ANALYSIS OF HYBRIDIZATION BETWEEN THE HIRUNDINID GENERA *HIRUNDO* AND *PETROCHELIDON* IN TEXAS

ROBERT F. MARTIN
Texas Memorial Museum and Department of Zoology,
The University of Texas at Austin,
Austin, Texas 78705 USA

ABSTRACT.—Breakdown of ecological segregation of nesting Cave Swallows (*Petrochelidon fulva*) at the northeastern margin of their continental range has been followed by nesting syntopy and hybridization with Barn Swallows (*Hirundo rustica*) at highway culvert sites. *Hirundo rustica* × *P. pyrrhonota* hybridization also may be involved at several culvert sites at which Cliff, Cave, and Barn swallows nest syntopically.

Employing morphological, observational, and biochemical techniques, 12 instances of hybridization (14 hybrid nestlings) between these genera have been identified and examined at sites near the periphery of the range of *P. fulva* in Texas. Hybrid individuals occurred alone in nests or together with young of *H. rustica* morphology. With one exception (*H. rustica, P. fulva* attendants), only adults of *H. rustica* phenotype were observed at hybrid-containing nests. Hybrids displayed general morphological and developmental intermediacy between parental species. When assessed by analyses of protein variation, genotypes of hybrids, their nestmates, and attendants were consistent with those inferred from their phenotypes.

No evidence of introgressive hybridization or of drastic changes in frequency of hybridization presently exists. Review of present behavioral, chronological, and spatial factors, as well as the history of contact between Barn, Cave, and Cliff swallows, suggests that, in situations of three-species syntopy, *P. fulva* is more likely than *P. pyrrhonota* to participate in hybridization with *H. rustica*. Data presented here are integrated with other evidence supporting the merger of *Petrochelidon* with *Hirundo*. *Received 15 February 1979, accepted 20 September 1979.*

ALTHOUGH a considerable literature concerning avian hybridization exists, relatively few works deal with the ecology, mechanics, and genetics of naturally and regularly occurring hybrid events in passeriform species and fewer with hybridization between nominate passerine genera (Cockrum 1952; Gray 1958, 1964; Short 1969). Recent human-mediated disruption of ecological segregation between Cave Swallows (*Petrochelidon fulva*) and other hirundinids in Texas (Martin 1974), however, has facilitated further investigation of such phenomena. Here, I report seven instances of hybridization between Barn and Cave swallows (*Hirundo rustica, P. fulva*) and five instances between *H. rustica* and species of *Petrochelidon* (*fulva* or *pyrrhonota*) subject to identification with less certainty, and describe morphologically, and in part biochemically, the 14 hybrid nestlings produced by these events. In addition, I present observations of the ontogeny and behavior of these individuals as well as that of their nestmates, parents (when known), and environment. Utilizing available data, I then hypothesize concerning the proximate circumstances surrounding each instance of hybridization, review the events leading to the breakdown of ecological and reproductive isolation between these species, and integrate these data with others that suggest the merger of *Petrochelidon* with *Hirundo*.

STUDY AREA AND METHODS

Our studies of comparative reproductive ecology of Cave, Cliff, and Barn swallows encompass various bridge, cave, and culvert nesting sites lying within that portion of Texas west of 98°E longitude and south of 31°N latitude; these boundaries approximate the range of *P. fulva* in this state (Fig. 1, Martin

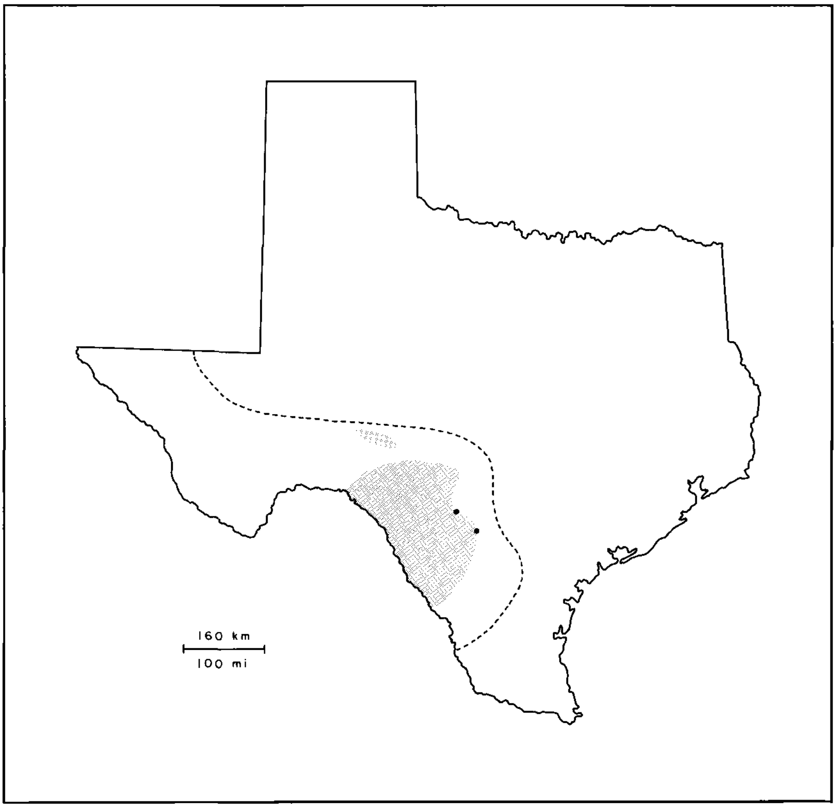

Fig. 1. Range of *Petrochelidon fulva* in Texas. Shaded portions of map indicate areas of essentially contiguous distribution; dashed line indicates approximate outer limit of noncontiguous distribution. Dots demarcate sites at which hybridization with *Hirundo rustica* occurs. Northern dot: Culverts 8 and 9, approx. 25 km W Hondo; southern dot: Culverts 300, 301, 302, vic. Moore.

1974, Martin and Martin 1978). Within this area, we visited culverts and gathered data most intensively (usually twice weekly) along a transect coincident with U.S. Highway 90, extending approximately 200 km E to W through Medina, Uvalde, Kinney, and Val Verde counties. Tributaries of the Nueces and Rio Grande rivers drain the Edwards Plateau and pass through concrete culverts beneath this highway. Barn Swallows alone nested in culverts at both ends of the transect, but culverts in its central portion were occupied by both Cave and Barn swallows, usually nesting in syntopy (see Martin 1974 for detailed distribution of syntopy). We checked less frequently other transects coincident with major north-south highways that intersect the primary transect.

We also gathered reproductive data twice weekly on syntopic, culvert-nesting aggregations of Barn, Cave, and Cliff swallows in three culverts (#s 300, 301, and 302) near Moore, Frio County, Texas. Although here the three species nested in the same culvert passageways, Cliff Swallows tended to nest in segregation near western passage ends.

Occasionally, young of disparate phenotype were found in a single nest. When possible, observations of nests containing these young were initiated, and nestlings of intermediate phenotype, nestmates, and attending adults were collected. Morphological comparison was made with two previously identified hybrids between *H. rustica* and *P. fulva* (Martin and Selander 1975). In many instances, tissue extracts of specimens were prepared and subjected to electrophoretic analyses of proteins whose mobilities could be utilized to discriminate between parental genera and hybrids (Martin and Selander 1975).

Hybrids occurring in culverts at which only *H. rustica* and *P. fulva* were syntopic (no *P. pyrrhonota* colonies existed within 40 km of these) were considered progeny of these species. Morphological and biochemical examination of hybrid nestlings occurring in culverts at which three species nested did not

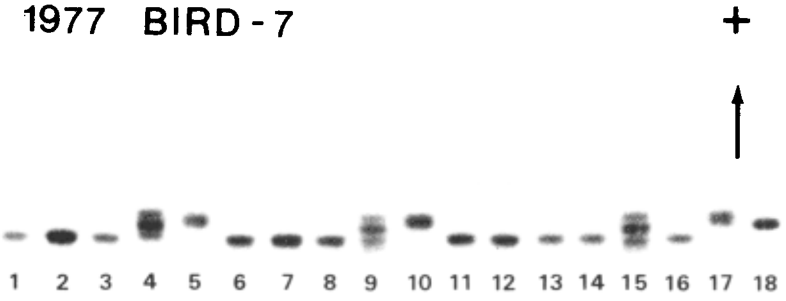

Fig. 2. Six-phosphogluconate dehydrogenase zymogram. Anode is at the top, origin at the bottom, and sample 1 at the left of the figure. Samples 1, 3, 8, and 16 are *H. rustica*; 5, 10, 17, and 18 are *P. fulva*. Samples 2 and 4, respectively, are the nestling *H. rustica* and hybrid from nest 8B5. Samples 6, 7, 9, 11, 12, 13, and 14, respectively, are the attending *H. rustica* adults, the hybrid nestling, and the 4 *H. rustica* nestlings from nest 301AE11. Sample 15 is the hybrid nestling from nest 301AW11. Note that two "fast" alleles occur in the *P. fulva* population.

permit differentiation between the (sibling) species of *Petrochelidon* involved in parentage. Attempts to determine the species of *Petrochelidon* involved in parentage of hybrids found in culverts with three-species syntopy and to determine the identity of individuals of *P. fulva* involved in parentage of hybrids found in culverts with two-species syntopy involved consideration of behavioral, chronological, and spatial factors concerning *Petrochelidon* males nesting proximate to the hybrid-containing nests. Specimens collected are housed at the Texas Memorial Museum.

RESULTS

Description of hybrids.—No adult putative *H. rustica* × *P. fulva* hybrids are described or available. Several putative adult *H. rustica* × *P. pyrrhonota* hybrids have been described (Trotter 1878, Mearns 1902); they are in general similar to *H. rustica* × *P. fulva* hybrid juveniles described below. *Petrochelidon fulva* and *P. pyrrhonota* presently are considered sibling species (Selander and Baker 1957), but adult plumages of both are sufficiently variable to prompt occasional questions as to their specific distinctness. Nestling plumages of these species vary to a greater extent, and considerable variation also exists in the nestling plumage of *H. rustica*. Hybrid nestlings reflect this variation, which is compounded further by differences in age at time of collection (when plumage is still erupting) and also by plumage soilage during attempts at hand-rearing. Nevertheless, a general description is possible.

At or near fledging, the plumage of hybrids is generally intermediate between that of nestling *H. rustica* and nestling *Petrochelidon fulva* or *pyrrhonota,* although earlier it more closely resembles that of the latter two species. Crown, nape, and back coloration is intermediate between the glossy blue-black of *H. rustica* juveniles and the dull brown of those of *P. fulva* and *P. pyrrhonota.* A chestnut collar is present at the lower nape as in *Petrochelidon* (but paler in coloration), not absent as in *H. rustica.* Upper breast coloration is darker than that of *P. fulva,* similar to or paler than that of *P. pyrrhonota,* and paler than that of *H. rustica.* Breast and abdomen

TABLE 1. Numbers of active nests of syntopic swallows at approximate time of laying of clutches containing hybrids.

Nest	Year	*H. rustica*	*P. fulva*	*P. pyrrhonota*
8B.5	1973[a]	4	1	0
8B5	1977	6	2	0
8B8	1977	6	2	0
9A6.2	1974	5	1	0
9A8	1974	7	1	0
300Bx13	1974	19	9	31
300Ay2.1	1974	21	9	31
300Bx12	1975	23	6	14
301Ae11	1977	22	5	4
301Aw11	1977	41	6	5
302RR1[b]	1974	16	7	1
403[c]	1974	25	3	0

[a] Records for nest 8B.5 from Martin and Selander (1975).

[b] Numbers for this site are from culvert 302, 30 m distant.

[c] Sighting of hybrid flying and vocalizing with scolding *H. rustica* and *P. fulva*. Hybrid assumed to be from 403. Active nest records from this culvert are approximate.

show less cinnamon than in *H. rustica,* but are not white (with some cinnamon laterally) as in *P. fulva* or *P. pyrrhonota.* Each of the outer two or three rectrices has a subterminal white or tan spot on its inner vane as in *H. rustica* and is not uniformly dark or dark with a terminal light spot as in *P. fulva* and *P. pyrrhonota.* The rump is buff or orange as in *P. fulva* and *P. pyrrhonota,* not black as in *H. rustica.*

Hirundo rustica and *P. fulva* show little protein variation. In 18 of 22 proteins examined electrophoretically, no intra- or interspecific variation was noted by Martin and Selander (1975); interspecific differences in 6-phosphogluconate dehydrogenase (6-PGD) and isocitrate dehydrogenase (IDH-1) banding patterns did exist, however, and could be used to confirm identity of the two *H. rustica* × *P. fulva* hybrids discovered initially. Further biochemical analyses indicated that *P. pyrrhonota* could not be distinguished from *P. fulva* on the basis of these enzyme systems (Martin and Zimmerman MS).

In the present study, only 6-PGD and IDH-1 systems were scored in all specimens that were examined biochemically (see Selander et al. 1971 for electrophoretic methodology). For both these enzymes, individuals of *P. fulva* displayed an adonal-positioned band migrating more rapidly than that characteristic of *H. rustica.* For 6-PGD, hybrids showed a three-banded phenotype (Fig. 2), with the heterodimeric band staining darker than the homodimeric bands. In hybrids, IDH-1 was represented by a three-banded phenotype, with the central heterodimeric band staining darker than homodimeric bands.

Distribution.—*H. rustica* is essentially contiguously distributed across the study area; the range of *P. fulva* is included within it. Colonies of *P. pyrrhonota* occur in (usually) widely disjunct fashion throughout the region, but usually at bridges and not culverts. All hybrid-containing nests detected during the study occurred at localities at which *P. fulva* was at or near the margin of its contiguous distribution (Fig. 1) and at which it was less common than *H. rustica* (Table 1). In 1974, *P. pyrrhonota* were more numerous than both *H. rustica* and *P. fulva* at Culvert 300, but this has not been true at any site of hybrid occurrence since then (Table 1).

TABLE 2. Summary of data for nests and culverts containing hybrids.

Date[a]	Nest	Species at site[b]	Eggs	Adults at nest	Young in nest (phenotype)[c]	Summary of observations	Specimens collected	Confirming protein	Diagnosis
1973									
23 April	8B.5[d,e]	Barn, Cave	5	Barn, Barn	1 Barn, 2 hybrids	Young of Barn Swallow phenotype fledged first. Adults escaped. Only 1 Cave Swallow nest in this culvert.	Young: 2 hybrids	6-PGD IDH	2 Barn × Cave hybrids
1974									
1 May	9A6[d]	Barn, Cave	5	Barn, Barn	3 Barn, 1 hybrid	Young of Barn phenotype fledged first. Only Barn young in subsequent brood in 9A6. Ten Barn, 1 Cave nest present in 9A6.	0	—	Barn × Cave hybrid event
19 June	9A8[d]	Barn, Cave	5	Barn, Barn	3 Barn, 1 hybrid	Young of Barn phenotype fledged first. Hybrid fledged before 21 days posthatch. Only Barn young in previous brood in 9A8. Cave parent probably also involved previously in hybrid event of Nest 9A6.	0	—	Barn × Cave hybrid event
24 April	300 Bx13	Barn, Cave, Cliff	5	Barn, Cave	3 Barn, 2 hybrids	Barn, Cave attendants also at this nest at night with subsequent clutch of 4; young missing before identification. Third clutch hatched: 3 Barn young from 4 eggs. Adult Barn at nest; positive association of Cave, nearby and scolding, could not be made. Alternative descriptive hypotheses avoiding invoking introgression available; reuse of nest by different pair for clutch 3 likely.	Young: 1 Barn, 1 hybrid	6-PGD IDH	1 Barn, 1 Barn × Cave hybrid
28 April	300 Ay21	Barn, Cave, Cliff	4	Barn, Barn	1 Barn, 1 hybrid	Subsequent clutch missing before hatch. Nearby Cave nests active synchronously with first clutch in 300 Ay21. Cliff nests active in 300, but 100 m distant at far end.	0	—	Barn × *Petrochelidon* hybrid event; Cave paternity more probable than Cliff
1 May	302 RR1	Barn, Cave, Cliff	5	—	3 Barn, 1 hybrid	Site visited irregularly. Nearby Cave nests active synchronously with 302RR1. Cliff Swallow colony 100 m distant postreproductive at this time. Previous clutch of 5 in this nest hatched 4 young of Barn phenotype; all fledged.	Young: 1 Barn, 1 hybrid	6-PGD	Barn × *Petrochelidon* hybrid; Cave parentage probable

TABLE 2. Continued.

Date[a]	Nest	Species at site[b]	Eggs	Adults at nest	Young in nest (phenotype)[c]	Summary of observations	Specimens collected	Confirming protein	Diagnosis
	Cul. 403	Barn, Cave	—	—	—	30 Barn, at least 2 Cave, bird of hybrid phenotype observed in flight. Site visited only once; located 5 km S Asherton.	—	—	Probable Barn × *Petrochelidon* hybrid
1975									
22 June	300 Bx12	Barn, Cave, Cliff	4	—	1 hybrid	Nearby Cave nest active semi-synchronously. Proximate Cliff nests fledged young several days before clutch in 300Bx12 initiated, but were not active after this time.	—	—	Barn × *Petrochelidon* hybrid. Cave paternity more probable than Cliff
1977									
22 April	301 Ae11	Barn, Cave, Cliff	6	Barn, Barn	4 Barn, 1 hybrid	Proximate Cave and Cliff nests active synchronously. Weights of young taken twice during nestling period (see Table 4).	Attendants + all young	6-PGD IDH	Barn adults, 4 Barn young, 1 Barn × *Petrochelidon* hybrid
23 May	301 Aw11	Barn, Cave, Cliff	5	—	1 hybrid	Proximate Cave nests active synchronously. A few Cliff nests active 100 m distant; declining reproductive activity in these.	Young: 1 hybrid	6-PGD IDH	Barn × *Petrochelidon* hybrid. Cave paternity more likely than Cliff
25 April	8B8[d]	Barn, Cave	4	Barn, Barn	3 Barn, 1 hybrid	Reproductive activity of 8B8 synchronous with that of Cave nest 3 m distant. No Cliff nests within 40 km of 8B8. Weights of 8B8 nestlings taken twice during nestling period.	Attendants + all young	6-PGD IDH	Barn adults, 3 Barn young, 1 Barn × Cave hybrid
9 May	8B5[d]	Barn, Cave	4	Barn, Barn	2 Barn, 2 hybrids	Two Cave nests active nearby. Attending adult from 8B5 made several attacks, each involving peck or wing strike, upon Cave Swallow attending young at nearby Cave nest. Cave response passive. No Cliff nests within 40 km of 8B5.	Young: 1 Barn, 1 hybrid	6-PGD IDH	1 Barn, 1 Barn × Cave hybrid

[a] Date laying of hybrid-containing clutch was initiated.

[b] Species that nested syntopically at culvert site; Barn = *H. rustica*, Cave = *P. fulva*, Cliff = *P. pyrrhonota*.

[c] Identifiable by morphological (plumage) criteria. Some nestlings missing from nests before this stage of development reached.

[d] No colonies of *P. pyrrhonota* existed within 40 km of culverts 8 and 9.

[e] Data for Nest 8B.5 from Martin and Selander (1975).

TABLE 3. Frequencies of occurrence of clutches containing hybrids and frequencies of hybrid young in 1974 and 1977.

Nature of syntopy and type of comparison	Approximate frequencies			
	All culverts		Sample[a]	
	1974	1977	1974	1977
Culverts with two species nesting in syntopy				
Number of clutches with hybrid(s)/ number of *H. rustica* clutches		0.004	0.012	0.019
Number of hybrid young/ number of *H. rustica* young[b,c]		0.001	0.003	0.007
Number of clutches with hybrid(s)/ number of *P. fulva* clutches		0.007	0.013	0.021
Number of hybrid young/ number of *P. fulva* young		0.003	0.003	0.008
Culverts with three species nesting in syntopy				
Number of clutches with hybrid(s)/ number of *H. rustica* clutches	0.013	0.016		
Number of hybrid young/ number of *H. rustica* young	0.005	0.004		
Number of clutches with hybrid(s)/ number of *Petrochelidon* clutches	0.021	0.040		
Number of hybrid young/ number of *Petrochelidon* young	0.008	0.010		

[a] Only eight culverts with two-species syntopy were visited regularly in 1974; 1977 data from these culverts are presented for comparison under this heading. Data for these years from this sample are comparable internally, but the sampling procedure is biased toward overestimation of hybridization frequency.

[b] Mean clutch size for each species is (under)estimated at 4.

[c] Several clutches contained more than one hybrid.

Hybrid events.—Data on nests containing hybrids or on hybrid sightings are summarized in Table 2.

Frequency of hybridization.—Frequencies of hybridization based on data taken in 1977 (main transect culverts + Culverts 300, 301, and 302) are considered unbiased in that they represent nearly all culverts along these survey corridors (Table 3). In addition to Culverts 300, 301, and 302, only eight main transect culverts were visited in 1974. To enable crude chronological comparison of frequencies, 1974 data plus a comparable subsample of 1977 data are presented (Table 3). Although comparable internally, these two subsamples overestimate true hybridization frequency in that they over-represent culverts at which hybridization occurred.

Most annual comparisons of frequencies (Table 3) indicate increases in hybridization between 1974 and 1977, but as hybrid occurrence is low (five in each year), these differences are sensitive to small changes in incidence and must be considered with caution.

Hybrid development.—Cave Swallow nestlings are heavier than Barn Swallows of similar age (Miller 1975) and normally fledge approximately 3–4 days later (Miller 1975, Martin et al. 1977). Although I have no weight data for Texas *P. pyrrhonota* (see Stoner 1945 for weights of nestling New York Cliff Swallows), their pattern of development appears similar to that of *P. fulva* (Martin unpubl. obs.). Hybrids also are heavier than their *H. rustica* nestmates and either are similar in weight to *P. fulva* of similar age or are intermediate in weight between *P. fulva* and *H. rustica* nestlings (Table 4). These data suggest that, at least until this time, no severe developmental disadvantages exist for hybrids. In three nests for which fledging records exist, hybrid young were last to leave the nest. This delay may be maladaptive in that it is incongruent with the normal half-sibling (*H. rustica*) fledging

TABLE 4. Comparisons among weights (g) of nestling hybrids, nestmates, and expected weights of nestling *H. rustica* and *P. fulva.*

Nest	Age (days post-hatch)	Weights in hybrid nest		Expected weights[a]	
		H. rustica	Hybrid	*H. rustica*	*P. fulva*
301Ae11	11–12	19.5, 19.5, 20.0, 20.5	21.0	20.3	23.4
	16–17	16.5, 17.0, 18.0, 18.0	20.0	18.1	24.0
8B8	9–10	16.5, 17.5, 19.0	21.0	18.7	21.6
	11–12	20.0, 20.0, 22.0	23.5	20.3	23.4

[a] Expected weights are averages from Miller 1975.

chronology and may result in inadequate parental care or other disadvantage (see Emlen and Demong 1975 for discussion of the advantages of synchrony in Bank Swallow breeding).

DISCUSSION

Development of syntopy.—Hirundo rustica and *P. pyrrhonota* are sympatric throughout much of the United States (A.O.U. 1957). Breeding syntopy of these species is extensive and long-standing (Bent 1942) and has been facilitated by their frequent dependence upon man-made structures for nest sites; a putative Barn × Cliff Swallow hybrid was reported in the 19th century by Trotter (1878).

Petrochelidon fulva reaches the northeastern margin of its continental range in the state of Texas. In this area, it recently has undergone breakdown in ecological segregation (Wauer and Davis 1972, Martin 1974). Once narrowly restricted in its nesting sites here to the twilight zones of caverns and sinkholes, it now nests commonly and successfully in highway culverts (Martin 1974), where it usually is associated with *H. rustica* and, occasionally, with *P. pyrrhonota.* A further consequence of this release from segregation has been the gradual expansion of its range into flatland noncave topography south and east of the Edwards Plateau, increasing further its syntopy with other hirundinids (Martin and Martin 1978). Potential hazards (disease, competition, hybridization) generated by this situation were listed by Martin (1974); since then, the first observation of hybridization between *H. rustica* and *P. fulva* has been reported (Martin and Selander 1975), and no catastrophic mortality attributable to disease has occurred in syntopic *P. fulva* and *H. rustica* populations. The reproductive consequences of competition presently are under investigation. *Hirundo rustica* and *P. fulva* usually employ markedly different height-specific foraging strategies in central Texas (Martin and Miller unpubl. obs.), and preliminary data (Miller 1975, Martin unpubl. obs.) indicate that reproductive success of both species nesting in syntopy is good. In situations in which three species nest syntopically, nesting success usually appears lower in *P. pyrrhonota* than in the other species (Martin, unpubl. obs.).

Pair formation, copulation, fertilization, paternity.—In comparing the breeding behavior of syntopic Barn and Cliff swallows in West Virginia, Samuel (1969, 1971) indicated that Cliff Swallows formed pair bonds and copulated at the nest; only nonstructured vocalization preceded copulation, and no highly involved colonial synchrony in copulation occurred. Emlen's (1954) observations on *P. pyrrhonota* are similar and indicate further that copulation also may be attempted away from the nest and that females may copulate at their nest with a male other than the one with which they are paired. Samuel (1971) reported that *H. rustica* paired and copulated near the nest site but not at the nest, that a more structured vocal sequence preceded copulation, and that colony copulation was synchronous. Miller's (1975) less detailed observations on Texas *H. rustica* are in accordance with those of Samuel. Miller's data on *P. fulva* are less complete but indicate that *P. fulva* do copulate at the nest. Lacking other data, I assume here that most elements of precopulatory and copulatory behavior are similar between West Virginia and Texas *H. rustica* and that in these behaviors *P. fulva* is more similar to Texas *P. pyrrhonota* than to Texas *H. rustica*. Hypothesizing from his behavioral data, Samuel (1969) suggested that hybridization, were it to occur in West Virginia, would be more likely between male *H. rustica* and female *P. pyrrhonota* than in the reciprocal pairing because of the more structured precopulatory vocalization behavior of the former species. Considering *only* homospecific precopulatory and copulatory behavior of the species involved, this would seem also to be the most logical hypothesis for Texas *H. rustica* and either species of *Petrochelidon*. Postcopulation observational data from nests containing hybrid juveniles reported here, however, largely do not support this hypothesis (Table 2). With the exception of the unsexed mixed-species pair of adults attending nest 300Bx13, only adults of *H. rustica* phenotype (which, if collected, also proved to be of *H. rustica* genotype) were observed attending nests that contained hybrids. With two *potential* exceptions (nests 300Bx12, 301Aw11), hybrids never were observed to be the exclusive nestlings occupying a nest, and nonhybrid nestlings were never of other than *H. rustica* morphology. All nestlings of hybrid morphology examined biochemically had protein patterns expected of *H. rustica* × *P. fulva* hybrids, and all nestmates of hybrids showed enzyme patterns characteristic of *H. rustica*. These data, if representative, support the reciprocal hypothesis, which posits that female *H. rustica* more commonly accept male *P. fulva* (or possibly, in some instances, *P. pyrrhonota*) in heterospecific copulation and that these unions usually are transitory. Emlen's (1954) observations that male *P. pyrrhonota* would attempt conspecific copulation away from nests or would copulate with conspecific females at nests that were the female's but not their own are relevant to this point if we assume that *P. fulva* males also share this characteristic.

Although the physiological and chronological relationships surrounding copulation and fertilization apparently have not been described for hirundinids, research on domestic and wild nonpasserine species indicates that single copulations may result in fertilization from a week to well over a month after mating (Schick 1947, Sturkie 1976). Although long-term delay in fertilization would seem disadvantageous to most (altricial) passerine species, short-term delays may be frequent, and it is possible that multiple hybrid young in hybrid-containing clutches may result from only single heterospecific copulations by homospecifically-paired females.

Events facilitating hybridization potentially occur one to several seasons before its actual occurrence. At culvert sites, subsequent syntopy and/or hybridization may be facilitated by greatly increased visual and auditory familiarity of nestlings with nearby nonconspecifics. In some instances, due to nest similarity and position, or to accidental or deliberate human intervention, heterospecific egg misdeposition may occur (eggs are similar among these species). To speculate further (behavioral data for hirundinids are lacking in this area), it is possible that such events may be followed by some degree of heterospecific "disruptive imprinting" that subsequently increases the probability of heterospecific pairing or copulation. It is attractive to assign male parentage of hybrids tentatively to transient or unpaired resident *Pe-*

trochelidon males, as even brief polygyny need not be invoked. This interpretation represents only one possibility, however, and lacks supporting observational data, while possibilities involving nearby paired males are supported by data that in several instances appear reasonably persuasive (Table 2, summary of observations). Additional information that applies to either interpretation is available and suggests that when three-species syntopy is present, *P. fulva* rather than *P. pyrrhonota* is the species more likely to enter hybridization: First, colonial activity appears more developed in *P. pyrrhonota* than in *P. fulva*. Second, *P. pyrrhonota* usually is single-clutched at the study sites, arriving later and leaving earlier than both *P. fulva* and *H. rustica,* which rear at least two broods. Third, marked differentiation exists between the closed globular nests of *P. pyrrhonota* and the open cup nests of both *P. fulva* and *H. rustica*; this should potentially reduce the incidence of (hybridization-facilitating?) heterospecific egg misdeposition involving *P. pyrrhonota* and also should decrease visual and auditory familiarization between *P. pyrrhonota* nestlings and nearby heterospecifics. Fourth, the geographically more extensive (and, in central Texas, longer) contact of *H. rustica* with *P. pyrrhonota* than with *P. fulva* theoretically should have permitted greater reinforcement of isolating mechanisms between these species.

Sources of bias.—Discovery of hybrids was cued primarily to observation of nestlings and not to their attendants. The initial identification of hybrid young occurring together with *H. rustica* young is facilitated by intra-brood morphological contrast (rump color dichotomy) that develops early in ontogeny. Should hybrids occur as the exclusive occupants of a nest, lack of intra-brood character contrast and relatively late development of nonrump hybrid plumage characteristics may delay their identification. This also would be true of hybrids (potentially) produced by the potential reciprocal cross. The situation would be complicated further if progeny of female *Petrochelidon* × male *H. rustica* crosses were more difficult to recognize than those of the reciprocal combination (see Gray 1964, for maternal effects in hybrids). These factors, interacting with human error, nest failure, or premature fledging, could result in under-recording of exclusive-nest-occupant hybrids or of hybrids of other potential classes. Our identification relatively early in the nestling period of the two hybrids that occurred alone in nests (Table 2), however, argues for confidence in our power of discrimination.

Evolutionary and taxonomic conclusions.—The present data, as qualified above, offer no evidence of introgressive hybridization. Although hybrid nestlings display variation among themselves (as do their half-siblings and other young of the parental species), they are in varying stages of development of juvenal plumage, which itself is more variable than adult plumage in the species involved. It is important that, although two loci that could be used to differentiate the genera involved were scanned in eight nestmates of hybrids and four attending adults (all of *H. rustica* morphology), only *H. rustica* genes were scorable in these, while all individuals identified morphologically as hybrids displayed both *H. rustica* and *Petrochelidon* genes at these loci.

Our observations indicate that the hybridization reported here usually is the result of transitory encounters between females of *H. rustica* and males of *P. fulva*. The geographic pattern of hybrid occurrence is similar to that frequently demonstrated by sympatric *intra*generic species hybrids: one in which one participant is at the margin of its range and one that, presumably, is promoted by restricted mate choice (Sibley 1961, Short 1969). In most instances of hybridization reported here, conspecifically paired *P. fulva* nested proximately to the nests in which hybrids occurred; if restricted mate choice actually is a factor, this may imply polygyny in *P. fulva* or may indicate that transient or nonpaired resident males are involved.

The hybridization clearly is an anthropogenic artifact and appears to be of recent occurrence in the study area. Hybridization occurs regularly but at relatively low and apparently relatively stable frequencies; the methodology employed here (nestling-, not adult-targeted) does not readily permit comparisons with frequencies existing in the literature. Although preliminary estimates of genic similarity of species involved in this study are high (Martin and Selander 1975) and more recent comprehensive research (comparisons of all U.S. swallows, Martin and Zimmermann MS) supports this conclusion, these data or those presented here do not weaken the specific validities of *H. rustica, P. fulva,* or *P. pyrrhonota.* The data do, however, raise questions concerning present generic allocations. Short (1969) indicated that sporadic or subsporadic hybridization of the magnitude reported in the present study would indicate proximate relationship of the genera involved; he indicated further that the presence of supportive data would suggest generic merger. Mayr and Bond (1943) questioned the reality of generic limits in the Hirundinidae, suggested that general morphological similarity clouded taxonomic decisions here, and indicated that grounds for separation of *Petrochelidon* from *Hirundo* were particularly weak. Thus, behavioral, frequency-of-occurrence, and genetic data presented here complement previously published material from other disciplines and seem to fulfill Short's criteria for generic merger.

ACKNOWLEDGMENTS

I thank the following for their contributions to the study: George D. Baumgardner, Peter Brussard, Guy L. Bush, John Ellison, Michael R. Lewis, Walter K. Long, Diane Neilsen, Richard D. Sage, Robert K. Selander, H. Eldon Sutton, and especially Earl G. Zimmermann. W. F. Blair, Lawrence E. Gilbert, Frank B. Gill, Terrell Hamilton, Clark Hubbs, Wesley E. Lanyon, Ernst Mayr, and Lester L. Short read and improved the manuscript. Particular gratitude is due my wife, Sallie, whose observations initiated our swallow research and whose support and insight contributed materially to its progress.

The project was supported in part by the National Geographic Society (Grants # 1301, 1418, and 1721) and The Texas Memorial Museum, University of Texas at Austin.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds, Fifth ed. Baltimore, Amer. Ornithol. Union.

BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.

COCKRUM, E. L. 1952. A checklist and bibliography of hybrid birds in North America north of Mexico. Wilson Bull. 64: 140–159.

EMLEN, J. T., JR. 1954. Territory, nest building, and pair formation in the Cliff Swallow. Auk 71: 16–35.

EMLEN, S. T., & N. J. DEMONG. 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. Science 188: 1029–1031.

GRAY, A. P. 1958. Bird hybrids. Farnham Royal, Bucks, England, Commonwealth Agricultural. Bureaux.

———. 1964. Hybrid. Pp. 385–386 *in* New dictionary of birds (A. L. Thompson, Ed.). New York, McGraw-Hill Book Co.

MARTIN, R. F. 1974. Syntopic culvert nesting of Cave and Barn Swallows in Texas. Auk 91: 776–782.

———, & S. R. MARTIN. 1978. Niche and range expansion of the Cave Swallow in Texas. Amer. Birds 32: 941–946.

———, & R. K. SELANDER. 1975. Morphological and biochemical evidence of hybridization between Cave and Barn Swallows. Condor 77: 362–364.

———, G. O. MILLER, M. R. LEWIS, S. R. MARTIN, & W. R. DAVIS, III. 1977. Reproduction of the Cave Swallow: a Texas cave population. Southwestern Nat. 22: 177–186.

MAYR, E., & J. BOND. 1943. Notes on the generic classification of the swallows, Hirundinidae. Ibis 85: 334–341.

MEARNS, E. A. 1902. Description of a hybrid between the Barn and Cliff swallows. Auk 19: 73–74.

MILLER, G. O. 1975. The reproduction of syntopic culvert nesting Cave and Barn swallows. Unpublished M.A. thesis, Austin, Texas, Univ. Texas.

SAMUEL, D. E. 1969. The ecology, behavior, and vocalizations of sympatric Barn and Cliff Swallows in West Virginia. Unpublished Ph.D. dissertation, Morgantown, West Virginia, West Virginia Univ.

———. 1971. Vocal repertoires of sympatric Barn and Cliff swallows. Auk 88: 839–855.

SELANDER, R. K., & J. K. BAKER. 1957. The Cave Swallow in Texas. Condor 59: 345–363.

———, H. M. SMITH, S. Y. YANG, W. E. JOHNSON, & J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus* I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in Genetics 6 (Univ. Texas Publ. 7103): 49–90.

SHICK, C. 1947. Sex-ratio-egg fertility relationships in the Ring-necked Pheasant. J. Wildl. Mgmt. 11: 302–306.

SHORT, L. L. 1969. Taxonomic aspects of avian hybridization. Auk 86: 84–105.

SIBLEY, G. C. 1961. Hybridization and isolating mechanisms. Pp. 69–88 *in* Vertebrate speciation (W. F. Blair, Ed.). Austin, Texas, Univ. Texas Press.

STONER, D. 1945. Temperature and growth studies on the northern Cliff Swallow. Auk 62: 207–216.

STURKIE, P. D. 1976. Avian physiology, Third ed. New York, Springer-Verlag.

TROTTER, S. 1878. Description of a hybrid (*Hirundo horreori-lunifrons*) between two North American swallows. Bull. Nutt. Ornithol. Club 3: 135–136.

WAUER, R. H., & D. G. DAVIS. 1972. Cave Swallows in Big Bend National Park, Texas. Condor 74: 482.