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VOCAL DIALECTS AND THEIR POSSIBLE RELATION TO HONEST STATUS SIGNALLING IN THE BROWN-HEADED COWBIRD¹

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Abstract. We describe dialects in the flight whistle of the Brown-headed Cowbird and contrast previous hypotheses for the maintenance of dialects with a new one that assumes that a male's ability to give the correct local dialect is an honest signal of relatively high male quality. The three dialects upon which we focus are part of an extensive dialect system along the eastern Sierra Nevada. The dialects are partially isolated by unsuitable habitat and are unusual because they differ via lexical rather than the less extreme phonetic differences that characterize song dialects in most other species. Because males whistle just before copulating, whistles may function in mate choice. Since flight whistles are also used over long distances, we predicted and confirmed that males within the same dialect have quantitative whistle differences of potential value for individual recognition. Other quantitative analyses indicated phonetic differences among homologous whistle elements from adjacent dialects. Recordings made between 1978 and 1980 showed no quantitative or qualitative differences from a large sample of 142 males recorded between 1983 and 1985. Such temporal stability is expected since the dialects are large, being 10 to 30 km in extent and probably contain hundreds of individuals. Historical records demonstrate that the dialect populations developed since the late 1930s.

Males banded in one dialect but recorded in another made up 13.0% of our adult sample and were more likely to have foreign whistles than adults banded and recorded in the same dialect. Yearling males were significantly less likely to whistle than adults, and yearlings that did whistle were significantly more likely to have foreign whistles. Thus possession of a locally appropriate whistle is a reliable indicator of a male's age which is a major correlate of male mating success and possibly of male quality, as nearly all copulations involve adult males. These age differences are consistent with our new "honest convergence" hypothesis and inconsistent with the local or genetic adaptation hypothesis which predicts that vocal ontogeny is closed by a male's first breeding season. Bilingual males and those with hybrid whistles combining elements from two dialects made up 0 to 8% of the males within dialect areas. By contrast, 38% of males in one contact zone between two dialects were bilingual and 54% of males in another contact zone gave hybrid whistles. These trends are consistent with the honest convergence hypothesis and inconsistent with hypotheses that dialects are maintained by isolation or because they contribute to local adaptation among populations.

Key words: *Brown-headed Cowbird; dialects; flight whistle; honest convergence; mate choice; Molothrus ater; Sierra Nevada; social adaptation; song; status signalling.*

INTRODUCTION

Numerous bird species show geographic variation in their vocalizations (reviewed by Mun-

ding 1982). Especially interesting are dialects, which by definition require well defined boundaries that separate adjacent populations with different vocalizations. The questions of how dialects are maintained and whether they have significant evolutionary consequences have been the subject of intense interest and controversy in recent years (summarized in Baker and Cunningham 1985 and Kroodsma et al. 1984). Partly

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responsible for this attention is an early hypothesis for dialect maintenance, the genetic or local adaptation model, which states that dialect differences facilitate reproductive isolation among dialects (Marler and Tamura 1962). This hypothesis implies that conspecific populations may be more genetically divergent than is currently thought and that dialects may even influence speciation (Baker 1981).

This paper has three objectives. First, we contrast the local adaptation and other hypotheses with a new one for the maintenance of dialects. This new hypothesis, termed the honest convergence model, assumes that a male's ability to give the correct local dialect is an honest signal of his relatively high quality as a mate. Males that do not give the local dialect are less desirable because they are either yearlings or are emigrant adults that have not been present long enough to learn the dialect and to establish site-based dominance.

Secondly, we describe dialects in the flight whistle of the Brown-headed Cowbird (*Molothrus ater*). We assess variation within and among three dialects and two overlap areas along 65 km of the eastern slope of the Sierra Nevada of California. To place these dialects into an overall perspective, we also briefly describe whistle variation over a 300-km span of the eastern Sierra, where cowbirds occur largely in a north-south series limited to the west and east by unsuitable habitat. Descriptions of dialects are made necessary (Brenowitz 1985, Jenkins 1985) by recent work showing that even the most well-studied dialect species, the White-crowned Sparrow (*Zonotrichia leucophrys*), has vocal variation that is more complex than assumed previously (Kroodsma et al. 1984, Baker and Cunningham 1985, Baptista 1985a).

Thirdly, we show that the whistle dialects are temporally stable and use our data to test various predictions arising from the different hypotheses for dialect maintenance. The whistle dialects are especially interesting because the cowbird is a brood parasite with no obvious mechanism by which juveniles learn vocal types from conspecifics. Nevertheless our evidence indicates that dialect differences are indeed learned in cowbirds, as in other bird species (Krebs and Kroodsma 1980, Mundinger 1982). Although learning in a parasite may involve some atypical processes, studies of another cowbird vocalization, the song, have produced new insights of general

importance (West and King 1985). Cowbird song varies macrogeographically (Eastzer et al. 1985, King and West 1983) but may not have localized dialects (Dufty 1985).

THEORETICAL FRAMEWORK: THE MAINTENANCE OF VOCAL DIALECTS

There is considerable consensus concerning the stochastic processes that seem to provide the origin of dialect differences (Kroodsma 1985). Because the ontogeny of song usually involves modification of an innate template following exposure to conspecific song models (Nottebohm 1970, 1975; Marler and Mundinger 1971; Kroodsma 1978, 1982), new songs may be introduced by an absence of adult models, or by mistakes in learning or in a genetic template (Andrew 1962, Thielcke 1973, Baptista 1975, Lemon 1975). A new dialect may be generated if a song variant is copied due to behavioral dominance (Jenkins 1978, Payne 1981b, Petrinovich et al. 1981) or if allopatric populations arise (Thielcke 1973, Baker 1975, Mundinger 1975, Adkisson 1981, Baker and Cunningham 1985). The maintenance of such dialects is the critical question that we address by briefly contrasting the following five hypotheses.

(1) *History or isolation.* Dialects are maintained merely by geographical isolation and are epiphenomena with no evolutionary consequences (Payne 1981a, Petrinovich et al. 1981, Wiens 1982). Genetic differences among dialects are those due only to present or past isolation by distance or barrier.

(2) *Genetic or local adaptation.* Dialects are maintained because they serve as population markers that local females use to identify and thus to preferentially mate with local males (Konishi 1965; Nottebohm 1969; Baker et al. 1981a, 1982c; Baker 1983). Because dialects maintain locally adapted or coadapted gene complexes via assortative mating (Marler and Tamura 1962, Nottebohm 1969, Baker 1982a), they result in "excess genetic differentiation," i.e., differentiation among dialects is greater than that due solely to spatial separation (Baker 1974, 1975, 1981, 1982a, 1982b, 1983; Baker et al. 1982b, 1982c; but see Zink and Barrowclough 1984).

(3) *Acoustic adaptation.* Dialects arise and are maintained because the dialect vocalization transmits best through the local habitat (Morton 1975, 1982; Bowman 1979; Gish and Morton 1981; Nottebohm 1985). Unlike the other hy-

potheses, this one ascribes direct adaptive significance to the specific vocal differences that characterize dialects (e.g., Anderson and Conner 1985).

(4) *Social adaptation.* Payne (1981a) developed the idea that dialects are maintained because immigrants and young males benefit socially by copying the song of established males (see also Verner 1975 and Baptista 1985b). Such social adaptation implies song learning after the juvenile period and even throughout a bird's life. The two remaining hypotheses propose different mechanisms by which social adaptation can occur.

(4a) *Deceptive convergence.* Payne (1982) proposed the following form of social adaptation and termed it "competitive mimicry." Others (McGregor and Krebs 1984, Baker and Cunningham 1985) have called it "deceptive mimicry" and we title it "deceptive convergence" to highlight the contrast between it and the next hypothesis. Dialects arise because males mimic the vocalization of a dominant male to facilitate interactions (Jenkins 1978, Payne 1981b, 1982, 1983). This mimicry may deceive other birds into responding as if the mimic is in fact the model. Thus, dialects correspond to interactive social units (Payne 1981a). Males disperse freely and adopt new dialects so ontogeny remains open. Dialects should be temporally unstable because dominant males gradually develop divergent vocalizations to counteract the mimicry (Rohwer 1982) and because dialects contain only a few males. Thus this hypothesis is primarily an explanation for short-term rather than long-term maintenance.

(4b) *Honest convergence.* Spatial variation arises through stochastic processes when a new population is founded. As the population expands, the local song variant (i.e., dialect) is maintained because the ability to give it is a reliably honest signal of high social status and mate quality. The signal is honest because the vocalization is too difficult to be copied immediately by recent immigrants (Craig and Jenkins 1982) and/or because some or all males have little or no contact with it as a juvenile and must learn it during their first breeding season (e.g., Kroodsmma and Pickert 1980). Thus males that do not give the local dialect are either newcomers or yearlings, both of which are likely to be inferior mates compared to long-term adult residents. Females learn to recognize the local dialect by

determining the predominant vocal type given by dominant males at the start of the breeding season and prefer to mate with males that give this vocal type. Also, males that frequently give a particular vocalization may be advertising their superiority by demonstrating that they can ward off male aggression elicited by the vocalization, as in the studies of West et al. (1981a). Giving the correct dialect is a status signal (Rohwer and Ewald 1981, Rohwer 1982, Fugle et al. 1984) that is resistant to cheating because by the time a male overcomes the learning or social restraints upon giving the signal, he is *on average* close in quality to other males that give the local signal correctly and superior to those that do not. Our honest convergence hypothesis differs from deceptive convergence in that males copy a particular class of males over a large area, not a particular dominant individual.

Vocal convergence and stability are maintained from year-to-year because if nondispersing adult males change their vocalization they no longer identify themselves as experienced members of the local population. Males that are recruited into the dialect, either by being reared there or by immigration, develop vocalizations that replicate those of resident adults thus contributing to temporal stability. Vocal convergence need not be due solely to male-female interactions. Both local and foreign dialects may elicit male aggression, the latter because they cannot be easily "ranged" (Morton 1982) or signal that a bird is a stranger (Falls 1982). According to the hypothesis, dialects contribute little to genetic differentiation because dispersing females prefer to mate with males that conform to their new dialect and dispersing males learn their new dialect. This hypothesis was prompted in part by our expectation that many yearling male cowbirds lack whistles because juveniles fledge after most adults have migrated from the Sierra (Rothstein et al. 1980, Verner and Ritter 1983) and therefore hear few whistles to copy. Similarly, Payne (1973a) noted that numbers of adult cowbirds dwindled in June while juveniles were seen through July in lowland California. Payne's (1965) and Norris' (1947) discussions of cowbird activity in Michigan and Pennsylvania also make it clear that adults withdraw from breeding habitat before many juveniles fledge. Adults do not migrate early from these eastern areas but they form large feeding flocks (Payne 1965), within which birds do not whistle. We

TABLE 1. Predictions of the five hypotheses for the maintenance of vocal dialects in birds. Underlined predictions are critical ones that are unique to one hypothesis and/or that indicate rejection of 2 or more hypotheses. Variables with asterisks are the most critical because for these, some predictions are so clear and testable that failure to confirm a prediction of a particular hypothesis in a single study is sufficient to invalidate the hypothesis for the species under consideration. See text for further discussion.

Variable	Hypotheses				
	Isolation	Local adaptation	Acoustic adaptation	Deceptive convergence	Honest convergence
*Dialect size:	variable	variable	variable	<u>small (conforms to social unit)</u>	variable
Related to past/present habitat patches:	yes	yes	yes	<u>usually not</u>	yes
Random dispersal among dialects:	<u>no</u>	<u>no</u>	? ^a	<u>yes</u>	<u>yes</u>
Excess genetic differentiation ^b :	<u>no</u>	<u>yes</u>	possibly	<u>no</u>	<u>no</u>
*Temporal stability:	<u>high</u>	<u>high</u>	<u>high</u>	<u>low</u>	<u>high</u>
*Assortative mating, by vocal type:	<u>no</u>	yes	some	yes	yes
Assortative mating, by natal dialect:	<u>no</u>	<u>yes</u>	?	<u>no</u>	<u>no</u>
Acoustic characteristics reoccur in disjunct dialects:	no	no	<u>yes</u>	no	no
Vocal ontogeny	?	closed ^c	?	open	open (but may close after first breeding season)
Adult-yearling differences in vocal ability	?	no	?	possibly	<u>yes</u>
High incidence of bilingual birds at dialect borders:	no	no	?	<u>yes</u>	<u>yes</u>

^a "?" indicates that no clear prediction is possible, or that the prediction depends on other variables.

^b See text for definition.

^c closed = vocal type normally determined before the end of the juvenile period.

conclude that some juvenile cowbirds in most, and perhaps all, regions are not exposed to adult vocalizations.

Our hypothesis is not limited to the cowbird because delayed song learning due to late hatching occurs in at least one nonparasitic songbird (Kroodsmma and Pickert 1980) and has been suggested in others (Wiens 1982). Furthermore, such delayed learning is not necessary to the hypothesis because conforming to local vocalizations will be adaptive for recent emigrants. Indeed, Craig and Jenkins (1982) argued cogently that a model similar to ours may apply to nearly all songbirds, although they framed their arguments solely in terms of intrasexual interactions. Feekes' (1977) "password" hypothesis, which is based on a nonparasitic species, is also similar to our hypothesis.

Contrasting predictions of the hypotheses. Alternative predictions for hypotheses 1, 2 and 4a were tabulated by Payne (1981a). We present here a much expanded table (Table 1) with predictions each of the five hypotheses makes for 11 variables. Many of the predictions in the 5 by 11 matrix are not useful in distinguishing

among the hypotheses. Critical predictions limited to one or two hypotheses are underlined in Table 1. The acoustic adaptation hypothesis is the only one that predicts the repeated occurrence of certain acoustic characteristics in disjunct dialects. If a particular type of sound (e.g., low frequencies) is transmitted most effectively in a specific habitat, it should reoccur if the species occupies that habitat elsewhere. The type of vocal ontogeny is important for discriminating among some hypotheses. Deceptive convergence predicts an open ontogeny. Only honest convergence predicts that yearling males are, on average, less competent vocally than adults (although this is not a necessary condition). Under the local adaptation hypothesis, ontogeny should be closed after the juvenile stage, otherwise birds could disperse from the natal dialect and successfully learn a new dialect, thereby breaking down the reproductive isolation among dialects. A high incidence of bilingual birds at dialect borders is inconsistent with the isolation hypothesis because development of two vocal types implies experience with, and therefore dispersal between, two dialects. Bilingualism is also inconsistent with

local adaptation because possession of two dialects implies that a male can breed successfully in both dialects. Although the deceptive and honest convergence hypotheses have certain conceptual similarities, they produce different predictions in terms of dialect size, relation to past or present habitat patches, and temporal stability (Table 1).

Table 1 distinguishes, with asterisks, those variables that allow the strongest tests of hypotheses. In these cases, predictions are so clear and testable that failure to confirm a prediction of a particular hypothesis is sufficient to invalidate that hypothesis for the species under consideration. Thus if dialects contain more than one social unit, they cannot be explained *solely* by deceptive convergence (Baker and Cunningham 1985). Similarly, if temporal stability is always low, only deceptive convergence can explain the dialects (unless there are population crashes during the time interval under consideration). Lastly, if females do not prefer males with the correct local dialect (i.e., no assortative mating by vocal type) only isolation can explain dialect maintenance. By contrast, other variables that make clear predictions do not always in reality allow for clear tests. For example, although the local adaptation hypothesis predicts excess genetic divergence, actual tests are difficult and open to alternative interpretations (Baker et al. 1982c, 1984; Zink and Barrowclough 1984; Hafner and Peterson 1985).

Payne (1973b, 1981b, 1982, 1983; Payne and Payne 1977) provided evidence consistent with deceptive convergence (but see McGregor and Krebs 1984) but did not confirm deception. The heightened success of males who transformed their songs to match local dominants may have occurred because these males were signalling honestly that they were not newcomers to the local social milieu. Most of the controversy concerning dialects has dealt with *Zonotrichia* spp., whose dialects have been explained in terms of deceptive convergence, isolation, and local adaptation (Baker 1974, 1975, 1981, 1982a, 1982b, 1983; Baker and Cunningham 1985; Baker and Mewaldt 1978, 1981; Baker et al. 1981a, 1981b, 1981c, 1982a, 1982b, 1982c, 1984; Handford and Nottebohm 1976; Petrinovich et al. 1981; Tomback et al. 1983; Baptista and Petrinovich 1984; Payne 1981a; Kroodsmas et al. 1984; Zink and Barrowclough 1984). The *Zonotrichia* results may conform to the honest convergence hypothesis, but our main objective here is to test

this and the other hypotheses with the cowbird dialects. We agree with Baker and Cunningham (1985) that different hypotheses can apply to different levels of variation within the same species. For example honest convergence could maintain large and divergent dialects within which small social units show relatively minor vocal differences (subdialects) that arise via deceptive convergence.

METHODS

RECORDING AND ANALYSIS OF VOCALIZATIONS

Recordings in 1978 and 1979 were made with Uher Report 4000 L and 4000 IC tape recorders and Uher M517 or Shur 565 microphones. Recordings from 1980 to 1985 were made with Marantz Superscope CD 320 or 340 or Sony Professional Walkman WM-D6 cassette recorders and Sennheiser ME-80 microphones. Whistles were analyzed with a Kay Elemetrics Sona-Graph machine (model 6061-B) using the narrow band filter and the 160 to 16,000 Hz scale. Frequency measurements were taken to the nearest 100 Hz. Measurements were analyzed with *t*-tests or ANOVAs using the Statistics Module on a T1-99-4A computer or with non-parametric tests in Siegel (1956).

Whistles were recorded by: (1) following birds but not disturbing them; (2) approaching and scaring off perched birds, which often elicits whistles; (3) eliciting whistles via playbacks of the female cowbird's chatter or rattle call (Friedmann 1929; Rothstein et al., in press).

SAMPLING CRITERIA AND RECORDING SITES

Radio telemetry demonstrated that cowbirds in our study area are dispersed during the morning throughout breeding habitats such as open forests where hosts are plentiful (Rothstein et al. 1984). The birds vacate their morning ranges, which cover up to 1.5 to 2 km, by early afternoon and commute up to 7 km to feeding sites where they spend the rest of the day in groups of 10 to >50 birds (Rothstein et al. 1980, 1984). Because of this high mobility, we could not assume that recordings made even 1 to 2 km apart represented different individuals. Thus we rely mostly on recordings of uniquely marked birds to describe whistle variation. Most of our data are based on 101 color banded birds recorded from 1983 to 1985. To this sample we added: (1) six

color banded birds recorded in 1981; (2) 15 unbanded birds recorded late in 1984 or in 1985 after all the banded birds had already been recorded; (3) 20 unbanded birds assumed to be different individuals because they were recorded from 1981 to 1984 in breeding habitat at least 2 km from the nearest site where another male was recorded. We doubt that any individual in the latter group was counted twice because no banded bird was recorded at sites >2 km apart in breeding habitat. We use this basic series of 142 birds to assess the current features of the dialects because 93.7% of the birds were recorded between 1983 to 1985. To assess temporal stability, we compare the "current data" with recordings of unbanded birds made between 1978 to 1980.

BANDING AND AGING MALES

Birds were captured in Potter traps at afternoon feeding sites such as horse corrals. Each was given a unique combination of three color bands and one Fish and Wildlife band. Males were aged as yearlings or adults (SY or ASY according to nomenclature of the Bird Banding Lab.) following criteria in Selander and Giller (1960).

ASSESSMENT OF RELATIVE COWBIRD ABUNDANCE

To assess relative cowbird abundance in different habitats, we used data on birds visually and/or aurally detected from a fixed point during a 10 min period. Counts were done from May to July 1978 with nearly all sites >1.6 km apart. Each site was sampled once between sunrise and 09:00 P.s.t. The method is described further by Rothstein et al. (1980) and Verner and Ritter (1983).

RESULTS

USE OF THE WHISTLE

As did Friedmann (1929), we found that solitary males in breeding habitat often whistle in flight, just after landing, or before taking flight. Although nonterritorial (Dufty 1982a, 1982b; Rothstein et al. 1984), males exhibit agonistic interactions in breeding habitat, apparently trying to dominate and perhaps drive off other males (Rothstein et al. 1986). Males whistle in response to distant whistles and approach the sound source which usually results in agonistic interactions involving songspread and head-up displays (Orians and Christman 1968). This male approach-behavior has been verified with experimental

playbacks of whistles, which also showed that males whistle in response to the playback (Rothstein et al., in press). Females respond to whistles with loud chatter calls after which males approach them. Sometimes females also approach males. The female response has also been confirmed with experimental whistle playbacks (Rothstein et al., in press; Fleischer and Rothstein, unpubl.). Furthermore, it is clear that males use whistles to communicate with females because experimental playback of the female chatter call (Rothstein et al., in press) showed that males of all three subspecies whistle as they approach such playback but rarely give the vocalization known as cowbird song (See Friedmann 1929). The uses and functions of the song and whistle are described further in Rothstein et al. (in press). Males whistle most in the morning but whistle in afternoon-feeding flocks if scared off by an approaching predator or human.

The whistle seems critical to mating. First, it is the chief way males and females make contact since they are usually apart (i.e., >30 m from each other) before most copulations. For example, the male and female were together for <5 sec before 81.6% of 76 copulations (Rothstein et al., in press; Yokel 1986). Secondly, males in our Sierran study area whistle just before mounting the female in most, 88.0%, copulations. Songs precede copulations significantly less often, 54.8% of the time (Rothstein et al., in press). By contrast, captive eastern males always sing before copulations (Eastzer et al. 1985) but rarely whistle (M. J. West, pers. comm.). These differences in precopulatory behavior are probably due to geographic variation and/or to artifacts of captivity (Rothstein et al., in press). Although males and females are apart before most copulations, mating is not a casual affair elicited by any male's whistle. Cowbirds in our study area are largely monogamous and nearly all copulations are limited to pairs that have had frequent contact over long periods (Yokel 1986). Although the whistle is rarely given in repeated broadcast fashion by perched birds, in contrast to the songs of most passerines, its use involves the functions ascribed to typical passerine song, namely agonistic male-male and sexual male-female communication. Furthermore, flying males whistle repetitively so the whistle can be called the aerial song of the cowbird. Thus hypotheses originated for song dialects (Table 1) are clearly applicable to the whistle.

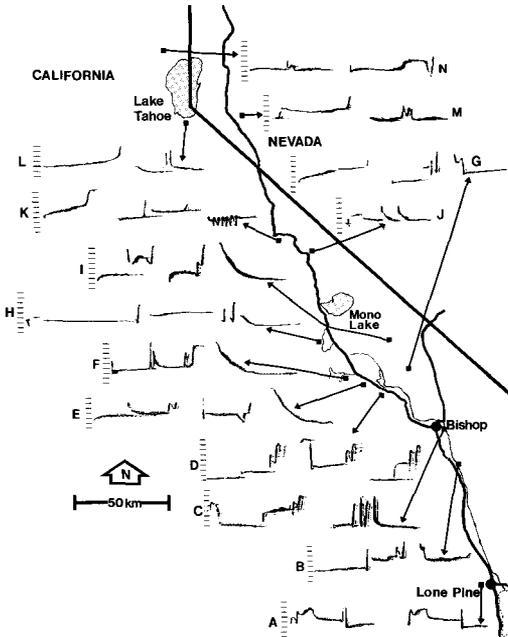


FIGURE 1. The series of diverse whistle types occurring along the east slope of the mid-Sierra. (Frequency scales begin at 3 kHz.) We have sufficient recordings ($n = >6$ males) from all sites to demonstrate that each is a distinct local dialect with the following exceptions: area C, Bishop, has at least five whistle types that co-occur (the only such "polymorphic" site on the figure); areas D, G, I, and K are based on three to five males. The three dialects under intense study are E, F, and H (Fig. 2). All other areas where whistles have been recorded in more than one year (A, C, D, J, and M) show constancy in whistle type except for area D where the whistle shown is apparently being replaced by the Convict type (E). The heavy dark line running from Lone Pine to Bishop and beyond is the major highway in the region (U.S. 395).

DIALECTS IN THE EASTERN SIERRA NEVADA

Most of the eastern Sierra and adjoining Great Basin are unsuitable for cowbirds because arid conditions prevail and because cowbirds prefer or even require modified environments such as towns and livestock for foraging (Verner and Ritter 1983). But cowbirds are locally abundant where host-rich habitats, such as riparian forests, occur near occasional foci of human activity, such as pack stations and campgrounds. Figure 1 shows most of the whistle types we have found in a 300-km north-south transect along the eastern slope of the central Sierra. Each type is limited to a single semi-isolated cowbird population and

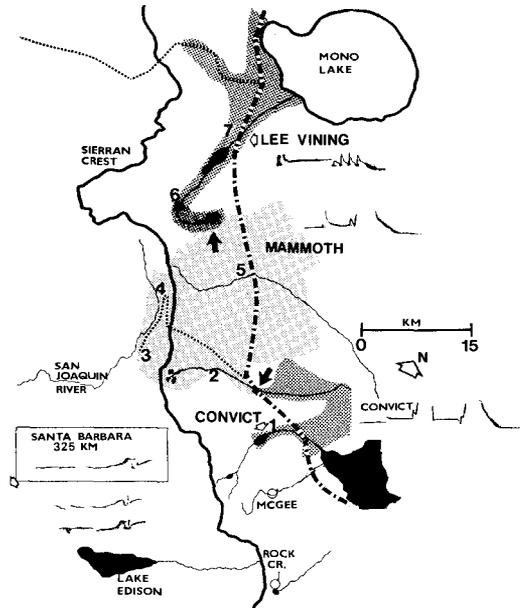


FIGURE 2. Flight whistle dialects in the eastern Sierra Nevada near Mammoth Lakes, Mono Co., California. Major dialects at or around Lee Vining, Mammoth Lakes, and Convict Lake are screened. Numerous examples of each dialect are shown in Figures 3-5. Areas of dialect overlap are delimited by broad, dark arrows. Sonograms of dialect whistles are at, or adjacent to dialect ranges except for the boxed off whistle. The latter is located in the general direction of the attached open arrow and at the distance noted within the box. For a relative time scale, the whistle labelled "Convict" is 1.1 sec in length. Note where the Mammoth dialect crosses over onto the western slope of the Sierra Nevada along the San Joaquin River and Devil's Postpile Road. "Coastal whistles," similar to those from very distant points such as Santa Barbara, occur within 25 km of the Devil's Postpile Road near Lake Edison. The dashed lines show the major roads in this region. The numbers represent major afternoon-feeding sites where we trapped birds. These are pack stations and ranches (1-4, 6, and 7) and a campground (5).

data are sufficient to indicate that at least 8 of the 13 whistle types represent local dialects (Fig. 1). Additional dialects probably exist since we haven't sampled every population in this region.

The dialects are generally separated by treeless expanses of desert scrub vegetation at lower elevations, or sagebrush above about 1,500 m. These habitats have only one to four potential host species and cowbirds were detected during none of 17 10-min counts within them. By contrast, cowbirds occurred at 101 of 337 count sites in other habitats (forests, riparian strips, etc.)

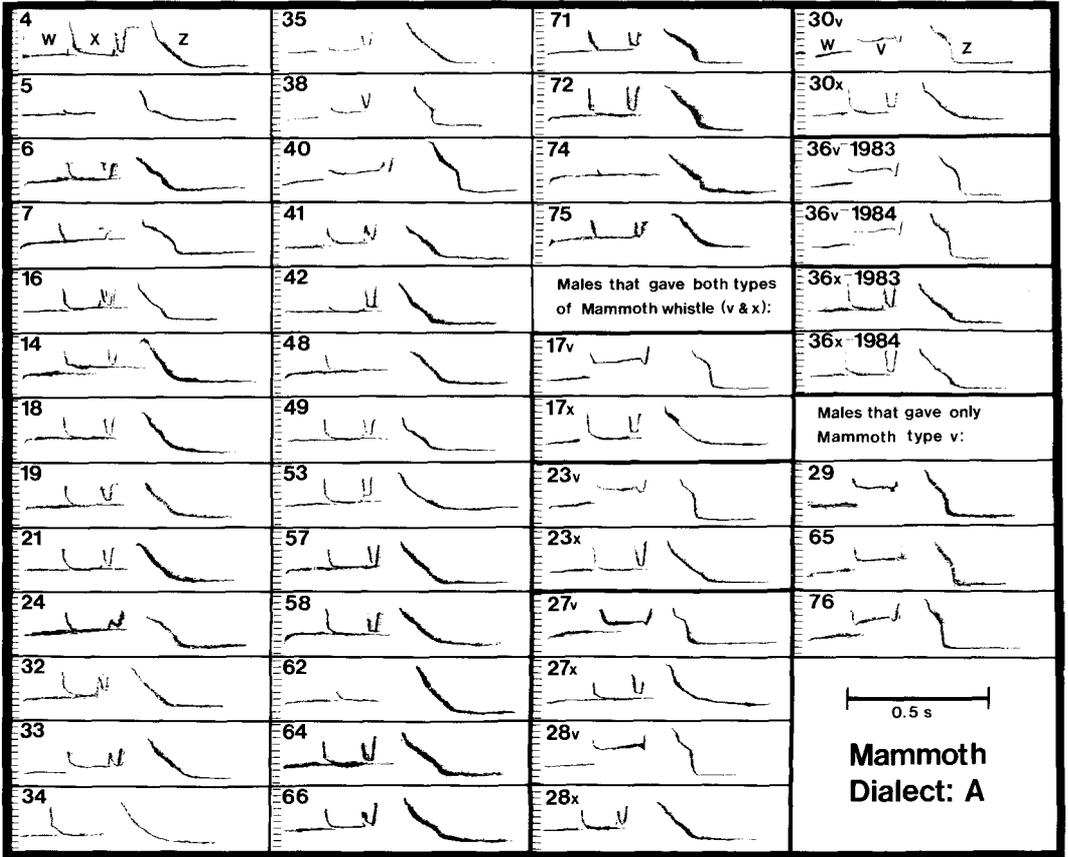


FIGURE 3A. Whistles of males that gave one or both of the two standard types of Mammoth whistles (WXZ or WVZ) within the Mammoth dialect area (Fig. 2). The sonograms shown are actual tracings that have been reduced via Xerox®. All the males that were recorded are shown except for a small number whose recordings were too poor to allow reproduction. Numbers within each panel are used to identify different individuals. Letters over whistle elements in the top panels identify code letters for these elements (see text). Frequency scales start at 3kHz.

within the area covered by Figure 1, resulting in a significant contrast ($\chi^2 = 5.73$, $0.01 < P < 0.02$). The remainder of this paper deals only with dialects E, F, and H (Fig. 1), which have been the subject of intensive studies.

THE THREE DIALECTS UNDER INTENSIVE STUDY

The “Mammoth” dialect corresponds to a large forest of Jeffrey pine (*Pinus jeffreyi*) as mapped by Griffin and Critchfield (1976) and as seen easily in Landsat photographs (Short et al. 1976). The dialect probably extends further east into the Glass Mountains than is shown (Fig. 2) but cowbird numbers and our data for this remote area are few. Extensive sagebrush flats occur north and south of the forest and cowbirds in the two

adjacent dialects, “Lee Vining” and “Convict,” occur in scattered riparian corridors and patches of forest surrounded by sagebrush. The Mammoth whistle has three syllables as opposed to four in the Convict type. The extra syllable in the latter is a unique third element as syllables 1, 2, and 3 in Mammoth whistles seem homologous with 1, 2, and 4 in Convict whistles (Fig. 2). The Lee Vining whistle is the most divergent and variable of the three. It ends with a unique element that starts with one to seven rapid frequency sweeps (two in H in Fig. 1, four in Fig. 2). This terminal element may be preceded by one (Fig. 2) or two (H in Fig. 1) simple elements, neither of which occur in Convict or Mammoth whistles. More descriptive detail is given below.

The Sierran crest occurs to the west of these

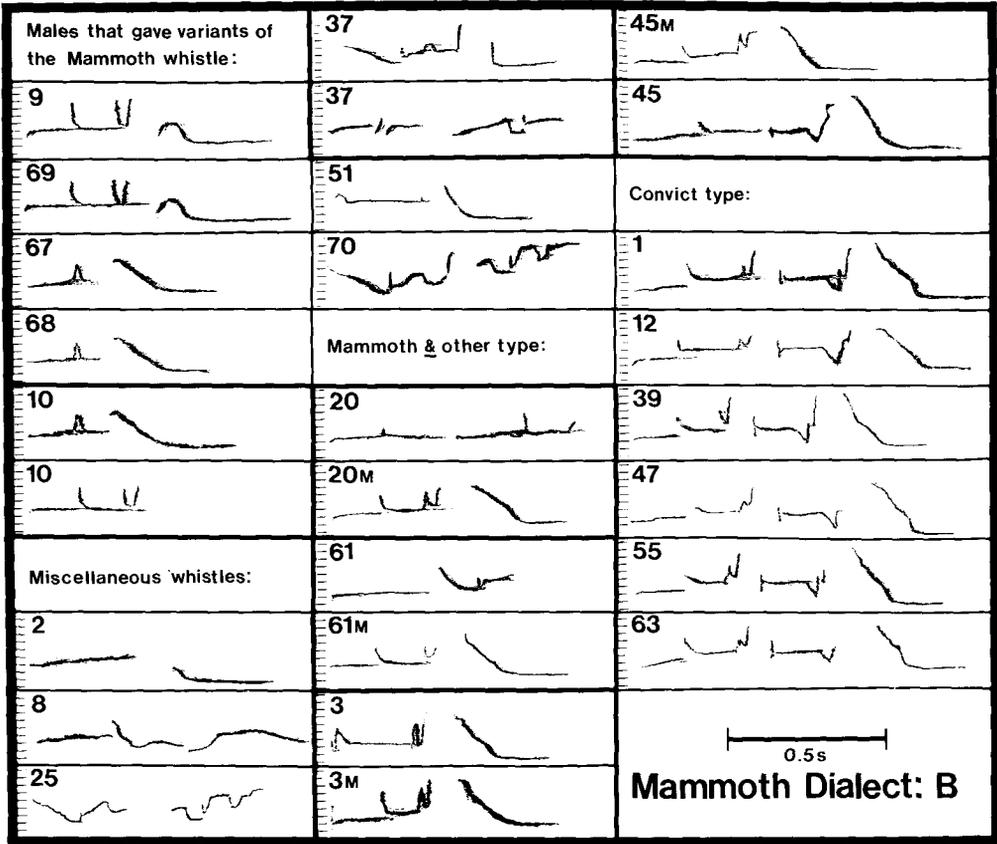


FIGURE 3B. Whistles by Mammoth dialect-area males that gave whistles atypical for the local area.

dialects. It usually corresponds to a gap in cowbird distribution because of both low-host densities above treeline and the low density of humans and livestock in wilderness areas (Verner and Ritter 1983). However, the crest is unusually low near Mammoth Lakes and is crossed by continuous forest and human influence in the form of the “Devil’s Postpile” Road and associated pack stations (3 and 4 in Fig. 2). Cowbirds along the road give Mammoth whistles. There is a 15- to 25-km gap in cowbird distribution west of the road and elsewhere along the crest until cowbirds again occur. These western slope birds are *M. a. obscurus*, as opposed to *M. a. artemisiae* on the eastern slope (Grinnell and Miller 1944). Their predominant whistle, “the coastal type,” conforms to a relatively constant type that *M. a. obscurus* shows over a 780-km north-south span west of the Sierran crest (Rothstein et al. 1986, see examples in Fig. 2 from Lake Edison). In contrast to the eastern Sierra, suitable cowbird

habitat is relatively continuous in most regions west of the Sierran crest and this is probably a major factor in the relative constancy of the whistle in these regions.

QUALITATIVE CONTRASTS AMONG THE THREE DIALECTS

To demonstrate the vocal constancy within dialects, Figures 3A, 3B, 4, and 5 show whistles of all 121 males in our basic series whose recordings were of sufficient quality to allow reproduction. The proportions of males that gave various whistle types are highly significantly different in the three dialect areas (Table 2). Furthermore, our sampling probably tended to reduce the dialect differences; 72.4% of our Mammoth sample was recorded within 1.5 km of site 2 (Fig. 2), which was within commuting distance (Rothstein et al. 1984) of the Convict-Mammoth overlap area. Breeders from the overlap area may have accounted for most of the 9.2% of Mammoth area

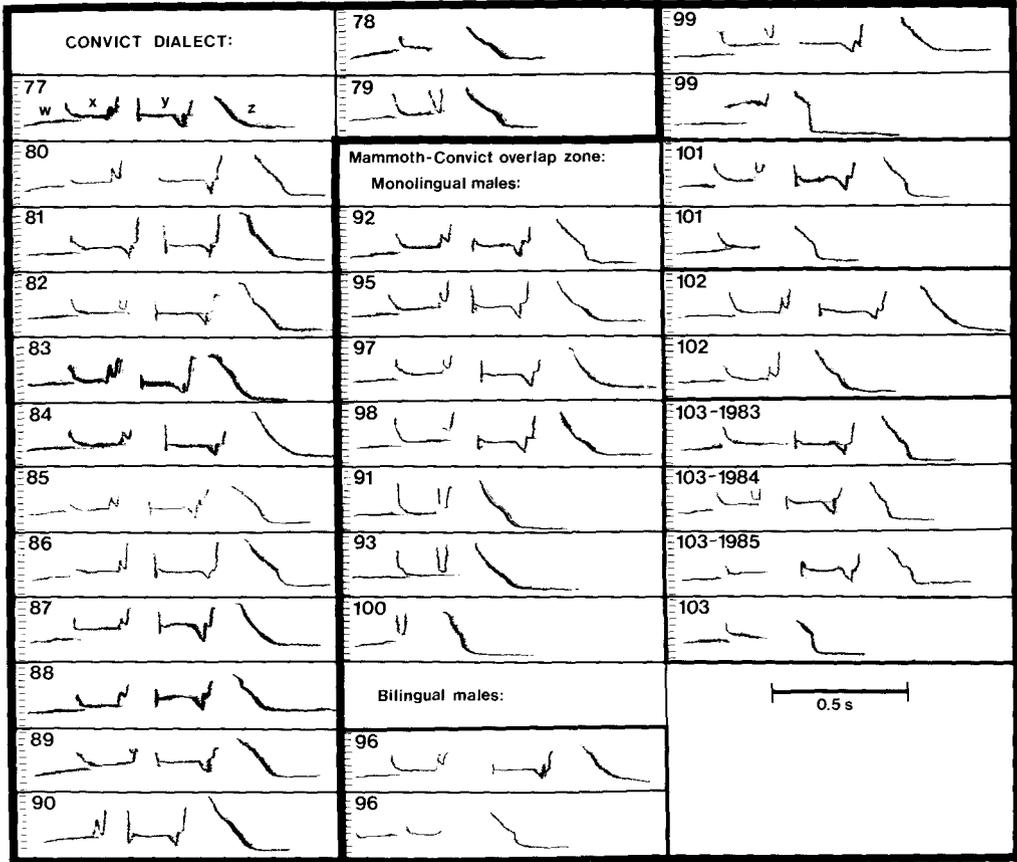


FIGURE 4. Whistles of males from the Convict dialect area and the Convict-Mammoth overlap area (Fig. 2). See Figure 3 for further details.

males that gave Convict whistles. Most birds in the two other dialects were also recorded in the afternoon near feeding sites (1, 6, and 7 in Fig. 2). Males recorded at afternoon feeding sites had the same whistles as males recorded in the morning in surrounding breeding habitat and radio telemetry data (Rothstein et al. 1984) indicate that the former males bred an average of 3.8 km from feeding sites (range = 1.4–6.7 km). Because the precise breeding sites of many males are unknown, we are unable to apply the isogloss method proposed by Mundinger (1982). In contrast to the samples for the three dialect areas, all males in the two overlap areas were recorded in the morning in breeding habitat. Bilingual males made up a significantly larger proportion of the males in the Convict-Mammoth overlap area than in both the Convict and Mammoth dialects (Table 2). Significantly more males gave hybrid

whistles that combined the last element of a Mammoth whistle with the initial one or two elements of a Lee Vining whistle (e.g., male 134, Fig. 5) in the Mammoth-Lee Vining overlap area than in either “pure” area to the north and south (Table 2).

Table 2 is based on 555 sonographed whistles ($\bar{x} = 3.9$ per bird, range = 1 to 40). Only one whistle was recorded from 50 of the 142 males but this has little effect on our sampling because: (1) Even if one whistle was recorded from each bird, statistical analysis would still reliably determine whether areas differ in predominant whistle types; (2) The majority of males in the nonoverlap zones had only one whistle type. We sonographed five or more whistles from 34 birds, only three of which gave more than one whistle type. All seven males that had samples of 7 to 15 whistles (Fig. 6) gave whistles of only one

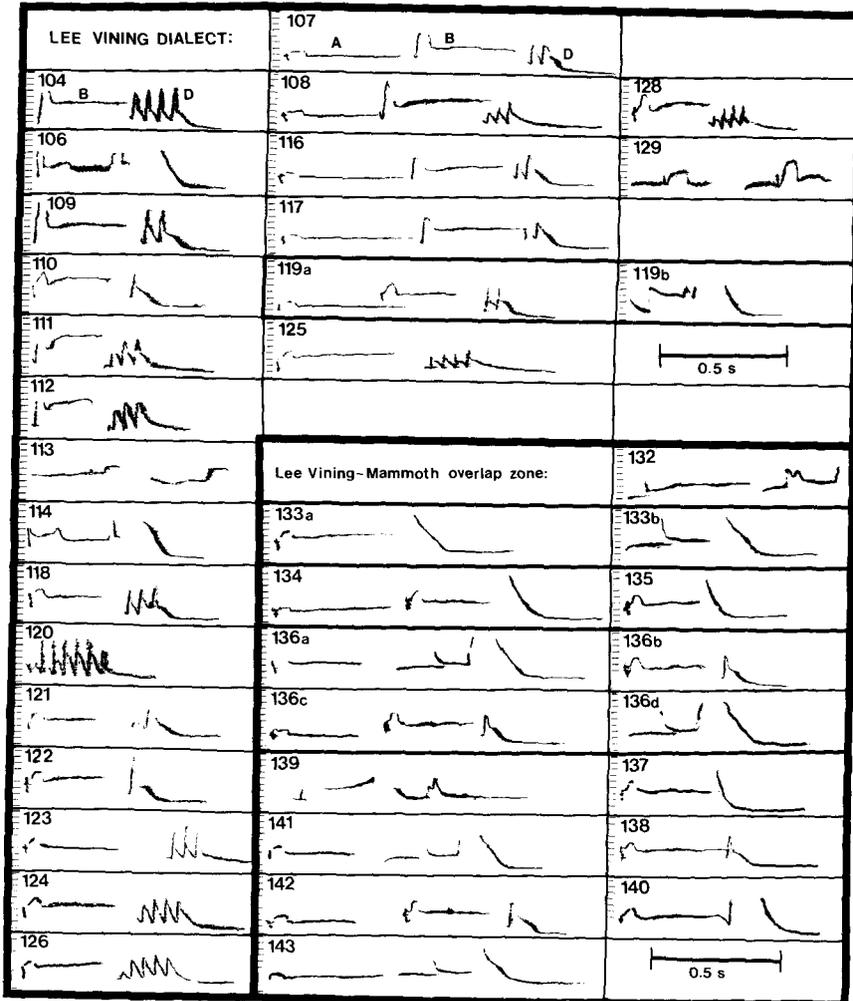


FIGURE 5. Whistles of males from the Lee Vining dialect area and the Lee Vining-Mammoth overlap area (Fig. 2). See Figure 3 for further details.

dialect. We cannot discount the possibility that some or most males can give an alternate whistle type but it is obvious that they do so very rarely, if at all. Otherwise, we would not have found such high conformity within the three dialects, e.g., males that gave only whistles that conformed to the local type made up 85.7%, 76.3%, and 80.8%, of the Convict, Mammoth, and Lee Vining samples, respectively (Table 2). Furthermore, if males can give alternate whistles but rarely do so, it would support our contention that there is considerable social contact between adjoining dialects (see below).

There were occasional variations on the basic whistle types, but these do not make the dialects

less objectively definable. To facilitate discussion, we coded the whistle syllables as follows: WXYZ = Convict (Fig. 4), WXZ = Mammoth (Figs. 3A, 3B) and ABD or BD or D = Lee Vining (Fig. 5). Occasionally, males in the Convict and Mammoth dialects gave short WX whistles (e.g., male 10, Fig. 3B). Such nondiagnostic whistles are not included in Table 2. Two males in the Convict dialect (Fig. 4) did whistles characterized as WYYZ (Male 81) and XYZ (male 90) instead of WXYZ. Since element Y is the only difference between the Convict and Mammoth dialects, these males clearly conform to the former.

There were two variants of the Mammoth

TABLE 2. Numbers of males that gave each whistle type in the three dialect areas and two overlap zones under intensive study.

Area (see Fig. 2)	Whistle Type						
	Convict	Mammoth	Lee Vining	Bilingual Mam. + Con.	Bilingual Mam. + Lee Vining	Hybrid Mam. - Lee Vining	Misc.
Convict dialect	12	2					
Con.-Mam. overlap area	5	3 ^a		5			
Mammoth dialect	6	58 ^b		1		1	10 ^c
Mam.-Lee Vining overlap area			3		1	7 ^d	2
Lee Vining dialect			21				5 ^e

Statistical Comparisons (Fisher exact or χ^2 tests on 2×2 contingency tables)

1. Proportions of bilingual and monolingual birds in the Convict-Mammoth overlap area vs. the Convict dialect: $P < 0.025$; vs. the Mammoth dialect: $P < 0.001$, $\chi^2 = 9.72$.
2. Proportions of birds doing Convict and non-Convict whistles in the Convict vs. Mammoth dialects: $P < 0.001$, $\chi^2 = 37.1$.
3. Proportions of birds doing hybrid Mammoth-Lee Vining whistles in the Mammoth-Lee Vining overlap zone vs. the Mammoth dialect: $P < 0.001$; vs. the Lee Vining dialect: $P < 0.001$.
4. Proportions of birds doing Mammoth and non-Mammoth whistles in the Mammoth vs. the Lee Vining dialect: $P < 0.001$.

^a Two males did typical Mammoth whistles; the third did a modified Mammoth whistle (male 100 in Fig. 4).

^b Fifty-three males did typical Mammoth whistles; another five did modified Mammoth whistles (males 9, 69, 77, 68, and 10 in Fig. 3B).

^c Four of these 10 males did a typical Mammoth whistle plus one other type of whistle (males 20, 61, 3, and 45 in Fig. 3B).

^d One of these males did a normal Mammoth whistle in addition to hybrid whistles (male 133 in Fig. 5).

^e One of these males did a typical Lee Vining whistle plus a Mammoth-like whistle (male 119 in Fig. 5).

whistle. Forty-one males gave only the predominant type, WXZ, whereas nine gave both WXZ and WVZ (Fig. 3A). Three males gave only WVZ but we recorded only one whistle from two of these so we suspect that all males that gave WVZ also gave WXZ. Thus there is no reason to designate WXZ and WVZ as separate dialects. A later subsection quantifies the consistent differences between WXZ and WVZ whistles.

Birds in the Lee Vining dialect gave the most variable whistles. The following types occurred: ABD—5 birds; BD—14; D—1; ABD and BD—1 (Fig. 5). Since one bird did both ABD and BD, some of the variation is due to intraindividual variation. The variation does not reduce the distinction between the Lee Vining and adjoining Mammoth dialects because none of the elements ABD occur in the latter. Nor does the variation reduce the cohesiveness of the Lee Vining dialect because some birds that gave only BD whistles also did A alone. Element A is the predominant “single syllable flight call” in the Lee Vining dialect. This call occurs in all cowbird populations but varies spatially (Rothstein and Fleischer, unpubl.). In contrast to the Lee Vining dialect, where whistles often began with single syllable calls, only 1 of 80 males in the Mammoth and Convict dialects began a whistle with a single syllable.

This single syllable was different from element A and occurred in only one of five whistles by this male.

Besides the Convict whistle, only three types of atypical whistles were done by more than one male in the Mammoth dialect. These are the types by males 9 and 69, by 67, 68 and 10, and by 25 and 70 (Fig. 3B). Males that gave each of these whistle types occurred together in breeding habitat or within 0.5 km of each other, thus suggesting that there may be occasional “subdialects” of variant whistles. Although some atypical whistles were variants of local types, such as those by males 9 and 69 and by males 67, 68, and 10 (Fig. 3B), others matched whistles from distant areas. One of the whistle types by male 37 (lower one in Fig. 3B) resembled western slope whistles (Fig. 2). Male 139 (Fig. 5) gave a whistle identical to ones given in the Carson Valley, 140 km to the north (site M in Fig. 1).

QUANTITATIVE ANALYSES OF INTRADIALECT VARIATION

We concentrated on the Mammoth dialect to elucidate patterns of intradialect variation. Because whistles are used over long distances, we hypothesized that males have individually recognizable whistles. To test this hypothesis, we did quantitative analyses of the whistles of all 14

males that did typical Mammoth whistles (WXZ, Fig. 3A) and for whom we had good recordings of at least four whistles. We limited this analysis to WXZ whistles because it seemed likely that less common types (Fig. 3B) could be easily distinguished by the birds. We measured five variables on each of 105 WXZ whistles by these 14 birds. Two variables measure the frequency of elements and two measure duration (Fig. 6). The fifth variable quantifies variation in the shape of element Z (see Figs. 3A, 3B) and is explained in Figure 6. We performed one-way ANOVAs on each variable to determine if the variance among males was greater than that within the whistles of individual males. Since a significant ANOVA could occur if 13 males were identical for a character and only one were divergent, a more appropriate analysis to assess individual variation was achieved by dividing the 14 males into three groups on the basis of sample size. This resulted in 15 separate ANOVAs (five variables \times three groups), 13 of which were significant (Fig. 6, most P s $<$ 0.001).

We also grouped the 14 males by recording locality and year. Males 6, 35, 42, and 57 were recorded within 1.5 km of site 2 (Fig. 2) in 1983 and males 16, 22, 27, 49, and 53 were recorded there in 1984. Two of five ANOVAs for the former group were significant as were three of five for the latter group. Males 71 and 72 were recorded in 1985 within 3 km of site 5 (Fig. 2) and four of five possible t -tests contrasting their whistles were significant. Lastly males 19 and 21 were recorded in 1983 2.4 km east of site 2 (Fig. 2) and one of five t -tests was significant. Overall, 23 of 35 ANOVAs and t -tests were significant. Thus, we conclude that most males are potentially individually recognizable by their whistles.

The fact that whistles were individually distinctive is also demonstrated by the means in Figure 6. Males with similar means for one character invariably showed strong differences in one or more other characters because most of the characters varied independently. We used data on WXZ whistles by all 55 males that did such whistles within the Mammoth dialect and found only two significant correlations among the ten possible for the five characters. The shape score (character 5, Fig. 6) was weakly correlated with characters 3 and 4 (Spearman's coefficients of rank correlation were $r = 0.30$, $P = 0.03$ and $r = 0.42$, $P = 0.002$, respectively).

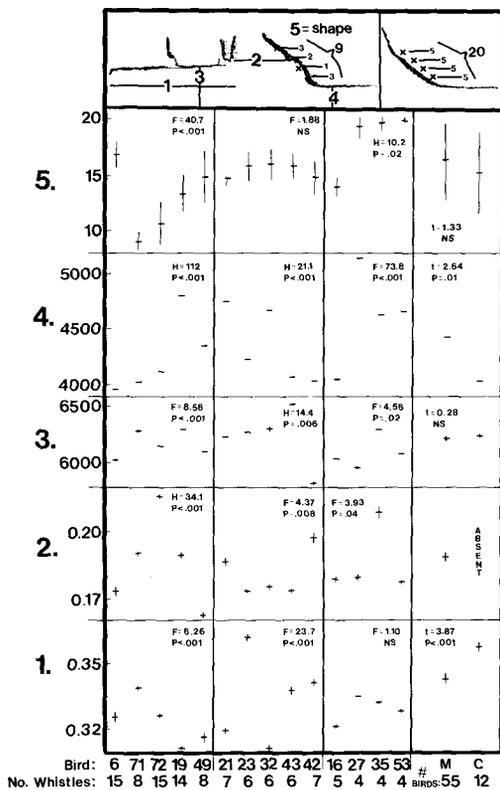


FIGURE 6. One way ANOVAs done on five quantitative characters measured on 105 Mammoth whistles by 14 males. Values shown are means and standard deviations for each male. (Some standard deviations are too small to be shown.) The 14 males were divided into three groups on the basis of sample sizes (see text). Each boxed-off area represents a separate ANOVA. Character 5, the shape of Z, the last whistle element, was calculated as follows: we placed one end of a ruler at the bottom of the downward frequency sweep at the start of Z and the ruler's other end at the top of the sweep. At points 1, 2, 3, and 4 cm from the ruler's lower end, we determined whether the ruler was to the left of the sweep (score = 1), touching the sweep's left side (2), within the sweep (3), touching the sweep's right side (4), or to the right of the sweep (5). Thus character 5 could range from 4 to 20 and divergent examples of 9 and 20 are shown in the figure. F -max tests were done to determine if variances were homogeneous. If variances were heteroscedastic, nonparametric Kruskal-Wallis ANOVAs were used (indicated by H values). The far right column uses t -tests to contrast measurements of homologous characters for all available Mammoth and Convict area birds. Character 2 does not occur in Convict whistles. Two of the other four characters show significant differences. Units are as follows: characters 1 and 2—sec; characters 3 and 4—Hz; character 5—unitless.

TABLE 3. Quantitative comparisons among males that did various whistle types within the Mammoth and Convict dialect areas shown in Figure 2.^a

Whistle types ^c (see Figs. 3 and 4)	Years	Parameter (see Fig. 6) $\bar{x} \pm SD^b$				
		1 (sec)	2 (sec)	3 (Hz)	4 (Hz)	5
1. Mammoth-WXY (55)	83-85	0.337 ± 0.019	0.188 ± 0.016	6,210 ± 40 ***	4,420 ± 40 ***	16.8 ± 3.3 ***
2. Mammoth-WVY (12)	83-85	0.348 ± 0.022	0.185 ± 0.026	7,960 ± 30 ***	3,740 ± 20 ***	11.0 ± 2.2 ***
3. Mammoth-WXY by males that also did WVY (9)	83-85	0.334 ± 0.019	0.182 ± 0.014	5,950 ± 20 *	4,620 ± 50	19.1 ± 1.5 *
4. Mammoth-WXY by males that did only WXY (46)	83-85	0.338 ± 0.020	0.189 ± 0.016	6,260 ± 40	4,390 ± 40	16.4 ± 3.4
5. Convict-WXYZ (12)	83-85	0.364 ± 0.021	—	6,240 ± 50	4,030 ± 60	15.4 ± 3.8
6. Convict-WXYZ (6)	78-80	0.381 ± 0.012 **	—	6,120 ± 20	4,200 ± 40	19.0 ± 1.7
7. Mammoth-WXY (11)	78-80	0.346 ± 0.014	0.178 ± 0.021	6,320 ± 30	4,370 ± 40	18.3 ± 2.2

^a Asterisks between values in adjacent rows indicate that these values differ significantly by *t* tests: * = 0.02 $P < 0.03$, ** = $P < 0.01$, *** = $P < 0.001$.

^b These data are based on the best recorded whistle for each male except that if a male was in the ANOVA series (Fig. 6) we used the means for his measurements.

^c Numbers in parentheses are the number of males in each sample.

Similarities within a male's whistles but divergence among different males also occurred in the Lee Vining dialect, where whistles had a variable number of brief frequency sweeps at the start of element D (Fig. 5). Four to 12 whistles from each of five males showed that the number of sweeps did not vary within each male's whistles but ranged from one to three among males ($P < 0.001$, $H = 24.5$, $df = 4$, Kruskal-Wallis ANOVA).

Data are available for seven Mammoth dialect males recorded on two days, with intervals ranging from one day to one year. Product-moment correlation coefficients for each of the five variables in Figure 6 showed that characters 1, 4, and 5 had significant correlations between the first and second time the males were recorded ($r = 0.694$, $P = 0.04$; $r = 0.838$, $P = 0.01$ and $r = 0.976$, $P < 0.001$, respectively). The correlation for character 2 was marginally significant ($r = 0.677$, $P = 0.07$). Because four of five characters showed correlations that were significant or nearly so, we conclude that temporal variation within a male's whistles is less than the variation among males. Temporal stability is also indicated by qualitative assessments of the whistles of males recorded in more than one year (see male 36, Fig. 3A and male 103, Fig. 4).

QUANTITATIVE CONTRASTS AMONG WHISTLE TYPES

The two standard types of Mammoth whistles (WXY and WVY, Fig. 3A) differed significantly in three of five quantitative characters (Table 3). The difference was especially strong for character 3, the midpoint frequency of elements X and V, which ranged from 5,300 to 6,900 Hz ($n = 55$ birds) and 7,500 to 8,500 Hz ($n = 12$), respectively. The WXY whistles by males that also gave WVY showed two significant differences from the WXY whistles by males that only gave WXY (Table 3). In both cases, the direction of the difference made the males' WXY whistles more divergent from the WVY whistles by these same males than was the case for WXY whistles in general. Thus birds with both WXY and WVY whistles appeared to make the former especially distinct from the latter.

Four of the five quantitative characters can be measured in both Mammoth (WXY) and Convict whistles (WXYZ). Among these, two showed significant differences (Fig. 6). Thus the two dialects differ qualitatively by the presence or absence of element Y, and quantitatively by differences between other elements that are clearly homologous. The only apparent homology between the Mammoth and Lee Vining dialects is

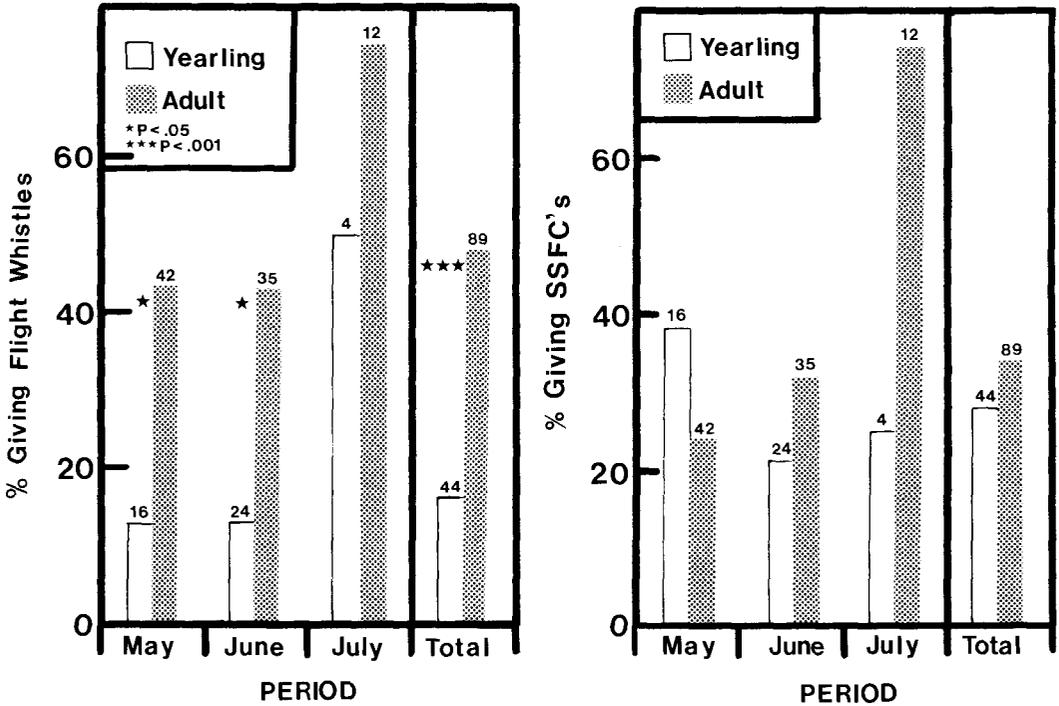


FIGURE 7. Proportions of banded adult and yearling males that gave flight whistles or single syllable flight calls (SSFCs) when approached by observers and eventually forced to fly off. Numbers of males are at the tops of bars. To avoid problems of inflated *ns* and conditioning effects, we included only data for the first time a bird was ever approached. This figure combines data for the three dialects, all of which showed concordant trends. *P* values are based on χ^2 tests. Note that adults and yearlings did not differ in their propensity to give single syllables but did differ in terms of whistles.

the terminal part of element D. Without its initial frequency sweeps, D is similar to element Z in the Mammoth dialect (Figs. 3A and 5). Thus the terminal frequency of D may be comparable to character 4 (Fig. 6) in Mammoth whistles. The mean for the character was $4,100 \pm 25$ Hz ($n = 22$) for Lee Vining whistles, which is significantly below the corresponding mean for the Mammoth dialect ($4,420 \pm 40$, Table 3; $t = 3.29$, $df = 75$, $0.001 < P < 0.01$). Again, probable homologous elements in adjacent dialects have significant quantitative differences.

TEMPORAL STABILITY

All 12 whistles recorded between 1978 to 1980 in the Convict dialect at site 1 (Fig. 2) were Convict whistles whereas 34 of 36 recorded in the Mammoth dialect at sites 2, 3, 4, and 5 were Mammoth whistles. The two discordant whistles in the Mammoth sample were one Convict whistle and one miscellaneous type never recorded

again. We attributed whistles in the 1978 to 1980 sample to different individuals if they: (1) were recorded at sites >3 km apart; (2) temporally overlapped on sonograms; or (3) had quantitative differences that exceeded those within the whistles of any male in the ANOVA series (Fig. 6). These criteria gave six males for the Convict dialect, all of whom gave Convict whistles. The Mammoth sample consisted of 11 males who gave the following whistle types: 9—Mammoth, 1—Convict, 1—miscellaneous. As in 1983 to 1985 (Table 2), the proportion of males that gave Convict and non-Convict whistles in the two areas is significantly different ($P < 0.01$ for 6 of 6 vs. 1 of 11, Fisher test). Our criteria for assessing the number of individuals in the 1978 to 1980 sample is highly conservative. These whistles were recorded by walking up to birds and scaring them off at afternoon-feeding sites. Work with banded birds in 1983 to 1985 demonstrated that this method usually elicited only one whistle from

TABLE 4. Relationships among a male's banding site and his age and whistle type when recorded.

Dialect in which male was recorded	Yearlings banded in dialect in which recorded		<i>P</i> ^c	Adults banded in dialect in which recorded		<i>P</i> ^c	Adults banded in another dialect	
	Local whistle ^a	Nonlocal whistle ^b		Local whistle ^a	Nonlocal whistle ^b		Local whistle ^a	Nonlocal whistle ^b
Convict	0	0	—	5	0	0.17	2	2
Mammoth	4	4	0.02	41	6	0.06	1	2
Lee Vining	5	1	0.69	7	1	0.07	0	2
Three dialects combined	9	5	0.04	53	7	<0.001	3	6

^a These males gave only local whistles.

^b Some of these males gave a local whistle in addition to a non-local type but most gave only the latter.

^c Probabilities are based on Fisher exact tests or χ^2 tests ($n > 20$) applied to 2×2 tables constructed from adjacent entries on each row.

each male (next section) so the total of 48 whistles from 1978 to 1980 probably represents much more than 17 males.

We measured the five quantitative characters described earlier (Fig. 6) on one whistle from each putative male in the 1978 to 1980 series. There were no significant differences among the 10 possible intradialect *t*-tests comparing 1978 to 1980 and 1983 to 1985 measurements (values in Table 3). Contrasts between Convict and Mammoth whistles in the 1978 to 1980 sample showed one significant difference. Character 1 was significantly larger in Convict whistles (Table 3), as also occurred in the 1983 to 1985 sample (Fig. 6). Overall then there is no evidence that the two dialects underwent quantitative shifts between the two time periods.

YEARLING-ADULT DIFFERENCES IN WHISTLE BEHAVIOR

We approached banded birds and determined whether they whistled before or as they flew away from us. Significantly more adults than yearlings whistled in May and in June and the difference is also highly significant for the combined May to July period (Fig. 7). Males gave up to six whistles as we approached them, but 73.5% that whistled did so only once. In contrast to their whistle behavior, yearlings and adults were equally likely to give one or more single syllable calls (Fig. 7), which are given in the same contexts as whistles. However, among males that gave single syllables, 9 of 12 yearlings gave more than one whereas only 10 of 30 adults did so, a significant difference ($P < 0.05$, Fisher test). Medians, means, and maxima are 1, 2.1, and 12 for adults and 2, 4.6, and 18 for yearlings. Thus yearlings may make greater use of the single syllable call than do adults.

RELATIONSHIPS AMONG AGE, WHISTLE TYPE AND BANDING AND RECORDING SITES

We were unable to determine the identities of 24 of the 107 banded birds in our 1983 to 1985 sample because we could not always see all four bands or some birds lost at least one band (but these 24 birds were known to be different individuals via process of elimination). There were two important trends among the whistles of the 83 identified males. A significantly higher proportion of yearlings than adults gave whistles that did not conform to the local dialect (Table 4). The whistles of four of the five nonconforming yearlings either matched whistles of another dialect or contained elements from another dialect (males 3, 12, and 51, Fig. 3B; and male 119, Fig. 5). Possibly these four yearlings were emigrants who still showed the effect of earlier experience in another dialect. The remaining nonconforming yearling (male 2, Fig. 3B) gave a possible variant of the Mammoth whistle.

Adult males banded in one dialect but recorded in another were significantly more likely to give foreign whistles than were adults banded and recorded in the same dialect (Table 4). Four of the six nonconforming adults in the former sample gave whistles similar or identical to the dialect in which they were banded. For example, males 78 and 79 (Fig. 4) were recorded in the Convict dialect but gave Mammoth whistles typical of the dialect in which they were banded. The other two males in this sample gave unique whistles (male 8, Fig. 3B; male 113, Fig. 5). The distances between the banding and recording sites of these six males ranged from 6.4 to 22.1 km ($\bar{x} = 13.4 \pm 6.9$ km).

POPULATION SIZES OF DIALECTS

The numbers of birds visiting feeding sites give a rough estimate of local population sizes. In

1984 we trapped 105 females and 129 males at site 2 (Fig. 2), the most heavily used feeding site in the Mammoth dialect. The sum of 234 is a minimum for the entire dialect because numerous birds remained unbanded and many birds banded in previous years visited site 2 but were not caught in 1984. Most importantly, site 2 attracted birds only from the southern half of the dialect. We estimate that the population size of the Mammoth dialect is at least twice the number we trapped at site 2.

DISCUSSION

SPATIAL AND TEMPORAL INTEGRITY OF THE DIALECTS

The whistle dialects are unusually well-defined relative to the song dialects described for most passerines because the whistle is relatively brief. Also, whistles that were atypical for each local dialect were rare (Table 2) and mostly limited to one or two birds. Furthermore, the whistle dialects are based on lexical or vocabulary differences rather than the less extreme phonetic or pronunciation differences that define dialects in most species (Mundinger 1982). Each of the three intensively-studied dialects differs by the presence or absence of at least one unique acoustic element. Some other species such as the House Finch (*Carpodacus mexicanus*) show lexical differences between adjacent dialects but their rarity is indicated by the fact that Mundinger's (1982) review of lexical variation was limited almost exclusively to macrogeographical, or nondialectal variation.

As Mundinger (1982) noted, most studies of dialects have not identified discrete borders where vocal types change abruptly. Even one of the few taxa Mundinger identified as having discrete dialect borders may in fact lack them. Baker and Thompson (1985) have shown that White-crowned Sparrow (*Z. l. nuttalli*) dialects have narrow borders only when dialects are defined on the basis of one song element. When two spatially varying elements are considered, there is a 1.5-km wide zone of "hybrid songs." This zone is significantly large in comparison to the small territory sizes of this species. The borders between the cowbird dialects seem to be especially clear-cut, perhaps as a result of low population sizes at dialect borders. Riparian vegetation along Mammoth Creek provides a narrow link of suitable habitat between the Mammoth and Convict

dialects (Fig. 2). Whistles along the creek change fairly abruptly from nearly 100% Mammoth type near site 2 (Fig. 2) to mostly Convict type at the overlap area (Table 2). While cowbirds are locally abundant along Mammoth Creek, the riparian corridor is narrow being less than 100 m in width and the breeding population of the 1- to 3-km overlap area may not exceed 20 to 30 birds. The Mammoth-Lee Vining overlap area is more extensive and covers about 6 to 7 km. However, it is only about 1 to 2 km wide, north to south, which is small compared to the north-south extents of the Mammoth and Lee Vining dialects, which are about 22 and 32 km respectively.

Most birds in the Mammoth-Lee Vining overlap area gave hybrid whistles (Table 2, Fig. 6), somewhat comparable to the hybrid songs described for White-crowned Sparrows (Baker and Thompson 1985). In contrast there were no hybrid whistles in the Convict-Mammoth overlap area but such whistles may be impossible, since the two dialects differ only in the presence or absence of a single element. Actually, the bilingualism common in the latter overlap area may have also been typical of the Mammoth-Lee Vining overlap area, where sampling was less intense than for other areas listed in Table 2. The overlap area male from whom we recorded the most whistles (male 136, Fig. 5) gave pure Lee Vining (b and c), Mammoth (d), and hybrid whistles (a). Other overlap-area males might also have been shown to be bilingual had we recorded more whistles from them.

The temporal stability indicated by our 1978 to 1980 and 1983 to 1985 samples is a key aspect of dialects that is absent in studies of most species, exceptions being the White-crowned Sparrow (Baptista 1975, Baptista and King 1980, Trainer 1983), and House Finch (Mundinger 1982). In other species, year-to-year stability has not been assessed or is known to be low (Feekes 1977, Ince et al. 1980, Payne 1985). The stability of the whistle dialects is especially impressive given that we were unable to find any temporal shifts in the frequencies and duration of whistle elements (Table 3). Furthermore, one of two quantitative differences between Convict and Mammoth whistles in 1983 to 1985 (Fig. 6) also occurred in the 1978 to 1980 sample (Table 3). The high population sizes of the whistle dialects, which number in the hundreds, undoubtedly contribute to temporal stability. Some Sierran

dialects are smaller and may be more ephemeral (Rothstein and Fleischer, unpubl.).

ORIGIN AND AGE OF THE DIALECTS

As have some other investigators (Lemon 1975, Mundinger 1982), we assume that dialect differences arise through founder and bottleneck effects and learning drift. Learned vocalizations might not be expected in a brood parasite but studies of cowbird song have shown considerable learning (West et al. 1981a). The yearling-adult differences in whistles (Fig. 7, Table 4) are *prima facie* evidence for learning in this vocalization.

With the exception of Mundinger's (1982) study of House Finches, investigators have not had historical records sufficient to determine the ages of dialects. The dialects we studied became established since the late 1930s as Rowley (1939) detected no cowbirds in our area between 1926 and 1939 despite observations at current hot-spots of local abundance such as Mammoth and Convict Creeks. However, there are records indicating at least small numbers of cowbirds before Rowley's time (Grinnell and Storer 1924, Rothstein et al. 1980). These apparently died out by Rowley's (1939) study although he did find one parasitized nest just north of the Lee Vining dialect in 1939. Cowbirds returned in good numbers by the mid-1950s as E. Eaton (pers. comm.) found them to be common at site 5 (Fig. 2) when she began to visit the area in 1955. The whistle types that characterize the three dialects may have developed *de novo* since 1939 because we have not observed them in nearby populations likely to have provided founders. However, some of their elements occur in possible founding populations to the north and south of the dialects (Fig. 1; Rothstein and Fleischer, unpubl.).

USE OF THE WHISTLE

As reported above, the whistle is used for both long- and short-distance communication. Given the former use, we expected and confirmed that even birds with qualitatively similar whistles have quantitative whistle differences of potential value in individual recognition (Fig. 6). The magnitude of individual differences in frequency and duration are within the range passerines can detect (Dooling 1982).

The various quantitative analyses indicate that development is geared to closely reproduce certain whistle characteristics and that these are, therefore, critical to communication. This view

is in accord with the significant quantitative differences between homologous elements in Mammoth and Convict whistles (Fig. 6). Similarly, the sharp quantitative differences between Mammoth whistle types WXY and WVY (Table 3) also indicate that whistle characteristics are critical, otherwise these two whistle types would merge. We are especially intrigued with the finding that the WXY whistles of males who also gave WVY are more quantitatively divergent from the latter than are WXY whistles by males who did not give WVY (Table 3). We suggest that this divergence allows males with WXY and WVY whistles to emphasize their possession of both of these whistle types.

The ways in which whistle characteristics may contribute to male fitness have been tested with playback experiments (Fleischer and Rothstein, unpubl.). These experiments and observations reported here suggest that both male-male and male-female communication are important. The consistent use of whistles in the seconds preceding copulations suggests that females require a final check on a male's vocalizations. Female cowbirds are likely to be very discriminating in mate choice because males outnumber females (Darley 1971, Dufty 1982a) and the sex ratio is especially biased in the Sierra (Rothstein et al. 1980). Rothstein et al. (1986) and Yokel (1986) discuss why a female brood parasite might prefer certain males even in the absence of any possibilities for paternal care of her offspring.

TESTING ALTERNATIVE HYPOTHESES FOR DIALECT MAINTENANCE

Tentative rejection of deceptive convergence and acoustic adaptation. The whistle dialects are clearly larger than a social unit as they contain hundreds of individuals. Afternoon-feeding concentrations (Rothstein et al. 1980, 1984) could create a lek-like situation where a few males control mating of birds breeding over a huge area. However, social behavior at feeding sites may have little significance (Rothstein et al. 1986) and virtually all copulations occur on the dispersed morning ranges (Yokel 1986, pers. observ.). Thus for the same reasons as did Baker and Cunningham (1985), we reject the deceptive convergence hypothesis since it requires that dialects conform to social units. This hypothesis is also weakened by the fact that the whistle dialects are temporally stable (Table 1). In contrast to the qualitative and quantitative stability reported

here, Payne (1985) reported that songs of Village Indigobirds (*Vidua chalybeata*), a species in which deceptive convergence may occur, change so rapidly that most song types are not recognizable after five years.

We also reject acoustic adaptation as an overall explanation for the maintenance of the whistle dialects although local sound environments may influence some general aspects of whistle variation (Rothstein and Fleischer, unpubl.). "Coastal whistles," such as occur on the Sierran western slope (Fig. 2) are found over a huge area with habitats ranging from coniferous forest to nearly treeless agricultural regions (Rothstein et al. 1986). Also, the Convict and Lee Vining dialects have similar unforested habitats yet disparate whistles and the former has a similar whistle to the forested Mammoth dialect. Given our rejection of deceptive convergence and acoustic adaptation, we limit further discussion to the isolation, local adaptation and honest convergence hypotheses.

Bilingualism and hybrid whistles. Thirty-eight percent of the males in the Convict-Mammoth overlap area were bilingual, whereas bilingualism was shown by 0% and 8% of the males in the two adjoining "pure" dialect areas (Table 2). Since such a large proportion of the overlap area males are bilingual and appear to have experienced both dialects, the trend is inconsistent with the isolation hypothesis. It is also inconsistent with local adaptation because bilingual males can presumably communicate successfully in both dialects (Table 1). By contrast, the honest convergence hypothesis can explain bilingualism. If females frequently hear two whistle types from older, dominant males, as might occur at a dialect border, they could learn both as indicative of high quality males. We are not implying that such females simply prefer males with a larger than average whistle repertoire, rather, that they prefer males who give one or both of the specific whistle types that occur in the overlap zone. Such female preferences would give bilingual males more potential mates than monolingual males in overlap zones and would lead to a bilingual zone that is stable over time so long as there are no population crashes.

Similar arguments apply to the high frequency, 54%, of males that did hybrid whistles in the Mammoth-Lee Vining overlap area. The hybrid zone, which may actually consist of bilingual males (above), is clearly most consistent with the

honest convergence hypothesis. The hybrid zone implies contact between the two dialects (*contra* isolation) and might serve as a conduit for gene flow between them (*contra* local adaptation). These arguments are similar to those that apply to analyses of secondary contact between differentiated populations. If more than half of the individuals in an apparent contact zone show character states intermediate between the two pure populations, it is likely that the populations are not isolated spatially or reproductively.

Adult-yearling differences in whistles. Adults were significantly more likely to whistle than were yearlings in our "approach experiments" (Fig. 7). The approach data do not give absolute proportions of adults and yearlings that whistle because even males with whistles do not always give them when approached (pers. observ.). Nevertheless, the results indicated that yearlings either use their whistles less often or that a larger proportion of them simply do not whistle. We favor the latter alternative because it is unlikely that the differences were due to social interactions. Yearlings may be subordinate in our area and dominant adults may inhibit vocalizations in breeding habitat (Rothstein et al. 1986). However, the approach data were collected at afternoon-feeding sites where birds do not respond agonistically to whistles. Nor is there much likelihood that the yearling's apparent subordination in morning-breeding habitat suppressed vocal behavior at afternoon-feeding sites. The only relevant data show that subordinate males, in captivity at least, are often more vocal in the afternoon than in the morning (Rothstein et al. 1986). This occurs because dominant males are more tolerant in the afternoon, perhaps because nearly all copulations occur in the morning (Yokel 1986). The fact that yearlings and adults gave single syllable calls in similar proportions is also consistent with our view that yearlings tend to lack whistles. Both vocalizations are given in similar contexts. The single syllable call is much simpler acoustically (e.g., see element A in Fig. 5) and its development may be less dependent on experience. The fact that those yearlings that gave single syllables gave significantly more of them than did adults, suggests that they did so to compensate for their lack of whistles.

The yearling-adult difference in propensity to whistle is a clear prediction of the honest convergence hypothesis (Table 1). It is inconsistent with the local adaptation hypothesis because it

implies that ontogeny is open until at least some point in a male's first breeding season. Such an open ontogeny would allow males to disperse from their natal dialect and learn a new one. Not only were yearlings less likely to whistle than were adults, those that did so were more likely to have foreign whistles (Table 4). Since most of the yearlings with foreign whistles had vocalizations appropriate for neighboring dialects, we suggest that they were emigrants. The greater conformity of adults could occur because yearlings continue to modify their whistles to match the local dialect or because yearlings with incorrect whistles disperse to the dialect that matches their whistle. The first possibility is inconsistent with the local adaptation hypothesis. Both possibilities are inconsistent with the isolation or epiphenomenon hypothesis because both indicate that some social process makes it adaptive for birds to conform to the local dialect.

If yearlings learn whistles during their first breeding season, we might have recorded numerous aberrant versions of the local dialect. Such was not the case, although one yearling, male 2 (Fig. 3B), may have done a crude Mammoth whistle. However, yearlings may practice whistles at low volume, as is typical during song development (Marler and Peters 1982), and seem to be less vocal than adults while in breeding habitat (Rothstein et al. 1984). Overall, yearlings seem harder to detect than adults (Rothstein et al. 1986) and may be comparable to floaters in territorial species (Smith 1978).

Inappropriate whistles in putative emigrants. Adults banded in one dialect and recorded in another tended to have foreign whistles in contrast to adults banded and recorded in the same dialect (Table 4). This is consistent with the honest convergence hypothesis because it implies that emigrants cannot quickly change their whistle to conform to the local dialect. They therefore "honestly" identify themselves as newcomers who are less desirable mates than males with greater local experience. The trend is also consistent with the local adaptation hypothesis because it could mean that emigrants are simply unable to change the whistle they developed in a prior dialect. But the fact that 13.0% of 69 adults were banded and recorded in different dialects suggests at least a moderate level of movement among dialects, which is not expected under the local adaptation hypothesis. These dispersal data are only suggestive because dispersal

must be assessed more rigorously by determining whether birds disperse less across dialect borders than across comparable distances within their own dialect and whether birds breed after dispersing (Baker and Mewaldt 1978). However, if cowbirds can't breed after dispersing to a new dialect, it is unclear why more than one in ten would show such dispersal. The 13% figure for dispersal is a minimum figure and is inconsistent with the isolation-epiphenomenon hypothesis. If 13% of the males move from one dialect to another and have done so since 1978, the dialects could not have remained stable from 1978 to 1985 unless some social process made it adaptive for males to conform to the local dialect. Such a social process would, by definition, mean that the dialects are not epiphenomena.

CONCLUSIONS

The data presented here are most consistent with the honest convergence hypothesis for the maintenance of dialects. Other results, such as an apparently high level of introgression between different subspecies (Rothstein et al. 1986, Fleischer and Rothstein, unpubl.), are also consistent with honest convergence and inconsistent with local adaptation and isolation because they indicate extensive interbreeding between populations with divergent whistles. The dialect populations we studied are less than 50 years old, so the dispersal and dialect contact that prevail today may be recent developments in expanding populations. If so, dialect differences may have been maintained until recently by isolation, i.e., the temporal stability we have demonstrated from 1978 to 1985 may be insufficient to confirm that the dialects will retain their divergent characteristics. A replication of our study 10 to 20 years from now should obviously be most informative in a system as dynamic as ours. For the present, the isolation and honest convergence hypotheses can be distinguished by playback experiments because, of the two, only the latter predicts female preferences for local whistles (Table 1; Fleischer and Rothstein, unpubl.).

Although honest convergence is the best explanation for the maintenance of the large whistle dialects we have identified (Fig. 2), different processes could explain variation at other levels. Males that bred near each other may have had more convergent whistles than males from different areas in the Mammoth dialect, although the evidence for such subdialects is much less

clear than in the case of the White-crowned Sparrow (Baptista 1985a). If subdialects exist, they could originate and be maintained by honest convergence operating at a local level or by deceptive convergence. Alternatively, the relatively minor differences that result in subdialect variation may be due to stochastic processes.

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