SOME BIOLOGICAL PRINCIPLES APPLICABLE TO SONG-BEHAVIOR

BY CHARLES HARTSHORNE

ALTHOUGH the singing of birds has been carefully studied in several countries, we are far indeed from a complete scientific understanding of this phenomenon. There are accurate descriptions, which I for one could not rival, of the songs of one or two regions (Saunders, 1935, 1951); there are some penetrating reflections upon general questions, such as why birds sing at all. (Perhaps the best is still the chapter by the great exponent of the role of territory in bird behavior, Howard, 1920; but see also Craig, 1943). What has been lacking is the attempt to use general principles to explain differences among species with respect to song development. I believe that sufficient information now exists to make reasonable a tentative effort to span the gap between specific or regional studies and broad generalizations about song birds, as a group and the world over. We should, for instance, be able to understand in some degree why song is little-developed in some species or families and well-developed in others; and, even, why some species have a certain complex mode of singing and others a very different though equally complex mode. Unless general principles expressing the biological bases and functions of song do thus help to illuminate particular aspects of song-behavior, they must be regarded as insufficiently established; for science is not content with blanket explanations which fail to particularize themselves in the direction of specific cases. The following are proposed as principles of singing which have enough of the self-particularizing power spoken of to deserve further consideration. (The order in which the generalizations are listed is not one of importance; thus 9c, concerning the role of territory, is perhaps the most important of all.)

1. CLASS LIMITATION

In every class of animals, e.g., insects, batrachians, and birds, in which some skill, such as singing, occurs, there are upper limits of flexibility, complexity, or other refinements, in the possible development of this skill—limits imposed by the basic anatomy, especially neural, of the class. In ability to produce "musical," or patterned sounds, birds have in most respects high upper limits, compared to batrachians, and perhaps still higher compared to insects. Nevertheless, even birds operate musically within narrow limits. Thus, whereas a human musician can learn by heart a composition occupying 50 minutes, or 3,000 seconds, the longest fixed bird song, proved to be such, that I happen to know of is the Winter Wren's (*Troglodytes troglodytes*) song of eight or ten seconds. There may (I doubt it) be a few twice as long—that is to say, less than 1 per cent of the human case. The vast majority of birds

is limited to patterns of less than four seconds' duration. Some birds can undoubtedly learn human tunes correctly, provided they are very short. I have heard a Talking Mynah (*Gracula religiosa*), in the Brookfield Zoölogical Gardens of Chicago, sing the musical refrain of "The Farmer in the Dell" with precision, save that the last portion, corresponding to the final repetition of the title phrase, was omitted. The performance took about seven seconds. In the achievement of pure musical tones (free from enharmonic partials), birds come far closer to us. Few if any musical tones are purer than those of some birds, for example, chickadees (especially *Parus atricapillus*), White-throated Sparrows (*Zonotrichia albicollis*), Woodlarks (*Lullula arborea*), Australian Pied Butcher-birds (*Cracticus nigrogularis*), many wrens and thrushes. Harmonic intervals in successive notes, even, in a few cases, simultaneous ones, are also found (Saunders, 1935, 1951), as in the Wood Thrush (*Hylocichla mustelina*), and Swamp Sparrow (*Melospiza georgiana*). In range of pitch, too, avian capacity is respectable, for the better singers dispose of at least one-half an octave, and some about three octaves, comparable to the best human voices, though not of course to an orchestra. In variety of singing a bird is vastly more restricted than a human musician. Yet an Eastern Meadowlark (*Sturnella magna*) was heard by Saunders to sing "53 different songs in less than an hour." These songs are simple, three to six notes each, making a total repertoire of somewhat less than 300 notes. Nightingales (*Luscinia megarhyncha*), with "24 stanzas," each containing on the average perhaps 11 notes, have a similar total, which is apparently somewhat exceeded by Carolina Wrens (*Thryothorus ludovicianus*), one of which according to Borror (1956) had 22 songs, each composed of at least 20 notes. Highly imitative birds have been known to sing, in individual cases, several dozen distinct imitations, besides some nonimitative passages, and it may be that the total would approach 500 or 600 notes. Very different is an insect repertoire, if one may speak of such a thing: usually a few notes, at most 20, would encompass it. Thus a species of katydid, or tree cricket, sang several little "songs," distinguished from one another only by the diverse numbers of repetitions of one sound within rhythmically separated groups. One individual had groups of 2, 3, and 4 notes; another of 5, 6, and 7. At the opposite extreme, a human musician may have a repertoire, performable from memory, of hundreds of thousands or millions of notes. The concept of class limitation can thus, in some of its aspects, be definitely quantified.

2. Species Limitation, or Specialization

The upper limits of skill in any one species are much narrower than in those of its entire class as a whole; for, although some species are close to the class limits in certain respects, none is close in all. No bird, no matter how "gifted," can equal the feats of all the others. There is and can be no

"lark and nightingale rolled into one" (Burroughs). Such statements are not made by careful observers, of proven accuracy in this field; and I hold that they contradict biological law. Animal skill is always specialized, a matter of doing some things well by sacrificing the ability to do various other things. Even the superiority of one entire class to another is not superiority in all respects. Achievement is always in some fashion exclusive or one-sided. The least creature in nature has some power not fully shared by any other, even our glorious selves. Birds can sing at higher pitches than we, and at high pitches they sound more musical than any of our instruments; also they can sing more notes per second. And a bullfrog (*Rana catesbiana*) has a better bass voice than perhaps any bird. Nevertheless, in most respects, we far surpass birds as musicians, and they surpass batrachians, though to a lesser degree. But the gap between these three classes of animals is worlds greater than that between one species of the oscinine suborder, the song birds, and the remainder. No songster is a super-bird, able to soar above the others in *all* respects of musical capacity. Of course, some species have an essential, over-all superiority to many others (indeed, of these others some do not sing at all); but we should expect to find, and we do find, if we look widely and with care, a considerable number of species that come so close to the avian limits in several respects—though never in all!—that our choice among these superior songsters is rather an exercise of taste than a contribution to knowledge. One could compile a long list of species which have been declared the finest in the world. Many birds in this country have been preferred to the Mockingbird (*Mimus polyglottos*), even by veteran Southern observers (see, for example, Wayne, 1910:181). One somewhat eccentric British writer prefers four other British songsters to the Nightingale, and quotes a farmer who preferred a fifth! The only dogma permissible here, I suggest, is, "There is no 'finest singer'!" But if this is rejected, then with Chapman I should nominate the Slate-colored Solitaire (*Myadestes unicolor*) of Middle America, known to me through recordings by Irby Davis. But its song, too, has limitations, compared to some others. It is still only a bird singing.

One may seek to evade the principle of exclusive specialization by holding that singing itself is a specialty. Yet no bird can sing as a human being can, and no insect or batrachian as some birds can; and this is enough to show that singing as such is not a definite specialty. A *particular way* of singing must be developed, and this always means that the door has been closed to other ways. Even of human performers this is true, much more of avian. Another, more subtle, evasion is to think of imitation as a specialty. This, too, will not do; we now know that imitation is no magic instinct by which what is done by one individual is simply duplicated by another. Rather an individual imitates, more or less closely, and after considerable groping and practice (often *sotto voce*, in the case of singing) only what it is, by its own

tendencies and structure, fitted to accomplish and find interesting; and in all this there are bound to be, and there observably are, sharp limitations, exclusive specializations. A highly imitative species must be one with no very strong fondness for any one musical pattern; it must have a rather loose sense of over-all musical form. It cannot care too much whether a sound be harsh, a sprawling handful of notes, a mediocre or brief tune, or an elaborate musical structure; except—and a notable exception this!—that it will disfavor the last. For even an imitative species has to have some style, some unity of pattern, of its own; hence like all medleyists, it must utilize other compositions (of any length) only in snatches. This is true of the Mockingbird (Nice, 1931) and of the Lyrebirds, *Menura* (Hartshorne, 1953): they prefer to copy brief, often unmusical songs or mere call notes; or to take bits, torn out of their musical context, from the more elaborate and highly organized songs. To take one of a Wood Thrush's five or six exquisitely contrasting, musically related phrases, almost never repeated immediately by the thrush, to stylize and simplify this phrase, missing something or much of its musical quality, to utter it two to four times in succession, and then to bury it in a medley of loosely connected, and often not very musical stanzas, is, I submit, a far cry from duplicating the thrush's musicianship. I once asked a veteran observer of Southern birds what he thought of the Mockingbird's imitations of the thrush. "Poor" was his entire reply. To the same query regarding imitations copying the Eastern Meadowlark (I have yet to note even an attempt at this), he answered, "Not very good." In Australia (Hartshorne, 1953:116f) I spent many hours listening to the stunning performances of both species of Lyrebirds, and to the several forms they were imitating; and I never once heard what seemed to me a full duplication of any of the most musical of Australia's other species. I conclude that vague or suspiciously absolute statements by enthusiasts, though acceptable as expressions of feeling, should not convince us that the principle of exclusive specialization can be transcended. Imitative species have their own remarkable skill, entirely deserving of admiration, but it is *their* skill, not that of the other highly developed songsters around them.

3. Necessary Versatility or Monotony Avoidance (Hartshorne, 1956)

There is a general minimum of flexibility or variability in singing for an entire class, and a special minimum for a species, below which individuals will not fall. There are two aspects of such variability: (1) contrasts in the musical patterns themselves; (2) pauses (measured in seconds: beyond that the bird is merely not singing) between utterances long enough to permit other activities, such as preening, listening to rivals, hopping to another twig, feeding, perhaps just idly sitting, or watching the surroundings. The anti-monotony tendency shows itself statistically in this, that as pauses grow

shorter (or as "continuity" of singing increases), the variety of utterances almost always increases. The shortest pauses (a second or so) are thus almost exclusively found in the most versatile singers—mockingbirds, lyrebirds, skylarks, numerous thrushes and wrens; whereas the longest pauses (5–10 seconds, even when the bird is stimulated by rival or lack of mate) are characteristic of the highly repetitive singers—e.g., most American warblers (Parulidae), most emberizine finches, and a host of other forms around the world (Hartshorne, 1956:184–185). (Outside the songbirds, the domestic rooster [*Gallus gallus*] is a good example.) Even within the same species, the law is often strikingly illustrated; for there may be two styles of singing, a repetitive style with long pauses, and a versatile style (usually occurring at dawn or dusk) with short ones. The most spectacular case is that of the Eastern Wood Peewee (*Contopus virens*), which Craig (1943) has studied with infinite care. However, the Canada Warbler (*Wilsonia canadensis*) and the American Redstart (*Setophaga ruticilla*) are only a little less striking in this respect (Hartshorne, 1956:185–187). A few species have unusually low minima of variability, or (the same thing) unusually high "monotony thresholds," but these are mostly non-Oscines, a fact significant in itself: thus the Least Flycatcher (*Empidonax minimus*) or the Whip-poor-will (*Caprimulgus vociferus*); but also, it seems, Hutton's Vireo (*Vireo huttoni*) and doubtless a few (a very few) other songbirds. The general trend is overwhelming; repetitiveness and short pauses are rarely combined.

4. Maximal Continuousness

Pauses tend to be as short as (subject to the previous principle) the bird's musical versatility permits; i.e., versatile singers do not regularly employ long pauses, just as repetitive ones do not use short pauses. Thus the two principles can be combined, into

3, 4. The Positive Correlation of Continuity and Variety

Most of the famous songsters of the world illustrate high values both in variety and in continuity; most of the "poor" singers illustrate low values in both; and it is rare to find a high value in one with a low value in the other. (It should be understood that "variety" here (like "continuity") means, in the short run: change in theme, or in rendition of a theme, within a dozen seconds or less. Birds with a repertoire, but which sing each song a good many times before shifting to another, do not count as highly versatile for the purposes of this law.) Why are these two variables thus correlated? The avoidance of the combination, short pauses with repetitiveness, seems simply to show that, like all creatures, birds require change to sustain interest in an object or activity. When a pattern has been sung, there is, therefore, a temporary inhibition lasting some seconds upon singing that pattern over

again (unless perhaps a few times, and even then, only if it be very short). But this inhibition fades rapidly, in birds much sooner than in us; for birds live in shorter time spans than we. Since the inhibition against repeating the same pattern does not hold against singing a contrasted one, a bird which performs several different songs or phrases is free to sing again immediately. Why, however, does it tend to use this freedom (principle 4)? One can think of three possible answers: (1) variety would be useless if pauses were so long that the bird (performer or listener), being a short memoried creature, no longer felt the effect of the previous utterance: (2) there may be competitive advantage for maintenance of territory, or of ethological isolation, or for finding a mate, in keeping up a steady stream of sounds; (3) if a bird likes to sing—otherwise, would it develop variety?—and if there is no disadvantage, why should it not keep at it uninterruptedly, provided the inhibiting effect of repetition can be avoided? These reasons seem mutually compatible, and amply explanatory of the fact that long pauses are as rare with variety as short ones without it, and that medium pauses and medium variety go together. As a result, one may in general, and rather closely, infer the degree of continuity normal to a species from its normal versatility, or vice versa. A corollary is that highly imitative birds, which of course are versatile, tend to be continuous singers.

5. Spatial Detachment of Continuous Singing from Place of Feeding

(I owe this to a suggestion of Dr. Olin Sewall Pettingill, Jr.) Species which sing with much variety, and hence continuously, sing from perches separated from their feeding grounds; whereas many, probably most, interrupted or discontinuous singers sing and feed in about the same places. Typical continuous singers: Skylarks (*Alauda arvensis*), feeding on the ground and singing in the air; numerous members of the thrush and the mockingbird-thrasher families, feeding on the ground and singing in trees or bushes (or —*Turdus merula*—from house tops); lyrebirds, singing from a specially constructed mound on which they also "dance", and feeding elsewhere, over a wide area, on the ground. Typical interrupted singers: Old and New World warblers (Parulidae, Sylviinae), Australasian whistlers (Pachycephalinae), which mostly sing and feed in the branches; American meadowlarks (*Sturnella*), which feed and often sing on the ground; flycatchers, in both hemispheres (Tyrannidae and muscicapids), which sing on perches from which they also sally out to catch insects. Reasons for the law seem clear enough. If food is immediately accessible, it tends to distract from song; also the system of interweaving snatches of song with bits of food-getting has advantages, since it provides song sufficiently continuous for most purposes, and enables food-seeking to go on without much interruption. In treeless areas, moreover, it is the natural alternative to prolonged

flight song, which is strenuous. Also, species living *entirely* in trees have little occasion to seek a special song perch; whereas ground-feeding species in areas not lacking in trees can sing much more safely and effectively from an elevated perch, whence they cannot, without loss of efficiency, descend every few seconds for moments of feeding. Interesting special case: Eastern Wood Pewee, which as a rule sings its special, continuous song, but not its usual discontinuous one, from a special tree, and at times of day (dawn and dusk) too dimly lighted for passing insects to be readily seen (Craig, 1943:36–37).

The Red-eyed Vireo (*Vireo olivaceus*) seems something of an exception to principle 5; for it often sings rather continuously in the trees in which it also feeds. However, its phrases are all short and without much musical connectedness, and in this sense its singing lacks continuity. Some of the Old World warblers which live in swamps (genus *Acrocephalus*) seem not to fit well either. Yet the general trend seems unmistakable.

6. The Correlation between Quantity and Quality

Many species (I believe the great majority) which sing elaborately and "well", by customary standards, also devote an exceptionally large part of the day, and ultimately the year, to singing. If we take the lengths of the songs or phrases in seconds, and multiply by the number of times the bird sings per minute, hour, and day, and take into account also the length of the song season, we find that the poorest singers do not have any such total output as the melodious singers. Many of the former sing less than one-fourth of each 60-second period, even when singing as steadily as they ever do. In addition, they tend to confine their singing largely to the breeding season, whereas many good singers perform both continuously and, as several writers have noted (Craig, 1943: 152–153; Zimmer, 1919), for an unusually large portion of the year. For example, Carolina Wrens and Mockingbirds are heard almost daily in the Atlanta area for twelve and nearly eight months, respectively. Out of 21 singers in the United States that seem to have been judged to have the most highly developed songs (I have heard 17 of them), eight sing most of the year, or, allowing for continuity, perhaps nearly three times the average total (taking data chiefly from Saunders' careful accounts of New England species); six sing at least 50 per cent more than the average; and the remaining seven have at least average outputs. This is hardly a chance distribution. In England, taking Nicholson and Koch's list (1936: 1, 70) of the songsters with the most "power and variety," five are permanent residents, and these (according to Nicholson's "calendar") sing on the average nearly eight months of the year, some of them very continuously (in each performance period), implying a total of more than twice the average output. The other five are migrants, and these sing at least the normal

amount while in England (the Nightingale making up through continuity and extra night singing for its short season). In addition, all but one (the Marsh Warbler, *Acrocephalus palustris*) are said to sing a good deal when wintering in Africa or while migrating. Again we have a decided correlation. In the Piedmont Plateau of Georgia, where I write, of the five good songsters wintering near our house (Mockingbird, Carolina Wren, White-throated Sparrow, Brown Thrasher, *Toxostoma rufum*, and Cardinal, *Richmondena cardinalis*) the first three sing freely much of the autumn; on the other hand, the five poor or mediocre singers (Towhees, *Pipilo erythrophthalmus*; Blue Jays, *Cyanocitta cristata*; titmice and chickadees, *Parus bicolor* and *P. carolinensis;* Flickers (*Colaptes auratus*) are almost songless from September to January. Nor do they "make up for the lost time" by resuming their singing correspondingly earlier in February or March.

The interest of this principle is that it constitutes evidence that our human classification, "good singer," has some biological meaning, since our enthusiasm for the performance of such a singer is matched by the performer's own more intense interest in it. He does not drop the activity the moment the climax of the life cycle is over, but continues it much longer, or nearly all the year; he does not spend most of a performance period in intervals of silence but sings as though, for the few minutes, or perhaps half an hour or more, singing were life itself. Naturally, if we use continuity as one criterion of quality as well as of quantity, our generalization becomes in part tautological; but only in part, since there are other criteria on both sides. The further fact that birds act as though to avoid monotony in their singing (principle 3), and sing as much during a performance period as this avoidance permits (principle 4), also gives some support to the view that they do in their way experience musical enjoyment, as does the evidence which imitation furnishes that they attend to the sounds they are making, and guide their utterances partly by their auditory impressions. Further, the standard explanation of harmony, first given by Helmholtz, I believe, is such as, in its simpler aspects, to apply to birds as well as to man; and as much can be said for explanations of the simpler effects of rhythm and melody. (Statements sometimes made that birds lack some elementary factor of musical utterance seem due to inadequate experience; somewhere in the world a bird turns up [or several] which exhibits the missing factor, provided it be not too elaborate or complex.)

The most notable exception I have heard of to the present principle is the Cactus Wren (*Campylorhynchus brunneicapillus*), an unmusical singer said to sing incessantly and all year. However, what total output is indicated by "incessantly" one can only guess. Another, opposite kind of apparent exception, from nearly the same desert region, is Leconte's Thrasher (*Toxostoma lecontei*), which sings a "musical" and powerful, yet "infrequent" song

(Hoffman, 1927:251; Peterson, 1941:137). It may be that this species is losing the tendency to sing, owing perhaps to extreme heat much of the day, or the high visibility of its habitat (see principle 9, below).

7. The Unequal Distribution of Musical Ability by Families

Since families represent specialization (some more than others), principle 2 should lead us to expect the present generalization. The crow family (Corvidae) has few even third-rate songsters, and no nearly first-rate ones, and this is true of a number of families. By contrast, the thrush subfamily has about 80 first-rate musicians, and the proportion in the wren family (Troglodytidae) is nearly the same (not far from 30 per cent). In the thrasher–mockingbird family (Mimidae) at least half are outstanding songsters. These dramatic differences are not plausibly ascribed to chance (see below, principle 9) or to bias or ignorance in my classification of species as outstanding musically (based on descriptions and, in representative samples, direct experience, at least of recordings). Nor are the differences very closely correlated with those in physical vocal equipment, since, for example, crows are well endowed in this respect (Miskimen, 1951).

8. The Relatively Equal Geographical Distribution of Musical Ability

Compared to the extreme contrasts between families, the geographical differences are unimpressive, if we rule out regions where species of perching birds are lacking or few, such as extremely cold, arid, or barren regions. The sometimes-maligned tropics, for example, contain about half the world's most highly musical species (the evidence for this must be reserved for another occasion), and yet the tropical areas total but one-third of the land surface of the globe. There are marked unevennesses in the distribution of good tropical singers, but every considerable region has some.

This universality of musical utterance, the world over, and in many widely-different families, shows how deeply grounded in bird life the phenomenon is. That there are everywhere some strikingly unmusical songs among oscinine birds may indicate that if, by chance, a species hits upon a distinctive, penetrating, but harsh utterance, there may not be much to gain by its transformation into a musical one. Examples: the Ovenbird (*Seiurus aurocapillus*), or the Australian Wattlebirds (genus *Antochaera*).

9. The Ecological Distribution of Musical Ability

The degree of musical development (measured by variety, purity of musical tone, pitch span, carrying power) tends to be correlated positively with most, if not all, of the following factors:

(a) Relative invisibility, as due to habitat (dense vegetation, clouds or fog), dull or protective coloration, smallness of size, secretive mode of life (flying swallows or hawks can usually see one another);

(b) Lack of sexual dimorphism;

(c) Degree of territorial possessiveness, and (up to a point) size of territory (hence, species which are gregarious in the breeding season are poor singers);

(d) Number of closely-related, especially like-sized, songbird species within hearing of one another;

(e) Scarcity of strong-voiced, primitive forms, such as parrots, cuckoos, toucans, doves, which, when abundant, may make such a racket that musical qualities tend to be imperceptible;

(f) Audibility as due to habitat (Beebe and others have thought that certain tall tropical forests, as in northern, lowland South America, absorb delicate sounds and put a premium upon harsher ones—see *e*, above);

(g) Efficiency of feeding methods, yielding surplus energy and time;

(h) Mild weather over much of the year.

As to (*a*, *b*), since song is vocal signalling, the need for it must be partly proportional to the ineffectiveness of visual cues; also, since song is above all territorial "advertisement," strong territorial habits (*c*) make signalling necessary for long periods of time and not merely during courtship, and over considerable distances, with the consequence that signals must be not only loud but distinctive enough to stand out, not simply from a few nearby sounds, but also from the more varied assortment coming from a greater distance. They must be different from mere calls, which tend to be alike in both sexes and sometimes in related species and which do not differentiate between an individual occupying a territory and one not so doing, but perhaps travelling in a flock. The number of like-sized species (*d*) in an area, especially if they are congeneric or of the same family, increases the need for distinctive patterns, rather than mere shrieks or chirps which tend to betray only the size and basic structure of the species.

Though the presence of many types of songbirds in an area is probably favorable to song-development, the presence of many primitive forms with unmusical voices (*e*) may be unfavorable. At dawn, especially, a critical time, it may be hard for the more exquisite voices to make themselves heard. Some observers with tropical experience doubt the validity of the argument. Yet we do need an explanation for the rather low yield of the Amazon Valley in musical species, even among Oscinines, compared to the highlands of Central America, Colombia, Africa, or Java. Possibly the tendency of lowland tropical birds to follow ant-armies, with resultant weakening of territoriality, is a factor. Possibly there are too many species, even of songbird

type, in the Amazon. Is there a saturation point in number of different songs that can be effective? Compare the hopeless confusion of sounds in bird houses in zoölogical gardens. On the other hand, the number of individuals in an area is not necessarily much greater in the tropics. It has been suggested by Keith Dixon that, as in trees, birds of tropical rain-forests may be thinly distributed, and thus mutual stimulation within species is diminished and the territorial functions of song reduced. Perhaps (as Professor Pettingill has suggested) the year-round combination of high humidity and fairly high temperature in lowlands along the equator inhibits song. The sound-absorbing character (*f*) of tropical forests perhaps differs from that of other forests. In any case birds of most tropical areas are fairly musical. As to (*g*), insectivorous birds may have an advantage (especially compared to those living chiefly on small seeds) in the high protein content of their food, and ground feeders have a further advantage, perhaps, in that worms and grubs are more rewarding than small flies, mosquitoes, and aphids. Or is walking or hopping on the ground more economical of energy than some other methods of locomotion while feeding? The enormous superiority of thrushes, musically speaking, to even the Old World flycatchers (nearly 30 per cent outstanding singers, compared to about 1 per cent), is strongly suggestive, though it may also be true that the flycatching habit makes the bird more visible to its fellows (*a*). Ground-feeding in forest or long grass also means relative invisibility, and this may well be the main point. There seems little doubt that ground-feeding does favor song (principle 5 is probably relevant here). Thus ground-feeding members of the Parulidae include nearly all of the loudest and most of the more musical songsters in this family. For instance, the two chats (*Icteria virens* and *Granatellus venustus*), the Ovenbird and the water thrushes (genus *Seiurus*), and Swainson's Warbler (*Limnothlypis swainsonii*) may be cited.

(h) Mild weather releases more energy for song, and mild weather for much or all of the year—by stabilizing the food supply and eliminating the necessity for migration—increases the opportunity (Robinson: 1949, 1956) to perfect complex types of singing, which to some degree have to be learned (see Principle 11). Perhaps this is why, in the far North, while some species sing sweetly, there is a lack of complexity and variety of singing. (The prolonged daylight, however, in part atones for the shortness of the season.)

Of the ecological principles, (*a*) and (c) are probably the most important, and certainly they are the ones most securely established by known facts. Colonial nesters, and gaudy, conspicuous birds living in well-lighted places, are not good singers; the typical songbird is, like the usual thrush or wren, a highly territorial form, feeding in dark substages of forests or thickets, with somber, protective coloration.

10. Sex Distribution of Musical Ability in Relation to Climate

The potentiality of song is innate in both sexes in many, possibly all, species, but is for the most part inhibited in the female under natural, and to a lesser extent artificial, conditions (as in caged birds), with the partial and notable exception that in tropical and subtropical areas scores, very possibly hundreds, of species exhibit female singing as a normal part of the life pattern. It often takes the form of "dual singing," antiphonal singing, or "duetting," according as the female sings a portion (usually, or perhaps always, the last) of a single unitary pattern, or replies to the male song with one of her own, or sings simultaneously with the male. The functions of such joint singing include that of maintaining the pair bond throughout the year. It is scarcely a mystery that the luxury of female singing occurs chiefly in uniformly mild climates, where migration and the struggle with severe cold are both absent. There is an additional, though I judge much less frequent, form of female song where winters occur but are not very severe, as in Britain and the southern United States: this is singing by females occupying individual winter feeding territories of their own, Robin Redbreast (*Erithacus rubecula*), Mockingbird. Female song as standard behavior occurs in many parts of the world (for instance, Mexico, Africa, Australia) and in widely-different families, but only, so far as I know, in non-migratory, and usually sub-tropical or tropical, species. It is then definitely associated with climate, plus some as yet undetermined factors.

11. Innately Guided Imitation and Learning

Evidence is accumulating that the songs of most, possibly all, species result from an inborn tendency toward the specific type of song, always, however, more or less influenced in its maturing by practice and by hearing songs sung by other individuals. Usually these individuals are of the same species but, in exceptionally imitative forms, or in captivity, of other species as well. It has yet to be strictly proved (and seems unlikely) that *any* species is wholly without innate disposition to sing a characteristic song; for it is not enough to show that, given early and exclusive exposure to a "foreign" song, the species will sing this foreign song rather than that of its species. One could only conclude from this that the exposure is a stronger force than the innate trend, if the latter exists. To prove the absence of such a trend one must show that, given exposure to no adult singing (nurtured in a sound-proof chamber), the individual will still not sing its proper song. This has been tried with the Chaffinch (Thorpe, 1954) and two other species (Sauer, 1954; Messmer and Messmer, 1956). The Chaffinches did sing the proper song; although, when other individuals of the same species were exposed solely to foreign songs, they adopted them and failed to sing the song of their own species. Further, when several distinct groups were brought up in isolated

chambers, each group developed its own version of the song of the species, thus beautifully showing the blend of innate and imitative factors. The other two species also sang correctly, although when examples were provided they always were responded to in some degree. Very likely all species have something innate and (in the wild) something learned in their singing—learned at least in the sense of perfected by practice, and probably also in the sense of having been influenced by the hearing of other individuals. The proportions of the three factors doubtless vary greatly in diverse species, and slightly in diverse individuals. Song apparently sums up nearly that a bird is, both of instinct and of plasticity or "intelligence." Birds are innately musical, as man is innately talkative, for as babies babble in speech-like sounds, so young birds (though within much narrower grooves of instinctive pattern) "warble," in rambling, exploratory fashion. That imitation plays a role, often an important one, and that songs develop with practice, show that birds are aware of, and in a manner judge, their musical efforts (Howard, 1952:177–199). Such judgment works within narrow limits, but it probably has something in common, though at a vast removal, with man's musical intelligence.

12. The Possible Light–Dark Influence Upon Exuberance

This idea, suggested by L. A. Fuertes (1914), is highly speculative, not to say nebulous, and scarcely susceptible of proof. The "gayest," most exuberantly joyous, songs are thought to occur in species living in the open sunlight, and the least gay, or the most solemn, plaintive, or "chaste" songs to characterize forest-dwelling forms, living in dense shade. In the United States, exuberantly joyous songs are those of: the Bobolink (*Dolichonyx oryzivorus*); American Goldfinch (*Spinus tristis*—a name referring evidently to the call notes, not the song); the House Finch (*Carpodacus mexicanus*); the Purple Finch (*Carpodacus purpureus*); the Western Meadowlark (*Sturnella neglecta*); Townsend's Solitaire (*Myadestes townsendi*); and the House Wren (*Troglodytes aedon*). Most of these live entirely, and all of them to some extent, in the sunshine, in well-lighted places. The songs perhaps most solemn or chaste are of the Varied Thrush (*Ixoreus naevius*); the Veery (*Hylocichla fuscescens*); the Wood Thrush, the Hermit Thrush (*Hylocichla guttatus*); the White-throated Sparrow; the Wood Peewee; the Eastern Meadowlark. Of these, only the last lives in anything like bright light; and perhaps not even it does in comparison with the Western Meadowlark, since, before the forests were felled, it must have often frequented partly-shaded stream valleys or grassy areas surrounded by forest; and it also inhabits the cloudier and moister parts of the continent, where the growth of grasses is taller and denser, affording more shade (Lanyon, 1956: 103–105). In England, the Skylark (*Alauda arvensis*) is an exuberant singer, while its relative, the Wood Lark, is decidedly chaste, and as its name indi-

cates, and I believe in fact, it lives more in the shadow of trees. (The contrast between Meadow and Tree Pipits, *Anthus pratensis* and *A. trivialis*, is less easily fitted into the scheme.) The Chaffinch (*Fringilla coelebs*) is also rather gay, and it lives largely in somewhat open places; while the Blackbird (*Turdus merula*), the nightingales (*Luscinia*), and the British Robin are apparently typical chaste forest songsters. Birds living much in tree tops, as do many warblers (Sylviinae), are intermediate in relation to sunshine, and so perhaps are their songs. It might of course be argued that our own impressions of the "gaiety," or the opposite, of the songs are largely determined by the environment in which we find them. But this would be an exaggeration. There are objective characteristics of "gay" music (rapid tempo, for one), and they are found in high degree in the Bobolink, for instance, and not at all in the Varied Thrush or the Veery, which seek the deep shade and are among the most solemn of our birds. Also, no one ever thought the Eastern Meadowlark, or the Vesper Sparrow (*Pooecetes gramineus*) particularly gay, yet these occur in our experience together with sunshine. (Both seem exceptions to the Fuertes principle, if it be a principle.) We may imagine that species which, for food-getting reasons and/or security, live in subdued light, and therefore have an instinctive preference for such conditions, may also have a bent toward subdued ways of feeling and acting. The forest thrushes not only have more solemn songs, they have perhaps a more solemn comportment than many dwellers in the open. Possibly (here again I am indebted to Dr. Pettingill) "chaste" songs carry better in the forest than other songs. In one way or another, then, there may be something in Fuertes' idea.

These are some of the reflections to which 40 years of attention to a delightful aspect of nature have led me. Even to begin to justify them would require assembling a great mass of facts, and the writing of a book. I hope to write this book. But meanwhile, it seems appropriate to invite others to join in the game; for numerous observers must know many relevant facts of which I am not aware. I have always believed that there must be laws in this area. If the foregoing are not the right ones, what should be put in their place? There must be elements of discoverable order in these matters.

Summary

The proposed generalizations or "principles" are as follows:

1. Class limitation, as determined by structure.

2. Species Limitation, or Exclusive Specialization: the impossibility that a species should excel in all the capacities of its class.

3. Minimum Versatility, or the Monotony Threshold: mutual exclusiveness of repetitiveness and continuity.

4. Maximal Continuity, or (in combination with the preceding) the positive Correlation of Continuity and Versatility.

5. Spatial Detachment of Continuous Singing from Feeding.

6. Correlation between Quantity and Quality: better singers produce more song.

7. Unequal Distribution of Musical Ability by Families.

8. Relatively Equal Geographical Distribution.

9. Ecological Distribution according to: invisibility; sexual monomorphism; territoriality; number of Oscinine species in the area; scarcity of strong-voiced, primitive species, sound-transmitting characteristics of the habitat; efficiency of feeding methods; mild weather.

10. Sex distribution according to Climate (female singing integral to the life-pattern of a good many species not subjected to cold weather or migration).

11. Innately-guided Imitation and Learning.

12. Possible Light–Dark Influence upon Exuberance in Song.

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