neighbourhoods of different density (Fig. 7). Most males matched a song even when only one or two males were nearby. Nevertheless, the proportion of first-year males that matched a song increased with local density (George Reserve, $G=16·8$, $df=4$, $P<0·01$; Niles, $G=13·4$, $df=4$, $P<0·01$).

Did first-year males copy when their neighbours had a common song? If copying varies with frequency of occurrence of the song in their area, then first-year males should be more likely to copy a song if their neighbours match each other. At the George Reserve the proportion of first-year males that matched a neighbour's songs differed with the proportion of neighbours that had the most common song ($G=14{\cdot}5$, $df=4$, $P<0{\cdot}05$), but at Niles no such difference was apparent ($G=7{\cdot}67$, $df=4$, NS) (Fig. 7). In the denser neighbourhoods more males matched a common song (George Reserve, $b=0{\cdot}66$, $P<0{\cdot}005$; Niles, $b=0{\cdot}71$, $P<0{\cdot}001$), but a lower proportion of the males had this particular song (George Reserve, $b=-0{\cdot}60$, $P<0{\cdot}001$; Niles, $b=-0{\cdot}47$, $P<0{\cdot}001$). The results indicate that first-year males do not conform to a common song.

The effects of local density and frequency of males with a common song were compared in a series of step-wise logistic regressions (Table VIII). The variable that accounted for the greatest difference in whether a first-year male copied a song was the number of days he was resident; either birds that remained longer were more likely to copy, or birds that copied a song remained longer in the area. The number of neighbouring males added significantly to the statistical description of song copying, but the number that matched the most common song did not.

Also, we compared conformity between males that matched a local song. Did a first-year male copy the most common song in his neighbourhood? For first-year males that copied another male at the George Reserve, 75 of 230 (33%) copied the most common song, 44 (19%) copied a less common song, and 111 (48%) copied one of two or more equally common songs. At Niles, 85 of 203 (42%) copied the most common song, 86 (42%) copied another song, and 32 (16%) copied one of two or more equally common songs. Many first-year males copied the most common song, nevertheless as many as half of them copied a less common song.

In summary, a first-year male was more likely to copy a neighbouring male in a densely-populated neighbourhood, but he did not generally copy the most common song in the neighbourhood. Whether he first settled there or he copied because the neighbourhood was densely populated is unknown. The results are consistent with the view that a first-year male copies the song of a certain individual, rather than the most common song in the neighbourhood.

DISCUSSION

We found little evidence that first-year males can predict the breeding success of the resident males and choose the successful ones as their own 'song models'. The cultural success of the potential 'model' male indigo buntings in transmitting their song was at best marginally associated with whether they were successful in breeding. Their cultural success in song transmission was more strongly associated with their date of arrival and their age. In one of two populations, the first-year males with bluer plumage were more likely to be copied as 'models' than were the browner males, consistent with the hypothesis that the first-year males as 'copiers' choose song models on the basis of the adult-like plumage of the 'models', although in the other population no such trend occurred, and in both populations most of the blue first-year males were not copied. The loose association of song transmission and breeding success is explained mainly by the date of arrival, and when this is taken into account, their breeding success had a negligible effect on whether a male transmitted his song to a first-year male.

A null hypothesis of song copying was rejected, as males differed more than expected at random in the number of buntings that copied their song. More males than expected at random had no success, or had three or more first-year males copy their songs, and fewer than expected had only one or two male copiers. These results suggest that the date of arrival in spring of the 'song models' influences song transmission through a founder effect, with the early singing males being copied by the early first-year males as well as by the later arrivals.

Of the three adaptive hypotheses of assessment, only the standard fitness hypothesis (1) contributed to a description of song transmission. First-year males may copy the song of birds that are aggressive and sing persistently, but age was the only standard trait that we identified, and it is apparently assessed by plumage colour. Nearly all adults were blue and sang, but not all were copied in song, so age and plumage are necessary but not sufficient indices of cultural success, because there were fewer first-year male buntings to copy than there were potential 'song models' in the population, and only 80% of the first-year males copied a local song (Payne et al. 1988; Payne 1989; Payne & Payne 1990).

The comparative assessment hypothesis (2) was not supported in our observations. Although males that are successful breeders tend to be the ones that are copied, the results can be accounted for by associated factors, including the date of arrival as the song of the first male to arrive can be copied earlier and more often. Other behaviour such as singing rate also might affect whether a male is copied. The singing rate of an individual male varies over several orders of magnitude with the time of day and the stage of nesting (Thompson 1972), so 'model' males with different rates of singing do not necessarily signal their subsequent success in breeding. Because song transmission was largely independent of density and local patterns of behaviour, our observations do not support the convention hypothesis (3). First-year male buntings appear not to compare and copy the best 'model' male, when the number of males sampled is the size of the study population. On a more local scale, buntings seem not to copy a neighbourhood song of convention, although density of neighbouring males may affect the length of time the first-year males remain and copy a song as a result. First-year buntings copied a song even if only a single neighbour sang it. An assessment of the neighbouring males' fitness as a guide to which song to copy may be inappropriate insofar as breeding success is indeterminate by the time the first-year buntings use a local song. The differences among neighbouring males in breeding success are not related to their accessible (to humans) behavioural, morphological or genetic traits (Payne & Westneat 1988; Payne 1989), and no obvious fitness cues are available to a first-year male bunting early in the season.

The costs and the lack of reliable cues to fitness of other males may limit assessment in buntings. As in mate choice by a female, the time spent in assessment is lost for breeding and other activities (Parker 1983; Slagsvold et al. 1988; Dawkins & Guilford 1991). Little or no cost is incurred when buntings hear their neighbours' songs in the same time and place. Buntings can feed and sing while they assess, and we saw no predation on singing or listening males. We question whether information gained by a male's more prolonged or active behaviour, such as intruding into his neighbours' territories and testing their responses to him, would pay the cost in attacks by resident males or in loss of the first-year male's own territory while he was away.

In indigo buntings, song may indicate a male's condition at a standard level. A male sings in defending a territory and attracting a female (Emlen 1972; Thompson 1972; Payne et al. 1988). The diversity between the song types themselves does not indicate a difference in fitness, as the annual survival and mean breeding success of males do not differ significantly when compared between song-type groups (Payne et al. 1988; Payne & Westneat 1988). Possible benefits to a first-year male in copying a neighbour's song are to address the neighbour and establish a social co-existence with him when they match his song in aggressive countersinging, and to deceive other males into misidentifying the copier as the experienced and aggressive defender of a territory (Payne 1983b). In buntings, however, breeding success is no higher in resident first-year males that copy a neighbour's song than in those that do not (Payne et al. 1988). Possible benefits to the male whose song is copied include an enhanced advertisement through song mimicry, a social analogue of a Müllerian mimicry complex (Fisher 1958; Moynihan 1968), with the shared song advertising that an area is occupied even when any one song-sharing male is not singing. Again, breeding success is no higher in adults that have neighbours singing the same song types than it is in adults that do not (Payne et al. 1988).

We did not systematically sample over long periods to test whether 'model' males that sing more are copied more often. Because song rate varies considerably with the time of day and stage of nesting (Thompson 1972), it is difficult to sample. Nevertheless, copying the song the males hear most frequently is unlikely to explain the patterns observed. First, we used one playback song to capture the first-year males. The last resident male with this song was in 1978. No other male in 1978–1991 gave it, even though we attracted and caught over 800 first-year and adult males when we used the song repeatedly in playback. The playback rate was similar to that of free-living buntings, with 100–200 songs in an hour early in the season (Payne 1983b). Some first-year males that were slow to be captured were presented with the song more than 200 times in a day and were tried again on other days. No males captured, nor any of the males that we failed to capture, copied this song, which we recognized well as we heard it often in playback. Also, the first-year males did not tend to copy a song type given by the majority of males in their neighbourhood, so again there was no reason to suspect that a first-year male simply copies the song he hears most often.

Rates of social interaction might affect a first-year male's decision to style his song after that of a certain 'model', but we did not systematically compare neighbouring males early and later in the breeding season. Our sampling methods were guided by our observations of naturally-occurring rates of behaviour. In the first 2 years of sampling the behaviour of focal resident males, we saw interactions between neighbouring males only infrequently (means of fewer than 0·4 intrusions or chases in an hour, Payne 1983b). However, when they first settle on a territory, the first-year males may interact at a higher rate (Walton & Nolan 1986). Captive first-year male indigo buntings copy more elements of song when they interact with a free-living male than when they have a caged tutor, and copy more from a caged singing tutor that they can interact with than from a recording (Rice & Thompson 1968; Payne 1981). The observations are consistent with these findings in that hearing a song is necessary, but not sufficient for song copying, and that social interactions are necessary for copying a song.

Social interactions may determine which songs a male will copy in other songbirds by the males assessing the song models by their behaviour, with the age of critical interaction varying among species. Captive zebra finches, *Taeniopygia castanotis*, style their song after the song of a male (their father) that is aggressive towards them at independence (Clayton 1987), and Darwin's finches, *Geospiza fortis*, also often copy their father's song (Gibbs 1990). Other species copy a male after natal dispersal. Marsh wrens, *Cistothorus palustris*, short-tailed tree-creepers, *Certhia brachydactyla*, and white-crowned sparrows, *Zonotrichia leucophrys*, in their first year all copy songs more readily and more completely from males they can interact with than from a loudspeaker of live birds which they can only hear, or from a tutor tape (Kroodsma & Pickert 1984; Thielcke 1984; Petrinovich 1985; Baptista & Petrinovich 1986; Baptista & Morton 1988). Prolonged social interactions between adult male colonial yellow-rumped caciques, *Cacicus cela*, throughout the breeding season accompany a continual copying of the song variants of the other males in the group (Trainer 1987, 1989). Finally, a prolonged assessment of neighbours is indicated in village indigobirds, *Vidua chalybeata* (Payne 1985). Males within an area of several km^2 visit each other at their singing sites. Within this area, one male has nearly half the matings while his neighbours have few or none (Payne & Payne 1977). When one male changes a song type, the other adult males may or may not copy the new variants, depending on that male's breeding success. Neighbouring males copy the song variants of the successful breeding male, and not the songs of unsuccessful males (Payne 1985). The direction of cultural transmission between males suggests an active behavioural assessment in these birds, in a continual process both within and between seasons.

These field observations and experiments point toward the importance of appearance and behaviour of the singing bird as a 'model' in transmitting its song. An hypothesis of assessment is consistent with the observation that some birds will copy a song from another individual with which it can interact, rather than a song from a tape-recorder with no opportunity to interact: the speaker may be assessed as lacking a standard condition. We suggest that the first-year indigo buntings copy a song only if the 'song model' meets a standard of appearance and behaviour, and will not copy if the standard is not met. Behavioural assessment may be a significant part of the process of social learning of song (Payne 1985; Petrinovich 1985; Baptista & Petrinovich 1986; Pepperberg 1988). The challenge remains to demonstrate the conditions under which songbirds assess their singing neighbours and interact with them in song copying and cultural transmission.

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