## Sayornis nigricans

FRENCH: Moucherolle noir SPANISH: Mosquero negro

# Black Phoebe

orth America's only small black-and white flycatcher, and a common breeding species from California through the southwestern United States to Middle and South America, the Black Phoebe is invariably associated with water. Coastal cliffs, riverbanks, the shorelines of lakes and ephemeral ponds, cattle tanks, and fountains in parks are all favored habitats. Almost any semipermanent source of water with an accompanying source of mud, required for nest construction, is attractive to this species. In many areas, natural nest sites, such as sheltered rock faces, streamside boulders, and hollow cavities in trees, have largely given way to artificial nest sites provided by human-made structures. Such artificial sites have greatly increased breeding densities of this species in habitats where the lack of suitable nest sites once limited breeding. The traditionally limited

The Birds of North America

Life Histories for the 21st Century

availability of suitable nest sites has promoted strong nest-site tenacity in this species; individuals often reuse the same nest or nest site year after year.

Black Phoebes are monogamous and frequently raise 2 broods of young during a breeding season. Their adherent nests are

composed of a mud shell lined with plant fibers, typically placed over water and plastered to a vertical wall within a few centimeters of a protective ceiling. Nest construction or refurbishment usually begins in March or April and takes from 1 to 3 weeks. After hatching, the





Figure 1.
Distribution of Black Phoebe in North and Central America. This species also breeds in South America. See text for details.

altricial nestlings are brooded by the female for several days, are fed by both adults, and fledge in about 18 days. After breeding, some individuals wander, tending to move downslope to lower elevations, but these patterns of movement are not nearly as pronounced or well known as those of the Say's (*Sayornis saya*) and Eastern (*S. phoebe*) phoebes.

Primarily an insectivorous species, the Black Phoebe forages in open areas over water, grass, or other substrates. It is a versatile forager, sallying from perches within a few meters of the ground and hawking prey from the air or gleaning it from the ground or the surface of a pond. Individuals are known to snatch small minnows from just below the water's surface and, rarely, to eat small berries.

Since Bent's (1942) summary of the literature, various aspects of the biology of the Black Phoebe have received extensive attention from researchers in California and Texas. These studies have focused primarily on reproductive biology (Irwin 1985, Schroeder 1985, Wolf 1991), song and behavior (Smith 1970a, 1970b), and foraging ecology (Verbeek 1975a, 1975b, Ohlendorf 1976, Irwin 1985). Migratory biology, physiology and molt, and other facets of the life history of this species remain poorly known, however, especially in Middle and South America.

## DISTINGUISHING CHARACTERISTICS

Medium-sized flycatcher, about 16 cm long; body mass approximately 18 g. The only small, predominantly black flycatcher in North America; black above and white below; seasonally and sexually monomorphic (Pyle et al. 1987). Male and female during breeding season (Mar-Aug) distinguished by cloacal protuberance (male) and brood patch (female). Sooty black head, breast, and upper back. Lower back, wings, and tail brownish slate with white undertail-coverts and belly. White on belly forms inverted V as it extends up into lower breast (northern populations only; see Systematics: geographic variation, below). Outer web of outer rectrix white. Juvenile has buffy cinnamon feather tips on body and buffy cinnamon wing-bars. Iris brown; legs, feet, and mandibles black.

Tail Wag, the rapid depression and fanning of the tail, often accompanied by Simple Vocalization (see Sounds: vocalizations, below), is a distinguishing behavioral characteristic for genus *Sayornis*. Say's Phoebe is grayish brown above, with orange brown belly and undertail-coverts. Eastern Phoebe whitish to pale yellow on underparts; only crown is sooty black.

## **DISTRIBUTION**

THE AMERICAS

Breeding range. Extensive (Fig. 1). Breeds in sw. Oregon in coastal portions of Curry Co. and in interior in Rogue Valley of Josephine and Jackson Cos. (Gilligan et al. 1994). In California, breeds from western slopes of Cascades and Sierra Nevada west in north and central regions, and through Coast Ranges in the south (sea level to 2,000 m), occurring sparingly in deserts of southeast; also breeds in valleys of Inyo and Mono Cos. and in Santa Barbara Channel on Santa Catalina, Santa Cruz, and Santa Rosa Is. Breeds throughout lower Colorado River valley (Rosenberg et al. 1991) and north through extreme s. Nevada, to extreme sw. Utah (Washington Co.), occasionally summering elsewhere in s. Utah (Behle et al. 1985). Also breeds in se., central, and nw. Arizona (Monson and Phillips 1981), s. and central New Mexico north to Mongollan Highlands, Espanola, and Santa Rosa (Hubbard 1978), and sw. Texas east through sw. Edwards Plateau (Oberholser 1974, Texas Breeding Bird Atlas unpubl.). Three confirmed breeding records for Pueblo Co. in s.central Colorado (Andrews and Righter 1992) and occasionally elsewhere just outside of regular range.

Breeds throughout Baja California (except central portion of peninsula), throughout interior Mexico and on adjacent slopes (sea level to 3,000 m), but not on Yucatán Peninsula; also breeds south through Guatemala to central Belize, w. Honduras, nw. Nicaragua, and all but se. El Salvador (Howell and Webb 1995). Breeds on slopes (600-1,850 m) throughout Costa Rica (Stiles and Skutch 1989), and locally throughout Panama (chiefly 900-1,800 m; Ridgely and Gwynne 1989). In South America, breeds in coastal mountains of n. Venezuela (east to Paria Peninsula) south through Andes of Venezuela, Colombia, Ecuador, Peru (south on west slope to Lambayeque) and w. Bolivia to nw. Argentina (south to Catamarca); Sierra de Perijá on Venezuela-Colombia border and Santa Marta Mtns. in Colombia (Ridgely and Tudor 1994).

Winter range. Occurs year-round throughout breeding range in Middle America and U.S., but in U.S. usually does not winter in Mongollan Plateau, upper Rio Grande valley (generally north of Socorro), and upper Pecos River valley (north of Roswell) of New Mexico (Hubbard 1978); e.-central and n. Arizona (Monson and Phillips 1981, Christmas Bird Count data); Colorado (Andrews and Righter 1992); valleys of Inyo, Mono, and Siskiyou Cos., California (Small 1994); and Rogue Valley of Josephine and Jackson Cos., Oregon (Gilligan et al. 1994).

Also winters in some areas not occupied during breeding season: e.g., coastal areas of s. Oregon,

including lower Coquille Valley of Coos Co. and occasionally farther north (Gilligan et al. 1994); desert areas of se. California (Garrett and Dunn 1981); Farallon Is. and other smaller offshore islands of s. California (Small 1994); valleys of lower Sonoran zone throughout sw. Arizona (Monson and Phillips 1981); central Baja California and Pacific slope of Mexico south to Nayarit (Howell and Webb 1995); and locally elsewhere. Range in Texas may also expand somewhat during winter.

Casual north to w. Washington, and east to se. Texas and Florida (Am. Ornithol. Union 1983).

OUTSIDE THE AMERICAS No reports.

#### HISTORICAL CHANGES

Breeding range may have expanded in some areas during twentieth century. In Oregon, breeding outside traditional area in Rogue Valley has increased in recent years to include coastal Curry Co., where species is now resident, and more recently Coos Co., where species now winters and occasionally breeds (Gilligan et al. 1994). Apparently did not breed in lower Colorado River valley until recent decades; considered rare breeder by 1950s, but now (1990s), fairly common local breeder throughout valley (Rosenberg et al. 1991). Originally nested in crevices and rock outcrops near water but now commonly uses bridges, buildings, and other human-made structures for nests (Small 1994). This flexibility may have facilitated expansion of breeding range.

FOSSIL HISTORY
No information.

## **SYSTEMATICS**

#### GEOGRAPHIC VARIATION

Trend toward reduced amount of white on wing and belly from northernmost populations to those on Isthmus of Tehuantepec, Mexico, with much more restricted amount of white south of there to w. Panama (Ridgway 1907). Abrupt reversal of this trend south of Isthmus of Panama, with birds from e. Panama south having white edging on tertials, inner primaries, and base of outer rectrices. Trend toward more extensive white edging southward; also increased body size north to south in South America (Ridgely and Tudor 1994).

#### SUBSPECIES

Two groups sometimes treated as species (Am. Ornithol. Union 1983): *nigricans* group (Black Phoebe) and *latirostris* group (White-winged Phoebe).

NIGRICANS GROUP. (1) S. n. semiatra (Vigors). U.S. south to w. Mexico including Baja California, to Zacatecas and n. Nayarit. Shows most extensive white on belly among all subspecies, white forms inverted V on belly, wings and tail have moderate pale edging. (2) S. n. nigricans (Swainson). Highlands of ne., central, and s. Mexico from Nuevo León and Tamaulipas across to Jalisco and south to s. Chiapas. Somewhat less white on belly than that of semiatra, forming inverted U, rather than an inverted V. Moderate pale edging on wings and tail. (3) S. n. aquatica Sclater and Salvin. Northeast Chiapas, Mexico; Belize; Guatemala; Honduras; and Nicaragua. White restricted to midbelly and vent; somewhat more restricted pale edging on wings and tail than on semiatra or nigricans. (4) S. n. amnicola Bangs. Costa Rica and Chiriquí, Panama. Darkest Black Phoebe; less white on abdomen. White edging of wings and tail much reduced, sometimes nearly absent.

LATIROSTRIS GROUP. (1) S. n. angustirostris Berlepsch and Stolzmann. Eastern Panama, Colombia, central Bolivia (Santa Cruz), and n. Venezuela from Táchira and Sierra de Perijá east to Sucre, south through Ecuador and Peru to n. Puno. Extensive white edging on tertials and primaries. Moderate amount of white on midbelly. (2) S. nigricans latirostris (Cabanis and Heine). Andes of central and s. Bolivia from Cochabamba to Tarija and nw. Argentina in Jujuy, Salta, and Tucumán. Extensive white edgings occupy half of outer web of tertials; more white on primaries, underwing linings, and base of outer rectrices.

## RELATED SPECIES

Among flycatchers (Tyrannidae), genus *Sayornis* placed in subfamily Fluvicolinae, which includes other chiefly Central and North American genera such as *Contopus*, *Empidonax*, and *Pyrocephalus*. The only congeners with Black Phoebe are Say's Phoebe and Eastern Phoebe, both of which have U.S. and Canadian distribution sympatric with Black Phoebe in some areas; no hybridization reported. *Pyrocephalus* closely resembles *Sayornis* in general form and in cranial characters; the 2 are believed to be closely allied on this basis (Traylor 1977).

## **MIGRATION**

## NATURE OF MIGRATION IN THE SPECIES

More sedentary than either Say's or Eastern Phoebe. Occurs year-round throughout most of breeding range, but partly migratory in north, where some breeding areas are evacuated during winter (particularly in interior U.S.) and some areas are occupied only during winter. Movement patterns

not well known. Within areas occupied year-round, some localized movements may occur upslope for breeding season (to 2,700 m in California) and then downslope to lower elevations after breeding (Stiles and Skutch 1989, Small 1994). Numbers increase in southern portions of year-round range in U.S. during winter, indicating some southerly migration to this area (Garrett and Dunn 1981).

#### TIMING AND ROUTES OF MIGRATION

Timing of migratory movements often difficult to determine, because species occurs year-round throughout most of range. Routes of migration largely unknown. In Oregon (northernmost portion of breeding range on West Coast), coastal breeding population in Curry Co. appears to be resident, with some birds wintering north to lower Coquille Valley (Coos Co.), but inland breeding population in Rogue Valley (Josephine and Jackson Cos.) migratory, rarely wintering within this area (Gilligan et al. 1994). In California, some seasonal movements occur as numbers increase in some southern areas and offshore islands during winter (these include some areas not occupied during breeding season; Garrett and Dunn 1981, Small 1994). Fall movements detected along coast, on offshore islands (e.g., Farallon Is., where species does not breed), and to lesser degree in eastern and southern mountain ranges, spring movements are rare on offshore islands (Small 1994). Fall transients occur on Farallon Is. early-mid-Sep (rarely Aug) through late Nov, peaking sharply in early Oct; rare spring transients noted in Mar, May, and Jun (DeSante and Ainley 1980). In lower Colorado River valley, influx of nonbreeding birds begins in Jul; these birds remain until Mar (Rosenberg et al. 1991). In Arizona, spring transients may occur as early as mid-Feb (Monson and Phillips 1981). Winter residents noted on Pacific slope of Mexico Sep-Mar (Howell and Webb 1995). Migrants rarely seen far outside of breeding and wintering areas but have been observed as far east as Florida, where there are 4 records from 26 Oct to 13 Apr (Stevenson and Anderson 1994). Also one Sep record for Minnesota (Janssen 1987).

MIGRATORY BEHAVIOR No information.

CONTROL AND PHYSIOLOGY No information.

## **HABITAT**

BREEDING RANGE

Invariably associates with water. Favored habitats include coastal cliffs; banks of rivers,

creeks, and streams; borders of lakes and ephemeral ponds; fountains in parks; cattle troughs (Grinnell and Storer 1924, Oberlander 1939). Forages in open areas over water, grass, and other substrates. Elevation ranges from sea level to 3,000 m (Willet 1912, Howell and Webb 1995). Almost any semipermanent water supply with accompanying source of mud, which is required for nest construction, is attractive to this species. Human-made structures have supplemented or replaced natural nest sites (e.g., sheltered rock faces, streamside boulders, dirt banks, and hollow cavities in trees), greatly increasing suitable habitat for this species. Grinnell and Storer (1924) note that irregular distribution of Black Phoebes in an area is probably due to their specialized nesting requirements. Similar in requirements to Eastern Phoebe (Weeks 1994); Say's Phoebe not associated with water. See also Food habits: feeding, and Breeding: nest site, below.

SPRING AND FALL MIGRATION No information.

## WINTER RANGE

Largely similar to breeding range. Some movements to lower elevations after breeding.

## **FOOD HABITS**

**FEEDING** 

*Main foods taken*. Insectivorous; mainly flying insects, but insects and other arthropods are often gleaned from various substrates. Some individuals readily adapt to capturing small fish. Sometimes eats small berries.

*Microhabitat for foraging*. Typically takes prey in open areas and from air, but also gleans from various substrates. A sit-and-wait predator, typically perches within 2.0 m of ground. Commonly forages over open grasslands, water, lawns, bare ground, dirt roads, yards, and parks. Uses any available substrate, including the ground, for perching. In Monterey, CA, median perch height varied from 0.9 to 1.2 m (range 0–25, n=371) through the year; 30% of flights initiated from lower outer canopy of trees (Verbeek 1975a). Resident in open pastureland and fields in n. California; 96% of foraging flights initiated from bush or wire fence, 3.7% from barn, and 0.3% from ground (n=3,183; Irwin 1985).

During breeding season, males forage in more open areas than females do. Females tend to forage inside and at canopy edge, males over open pasture. After pair separates in fall, no difference observed in selection of foraging microhabitat (Irwin 1985). Juveniles forage in more closed habitats than adult

birds do. In Jan, 1 juvenile captured 35.0% of its prey in closed habitats; an adult female on adjacent territory captured 9.0% of her prey in closed habitats (Irwin 1985). In early morning and late afternoon, prey captured primarily in closed microhabitats (canopy); at midday, 90% of prey captured in open grassland.

In Trans-Pecos, TX, observed feeding only in riparian habitat within a few meters of water; adjacent desert scrub habitat ignored (Ohlendorf 1976). Individuals foraged from perches within 2 m of ground and used shaded lower branches of willows (*Salix* spp.), baccharis (*Baccharis* spp.), and

mesquite (Prosopis spp.).

Food capture and consumption. Forages throughout day and occasionally in evening around electric lights (Judson 1901). Usually initiates flight from low perch. Visually locates prey from perch and pursues it until capture, in short (<2.0 m), direct flights (Oberlander 1939, Verbeek 1975a, Irwin 1985, BOW). Typically, only 1 prey item captured on each flight, but sometimes more (Oberlander 1939, 8.0% Irwin 1985). Eats small prey in flight; carries larger prey (i.e., grasshoppers [Orthoptera], and butterflies and moths [Lepidoptera]) to perch, beats it, and then swallows it whole. Individuals move among perches while foraging and return to same perch infrequently (23% of all flights, n = 133; Verbeek 1975a). Occasionally, in a manner similar to Say's Phoebe, Black Phoebe hovers 2–5 s while examining grass or vegetation for prey (Oberlander 1939, BOW). In Monterey County, CA, during Jul and Aug, 76% of prey captured in flight, 8% from grass, 8% from ground, 5% from buildings, and 2% from tree leaves (n = 133; Verbeek 1975a). Foraging behaviors very similar to those of Eastern Phoebe.

In n. California, prey capture rates varied with weather conditions; in fair weather, prey captured at mean rate of 1.21 items/min (range 1.0–1.34, n=1,181; Irwin 1985). Forages throughout day; rates peak in midmorning and midafternoon. Imminent rain amplifies foraging rates: Capture rates average 1.74 prey items/min (range 1.44–2.09, n=922); rainfall suppresses capture rates: mean 0.61 items/min (range 0.53–0.67, n=244). Capture rates higher prior to heavy rainfall than prior to light rainfall (Irwin 1985).

DIET

*Major food items*. Wild bees and wasps (Hymenoptera), flies (Diptera), beetles (Coleoptera), damselflies and dragonflies (Odonata), and spiders (Arachnida).

*Quantitative analysis*. Stomach contents of individuals from California (n = 344) contained 99% animal matter (Beal 1912); berries from blue

elderberry (*Sambucus gluaca*) found in 16 of 344 stomachs (see also Gander 1928). Of the total prey items observed, hymenopterans (primarily wasps and various wild bees) accounted for 31% (in Aug, 59%); flies, 28% (whose percentage remained the most constant throughout year, peaking in Apr at 64%); beetles, 13%; bugs, 11%; butterflies and moths, 8%; grasshoppers, 2%; and other arthropods, 6%. Honeybees (*Apis mellifera*) absent from stomachs examined by Beal (1912). Death of a Black Phoebe after consuming a honeybee suggests that bees are potentially dangerous prey (Ross 1933).

Stomach contents (n = 14) of phoebes collected from riparian areas between May and Aug in Trans-Pecos, TX indicate that termites (Isoptera) are the most frequent prey (48% of individual prey items), and account for 21% of total prey volume (Ohlendorf 1976). True bugs (Hemiptera) represented 15% of total prey items and 10% of prey volume; beetles, 14% and 13%; bees and wasps, 14% and 13%; damselflies and dragonflies, 5% and 21%.

Major differences in prey type as function of prey volume were found among sympatric Black and Say's phoebes (Ohlendorf 1976). In contrast to major prey taxa used by Black Phoebe, total prey volume of Say's Phoebe divided as follows: grasshoppers, 47%; beetles, 17%; bees and wasps, 17%; and flies, 15%. Along Colorado River, AZ, only arthropods (represented primarily by beetles, dragonflies, flies, bees and wasps) were found in stomachs of 6 Black Phoebes (Rosenberg et al. 1991).

Black Phoebes also capture fish; for example, at goldfish pond in Pasadena, CA, an individual repeatedly dove into pond, apparently trying to capture young fish (Howell 1924); in Berkeley, CA, minnows taken (Oberlander 1939); in Clark Co., NV, 1 individual observed hovering above water of sewage pond, immersing its bill and capturing mosquito fish (*Gambusia affinis*; Lawson 1975); and at a fish hatchery in Humboldt County, CA, individuals fished regularly and used fingerlings to provision nestlings (Irwin 1985).

Food items given to nestlings differed in proportion from those found in stomachs of adults. "Soft" food items (bees and wasps, flies, and butterflies and moths) accounted for 88% of total items in nestlings, versus 67% of total items found in adult stomachs (Beal 1912).

FOOD SELECTION AND STORAGE No information.

NUTRITION AND ENERGETICS
No information.

METABOLISM AND TEMPERATURE REGULATION No information.

DRINKING, PELLET-CASTING, AND DEFECATION

Perched birds observed to drink. Dips bill into water and then elevates head to facilitate swallowing (Oberlander 1939). Drinking frequency and intake unreported.

Casts pellets during day and while on roost at night; may do so less frequently during rainy periods. Pellets not cast every night; found under roost sites and within old nests used as roosts (Oberlander 1939, BOW). Pellets are spherical or conical and 4–9 mm in diameter (mean 7–8, n = 14; Oberlander 1939); composed of beetle forewings (most common item), insect femora and tibiae, parts of compound eyes, simple eyes, spurs and spines, setae, cranial parts, cocoon, and strings of woody material. Perched birds observed to eject pellets after stretching necks up and down while mouth is open; ejects pellet from or throws it out of mouth by whipping head to side. Pellets ejected >25 cm away from individual (Oberlander 1939, Irwin 1985). No information on defecation.

## SOUNDS

**VOCALIZATIONS** 

**Development**. No information. See Weeks 1994 for discussion of vocal development in Eastern Phoebe.

Vocal array. Variety of stereotyped calls and songs, presumed context and potential meaning of which are described in detail by Smith (1969, 1970a, 1970b) for Eastern Phoebe and in lesser detail for Black Phoebe and Say's Phoebe (Smith 1969, 1970a, 1970b). Outlined below are the most commonly used vocalizations.

PRIMARY SONG. Consists of series of Regularly Repeated Vocalizations (RRV) employed for predawn song, patrolling, countersinging, stationcalling, and mate association (Smith 1970b, BOW). Song typically has 2 alternating elements (Fig. 2A), described as Tee-hee Tee-hoo by Oberlander (1939), or RRV1 RRV2 (Fig. 2a and b in Smith 1970b). Song bouts are made up of combination of these 2 elements in varying frequency; single bout may contain series of repeated RRV1 elements or, to lesser extent, repeated RRV2 elements. Typical songs are about 50% RRV1 and 50% RRV2. Females rarely engage in RRV bouts (Smith 1970b). Songs also may contain Initially Peaked Vocalizations (IPV; Fig. 3a-e in Smith 1970b), or Tieur call (Oberlander 1939) as element of song bout. Tieur is used most commonly during mate association, and prior to or immediately after RRV1 RRV2 song. Different forms of IPVs and their contexts are described by Smith (1970a, 1970b). Primary Song

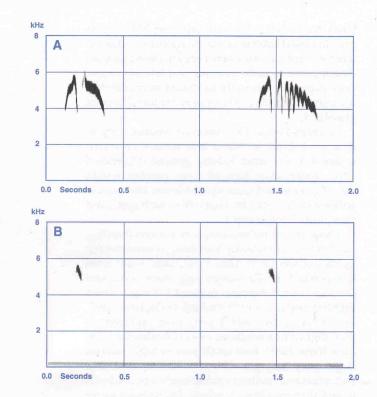


Figure 2. (A) Typical RRV1 RRV2 (*Tee-hee Tee-hoo*) part of Primary Song of Black Phoebe. (B) Simple Vocalization (*Tsip* call note). Prepared by staff of Borror Laboratory of Bioacoustics, Ohio State University. (A is BLB No. 7147, Cochise Co., AZ, 29 Jun 1964; B is BLB No. 7124, Cochise Co., AZ, 28 Jun 1964).

similar in complexity to that of Eastern Phoebe and greater in complexity than that of Say's Phoebe.

SIMPLE VOCALIZATION. Figure 2B. Simple Vocalization (Fig. 2a–d in Smith 1970a), or *Tsip* call, as described by Oberlander (1939), is the most common call. Forms of this vocalization are used throughout year and in several different contexts (e.g., during flight, foraging, interaction with potential nest predator).

CHATTER VOCALIZATION. Chatter Vocalization (Fig. 3a in Smith 1970a) is described as soft, wheezy sound (Oberlander 1939); used by males when approaching females and during Nest-Site-Showing Display (see Behavior: sexual behavior, below; Smith 1969, Irwin 1985, Wolf 1991).

BIPEAKED VOCALIZATION. Bipeaked Vocalizations (Fig. 4a–d in Smith 1970a, Wolf 1991) are used during chases of mates and conspecific intruders. Oberlander (1939) describes this call as *Tweedle-deedle-eek*.

*Phenology*. In n. California during winter, males sang Primary Song for 10–30 s an average of once every 7.3 h (Irwin 1985). By early Mar, bout frequency and song duration increased to average of

1 song every 43 min, with song duration of up to 7 min. From week preceding laying to posthatching period, vocal activity near nest is greatly suppressed (Oberlander 1939, Irwin 1985). General decrease in vocal activity also observed at end of breeding season, with onset of summer. Phoebes use Simple Vocalizations and IPVs throughout the year, although Oberlander (1939) notes IPVs abandoned Nov-Jan. Chatter Vocalizations heard only during breeding season near nest or mate (Oberlander 1939, Smith 1970a, Irwin 1985, Wolf 1991). Bipeaked Vocalizations also associated with breeding season and occur primarily during mate-chasing or chasing of conspecific intruders. In Humboldt Co., CA, Feb-Mar, mate-chasing and Bipeaked Vocalizations observed an average of once every 124 min (Irwin 1985).

Daily pattern of vocalizing. Predawn song by males typical during breeding season (Oberlander 1939, BOW). Late Jan–early Apr, Oberlander (1939) observed predawn songs on 26 out of 27 mornings. Males on breeding territories sing intermittently throughout day, often in response to males singing on adjacent territories or after intrusions by conspecifics. Predawn songs absent after onset of summer (Oberlander 1939). Simple Vocalizations and IPVs used throughout day.

Places of vocalizing. Songs localized around nest site and at territorial boundaries when males are countersinging. Most singing directed from top of bush, fence, tree, or other prominent object. Sometimes sings during flight displays (Irwin 1985, BOW). Gives Chatter Vocalizations and Bipeaked Vocalizations while in flight; gives Simple Vocalizations and IPVs while perched or in flight (Smith 1970a, BOW).

Repertoire and delivery of songs. Song repertoire limited; variation primarily in relative frequency of RRV1 and RRV2 elements and presence of IPVs in song (Smith 1970b). RRV2 elements often dominate songs. IPVs most often are prelude to Primary Song, but song bouts composed entirely of IPVs are not uncommon (Smith 1970b).

Social context and presumed functions of vocalizations. Primary Song apparently used primarily for attracting female, territorial advertisement, countersinging at territorial boundaries following agonistic encounters, and sometimes in flight songs. Smith (1970b) suggests that message or intent of song may be determined by relative frequency of RRV1 and RRV2 elements. Gives Chatter Vocalizations when approaching mate or during Nest-Site-Showing Display (see Behavior: sexual behavior, below; Oberlander 1939, Smith 1970a, Irwin 1985, Wolf 1991). Uses Simple Vocalizations in variety of situations and contexts, during flight, when perched while foraging with Tail Wag,

and when repelling potential nest predators. Context and function of IPVs variable; part of Primary Song and an association call during non-breeding season, as replacement for Simple Vocalization (Oberlander 1939, Smith 1970a).

#### NONVOCAL SOUNDS

Like other tyrannids, produces loud snapping sound by swiftly closing mandibles. Used as threat display during agonistic encounters with intruders near nest, and sometimes heard during prey capture attempts (BOW).

## **BEHAVIOR**

#### LOCOMOTION

Accomplishes most locomotion via flight; rarely moves on ground or even pivots or adjusts feet while perched. Rarely hops on ground, but occasionally lands on ground near potential prey and hops several centimeters to capture prey item. Flight movements are direct, with steady wing-beats and no undulations in flight path. Hovers during cold periods while gleaning prey from various substrates (e.g., fishing over water) or sometimes within clouds of flying insects; also during Nest-Site-Showing Display and during vertical zigzag flight display during breeding season (see Sexual behavior, below). May also hover over intruder during encounters near nest (BOW).

## SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Both sexes preen frequently, throughout day, often during or between foraging bouts or after leaving nest during incubation. May include scratching and alternate stretches of left wing and leg (simultaneous) and then the right wing and leg. Typical bout starts with head-scratching over wing on alternate sides and progresses to preening of rectrices or primaries on alternate sides (BOW). Holds wing upward with primaries partly folded, then rocks wrist inward and preens greater-coverts. Preens wing- and tail-feathers with greatest frequency. Stretches less frequently; sometimes elevates wings directly above back, folding primaries while stretching arm. This sequence often followed by stretching of wing and collateral leg of first one side then the other. Tail fully fanned and wing and leg stretched down and outward at 45° angle from vertical. Wing is stretched back so that it overlaps fanned tail. Preening bouts typically last 15-90 s (BOW). Bathing integrated with preening bouts.

Sleeping, roosting, sunbathing. Roosting locations largely unknown; some birds roost on old

nests or at old nest sites year-round. Also roosts in and around open buildings and other human-made structures, as do the other *Sayornis* species. Individuals show moderate variation in time of entering and leaving roost, with most variation confined to entering; limited observations suggest that male may enter roost later and leave roost earlier than female (Oberlander 1939). Time of entering and leaving roost also apparently associated with physiological status, proximity of another phoebe, and food availability. Time of leaving the roost in morning less variable than entry time.

On awakening, pumps and fans tail, stretches, looks around, and calls softly before leaving roost. Vocalizations may start with soft Simple Vocalizations (see Sounds: vocalizations, above) before bird leaves roost and flies to a favorite perch. During breeding season, Simple Vocalizations escalate to louder IPVs followed by Primary Song. No information on sunbathing.

*Daily time budget*. Needs study. In California, during Feb and Mar between 0700 and 1200, limited observations indicate that individuals spent average of 9% of each hour in flight (range 3–13.3, n = 19), mostly foraging (BOW).

#### AGONISTIC BEHAVIOR

From Wolf 1991. Early in breeding season, frequent territorial encounters; include chasing and vocalizations. Aggressive displays include wingflicking, wing-drooping, crest-raising, tail-pumping, tail-fanning, and chasing. Territorial disputes sometimes involve face-offs between birds after chases, if intruder remains. Birds may flutter from perch to perch maintaining separation of 0.5-2.0 m, crests erected, tails pumping and fanning briskly; wings are fluttered during movements and drooped while sitting; movements of <1 m occur every 3-4 s, and combatants may move all over bush or tree in 1 minute or less. Dispute may be settled with rush and chase by territorial bird. Chases normally include Bipeaked Vocalizations (see Sounds: vocalizations, above). Territory holders and intruders sometimes hover face to face with bodies held upright, tails fanned. Many of these disputes occur at territorial boundaries, and usually neither bird gives ground.

#### **SPACING**

Territoriality. Territories are aggressively defended against conspecific intruders. Minimum distances reported between nests range from 40 to 160 m (Ohlendorf 1976, Irwin 1985, Schroeder 1985, Wolf 1991). Similar distances reported for Eastern Phoebe (Weeks 1994); nests of Say's Phoebe more dispersed. Nonbreeding phoebes (Aug–Jan) main-

tain well-defined territories, and pairs may remain together or reside on adjacent territories (Irwin 1985, Schroeder 1985, BOW). Former breeders tend to stay on or very near previous year's territory (Schroeder 1985). Territorial maintenance consists primarily of mutual avoidance, except during establishment of territories when direct confrontations, flight displays, and chases take place with regularity (Grinnell and Linsdale 1936, Oberlander 1939, Verbeek 1975a).

*Individual distance*. Mated birds rarely perch less than a few meters apart. During incubation, males perched near nest throughout the day (Wolf 1991).

#### SEXUAL BEHAVIOR

Mating system and sex ratio. Primarily monogamous; female probably chooses mate. Polygyny uncommon; out of several hundred nestings, only 1 verified case and 1 suspected case (Schroeder 1985); both occurrences involved females on adjacent territories. Infrequent switching of sites and mates by either sex; pair bonds may last as long as 5 yr (Schroeder 1985). Pairs together from previous breeding attempts and seasons nest 2–4 wk earlier than new pairs (Irwin 1985).

Pair bond. Maintained at least through breeding season; typically double-brooded. Pairing initiated Jan-Feb by infrequent approaches by male (e.g., 2 interactions/day; Irwin 1985) that often result in chase as female is displaced from perch. Increasing frequency of interactions and attempts by male to perch near female characterize next phase of courtship. Male frequently approaches perched female in fluttering flight, and female usually leaves perch, typically when male has approached to within 1 m. When female refuses to be displaced, male is driven away from perch as he attempts to land. Male may perch 6–15 cm from female. Female squats down and assumes submissive posture, head lowered and retracted and feathers fluffed. Male tries to hover in front of and behind female; female intolerant at first, but after several days to weeks, female allows male to land on her back briefly for copulation (1-2s). Male engages in infrequent flight displays during this period.

Flight displays often start with male leaving perch at nest site and hesitantly flying almost straight up, with tail fanned and wings fluttering; may also make series of short zigzags or spirals. Climb sometimes accompanied by Bipeaked Vocalizations (see Sounds: vocalizations, above). Climb ends with bird reaching plateau at 20–30 m from ground; bird then either flutters to top of nearby tree, singing Primary Song (see Sounds: vocalizations, above), or drops straight down to perch near nest site. Upon landing, may immed-



iately start Primary Song (Oberlander 1939, Irwin 1985, BOW).

In n. California, courting males engage in Nest-Site-Showing Displays (Fig. 3) mid-Feb-early Mar (Wolf 1991). Male flies to nest site and hovers for 5-10 s, holding body vertically and fanning tail in front of old nest or section of bare wall; female often immediately follows male, either landing on old nest or hanging from wall of nest site. Frequently, male repeatedly hovers and lands on old nest before returning to perch above nest site. Displays sometimes accompanied by soft Chatter Vocalizations (Smith 1969) while birds are at nest site and often occur several times in 0.5-h period. Occasionally, female initiates display by flying under culvert; male immediately follows. Chasing often occurs when female leaves roost in morning and approaches mate; either sex may initiate chase (Wolf 1991).

Extra-pair copulations. No information.

## SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Nonsocial, except in association with mate during breeding season. In small percentage of breeding territories, apparently unpaired adult birds are present during breeding period; their role is unknown (Schroeder 1985, BOW). May occasionally forage near previous year's mate during nonbreeding season (Irwin 1985).

Play. No information.

Nonpredatory interspecific interactions. Around nest, nonpredatory intruders are repelled (Irwin 1985, Schroeder 1985, Wolf 1991). Black Phoebes observed chasing Western Wood Pewees (Contopus sordidulus), Rough-winged Swallows (Stelgidopteryx

Figure 3.
Nest-SiteShowing
Display of male
Black Phoebe,
typical behavior
seen during
courtship.
Drawing by N.
John Schmitt.

ruficollia), Barn Swallows (Hirundo rustica), House Finches (Carpodacus mexicanus), Whited-crowned Sparrows (Zonotrichia leucophrys), Brewer's Blackbirds (Euphagus cyanocephalus), and Audubon's Warblers (Dendroica coronata).

Aggressive behavior toward and attacks against Black Phoebes by Ash-throated Flycatchers (*Myiarchus cinerascens*), Western Kingbirds (*Tyrannus verticalis*), and House Finches (Schroeder 1985). Joint tenancy of a pair of Black Phoebes and House Finches after finches encroached on Black Phoebe's nest resulted in alternate periods of incubation by females of both species over period of 1 wk. Ultimately both species abandoned nest; phoebes had laid 6 eggs, finches 5 eggs (Holland 1923).

## PREDATION

Few observations. Individuals respond with alarm vocalizations and flight to Cooper's Hawks (Accipiter cooperii), Northern Harriers (Circus cyaneus), and American Kestrels (Falco sparverius; BOW). American Kestrels prey upon nestlings (Cowles 1928); Scrub Jays (Aphelocoma coerulescens) known to take eggs (Schroeder 1985); other corvids (Corvus) and Loggerhead Shrikes (Lanius ludovicianus) are probably common nestling predators. Nests are generally less accessible to terrestrial predators, but in some situations small carnivores, e.g., red fox and coyotes, may depredate accessible nests. Rodents such as California ground squirrels (Spermophilus beecheyi) are also potential nest predators (BOW).

Incubating birds, when disturbed by potential nest predator, frequently leave nest and perch at a distance (5–10 m away) with little vocal activity.

During nestling stage, adults respond to potential predators with Simple Vocalization (*Tsip* call; see Sounds: vocalizations, above) and usually patrol (10–12 maway) while calling frequently; may swoop down at terrestrial predators and snap bill (BOW). No distraction displays reported.

## **BREEDING**

#### PHENOLOGY

Pair formation. In California, starts early—mid-Jan and continues through late Feb (Irwin 1985, Schroeder 1985, Wolf 1991). Pairs from previous seasons often winter on adjacent territories, interact occasionally and maintain casual association through fall and winter. These pairs progress through courtship 2–4 wk earlier than pairs mating for first time (Irwin 1985).

**Nest-building.** First nest attempts: Santa Clara Co., CA, early Mar, median date 15 Mar (range 4–28 Mar, n = 15; Wolf 1991). In Berkeley, CA, start of nest construction observed as early as 28 Feb (Oberlander 1939).

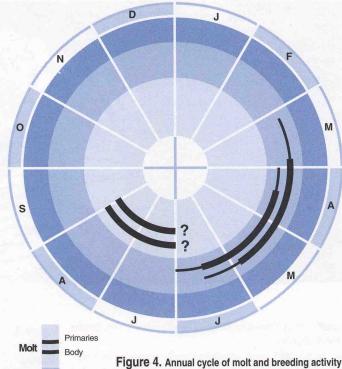
First brood per season. Figure 4. In Humboldt Co., CA, eggs laid 20 Mar–24 Jun (Irwin 1985); in Santa Clara Co., CA, 18 Mar–6 May (Wolf 1991); in Santa Barbara Co., CA, 6 Mar–28 Jun (Schroeder 1985). Egg dates for California as a whole, 17 Mar–15 Aug (n = 126; Bent 1942; see also Tyler 1913, Fraser 1931, Davis 1933); for Arizona, 16 Apr–26 Jun (n = 8, Bent 1942). Typically lays first eggs 2–4 wk earlier than Eastern (Weeks 1994) and Say's Phoebes (Shukman and Wolf in press).

Second/later broods per season. Second broods common in U.S.; in Santa Barbara Co., CA, approximately 50% of breeders renested or had second broods (*n* = 606; Schroeder 1985); in Santa Clara Co., CA, approximately 66% of breeders renested or had second clutches, 13 Apr–31 May (Wolf 1991). Third attempts rare; most frequent after nest loss (Schroeder 1985, but see Irwin 1985).

#### **NEST SITE**

Selection process. By female. Male engages in Nest-Site-Showing Displays (accompanied by female) during courtship; occur at potential nest sites (see Behavior: sexual behavior, above), but female selects actual site and determines nest placement.

*Microhabitat.* Nest cemented with mud to vertical wall of site, 1–3 m off ground (Bent 1942, Irwin 1985, Wolf 1991). Top of nest most often within 30–70 mm of protective ceiling (Wolf 1991). If placed in culvert or under bridge, nest is usually >2 m from outside. Placement of nest affords concealment, and proximity to ceiling may



Young

Breeding

Migration

Figure 4. Annual cycle of molt and breeding activity for a California population of Black Phoebes (latitude 37°N). Thick lines show peak activity, thin lines offpeak. See text for details on timing of breeding in other parts of this species' range.

discourage larger avian predators. Nests are placed above high-water mark even when actual water level is well below high-water mark (Wolf 1991).

Site characteristics. Common to all nest sites are (1) ceiling that protects nest from weather and may provide concealment, (2) placement near or directly over water (nests placed above ground tend to be situated higher than those over water), (3) placement close to source of mud for construction materials, (4) area surrounding site suitable for foraging (Ohlendorf 1976, Irwin 1985, Schroeder 1985, Wolf 1991). Natural sites include dirt ledges along streams (Bendire 1895, Hoffman 1927), sheltered pockets on large rocks over water (Tyler 1913, Baily 1921, Grinnell and Storer 1924), and in tree under broken limb (Robertson 1933). Human-made sites include under eaves of buildings (Ohlendorf 1976, Irwin 1985), on bridge stringers (Tyler 1913), in irrigation and drainage culverts, in abandoned wells (Bendire 1895), and in sluice boxes (Ray 1906).

In coastal Santa Barbara Co., CA, only 2% of nest sites examined were on natural structures (n = 168; Schroeder 1985); bridges and culverts were most frequently used (58%), then buildings (39%); overall, only 6% of 728 nesting attempts used natural structures for nest sites (Schroeder 1985). On Santa

Cruz I., CA, 59% of 29 nest sites were natural structures. Nest-site data are undoubtedly biased, because of difficulty of locating natural sites (Schroeder 1985, BOW). In Humboldt Co., CA, 22 of 23 nests were located under eaves of buildings; of the 21 bridges located within the study area, only 1 was used as nest site (Irwin 1985). In Trans-Pecos, TX, 14% of 36 nests were on natural structures; remaining 86% were placed under bridges and within culverts (Ohlendorf 1976).

#### NEST

Construction process. Female gathers material (Irwin 1985, Schroeder 1985, Wolf 1991). The following description is from Wolf 1991. Female flutters near or clings to wall and places or flings mud pellets onto vertical surface, forming horizontal line or shallow upward arc; builds base of nest out from wall into platform. Builds nest cup up from platform and lines nest. Initially, mud base may be started at several locations at nest site or at multiple sites, but usually by second day of construction a single site is focus of construction efforts. Gathers mud and plant material from distances of 1–75 m from nest site, often not from closest source. Construction bouts last 6-15 min, interrupted by periods of foraging. During one 75-min period, a female made 39 trips to nest with material, stayed on nest for 3-87 s (mean 32 s) and was away from nest for 4-284 s (mean 79 s). Nest construction sporadic throughout day and alternates with periods of foraging and other maintenance behaviors.

Construction of new nest takes  $5 \, d$ – $3 \, wk$  (Irwin 1985, Schroeder 1985), average 18.8 d (n = 6; Wolf 1991). Refurbishment of nest for first brood takes on average 7.5 d (1–10, n = 8; Wolf 1991); refurbishment of nest for second brood  $5.4 \, d$  (n = 5; Wolf 1991; see also Oberlander 1939, Irwin 1985).

Structure and composition matter. Half hemispherical in shape; side of nest cemented to vertical wall. Supporting base and outer shell of nest composed mostly of mud mixed with grass stems, small roots, or other dry vegetation; horse or animal hair (Tyler 1913) also sometimes incorporated (Bendire 1895, J. Froke pers. comm.); human-made fibers also used. Upper half to third of cup often composed primarily of tightly woven fibers with small amounts of mud; shows greatest variation in proportion of mud and plant fibers used. Nest lined with woven plant fibers (Bendire 1895, Irwin 1985, Schroeder 1985, Wolf 1991).

Eastern Phoebe builds 2 nest types: adherent (cemented to vertical wall, as just described) and statant (supported on the bottom), the former of which is similar in material and composition to nest of Black Phoebe (Weeks 1994); Say's Phoebe

constructs only a statant nest (rarely is mud used for construction).

*Dimensions*. Nest height (at attachment surface): mean 130 mm (range 80–210); width (at attachment surface): mean 100 mm (90–120); depth (distance from outer edge of nest to attachment surface): mean 125 mm (100–170); inside cup diameter (top of cup): mean 65 mm (63–68); inside cup depth: mean 31 mm (30–33); nest lining 10–20 mm thick (n = 8; Wolf 1991; see also Bendire 1895).

*Microclimate*. Away from prevailing winds and often above water; not typically exposed to direct solar radiation (Wolf 1991).

Maintenance or reuse of nests, alternate nests. Strong tendency to reuse old nests; reuse rates vary from 41 to 85% (Oberlander 1939, Irwin 1985, Schroeder 1985, Wolf 1991). In 76% of first nesting attempts (n = 21) and 85% of second nesting attempts (n = 13), individuals rebuilt existing nests (Wolf 1991). Readily relines nests with addled eggs from earlier attempts. Irwin (1985) found nest reuse in 16 of 23 cases, and in 1 case nest was reused in 6 of 7 consecutive years; 4 of 7 pairs that built new nests had second broods in same nest; 2 of the other nests were destroyed, and in the third, nestlings died from starvation. New nests used for 59% of 279 breeding attempts, and used more commonly for first clutches than for second clutches (Schroeder 1985).

Nonbreeding nests. Not constructed.

#### EGGS

*Shape*. Ovate to short ovate, occasionally short subelliptical.

*Size*. Mean length and breadth (mm), San Francisco Bay, CA: 18.90 (range 17.50–20.14)  $\times$  14.56 (range 13.64–15.31, n = 123; Wolf 1991); 18.7 (17.3–20.3)  $\times$  14.4 (13.2–15.2, n = 50; Bent 1942). Egg size (volume, as calculated using Hoyt 1979) increases significantly from first to second clutches for eggs with same position in the laying sequence; tendency for egg size to increase with laying sequence. Total clutch volume increased 2.9% from first to second clutches (Wolf 1991).

*Mass*. From Wolf 1991. Fresh-egg mass 2.1 g (range 1.7–2.4). Egg volume 2.05 ml (range 1.7–2.4, n = 122). Fresh-egg mass averages 10–12% of female body mass. Eggs lose average of 17.5% (range 13.1–28.5, n = 39) of mass during incubation period.

Equal in size to Eastern Phoebe eggs; eggs of Say's Phoebe approximately 25% heavier.

Color. Ground color pure white and moderately glossy, immaculate to lightly spotted around large end. Variation in spotting with laying sequence first noted by Tyler (1913). Presence of spots varies significantly with position of egg in laying sequence; last egg spotted more frequently and intensely

than other eggs in clutch; 38% of all eggs spotted to some degree. In 3 of 26 clutches, all eggs had no spots and in 4 of 26 clutches all eggs were spotted to some degree. Eggs in 5-egg clutches are more frequently and intensely spotted than eggs in 4-egg clutches (Wolf 1991). Irwin (1985) reported all eggs immaculate white (n = 119). Very similar to eggs of both Eastern and Say's phoebes (Weeks 1994, Shukman and Wolf in press).

Physiological cause of variation in egg-spotting with laying sequence is not known. Longer retention in shell gland, because of tendency for last egg to be laid 1–2 h later than other eggs within clutch, could account for increased pigmentation found on later eggs (Warren and Conrad 1942); needs study.

Surface texture. Smooth.

Eggshell thickness. Not known.

Clutch size. Varies from 1 to 6 eggs. In Santa Barbara Co., CA, mean clutch size 4.20 eggs (range 3–5, n = 402; Schroeder 1985), last-quartile clutches (26 May–28 Jun) significantly smaller than earlier clutches. In Santa Clara Co., CA, mean clutch size 4.55 eggs (range 4–5, n = 38; Wolf 1991); in Humboldt Co., CA, 4.3 eggs (range 3–6, n = 33; Irwin 1985). In Trans-Pecos, TX, 3.57 eggs (range 1–4, n = 21; Ohlendorf 1976). Food availability may limit clutch size and number of breeding attempts in season (Irwin 1985). Female with access to hatchery fingerlings laid more clutches (3 vs. 2) and fledged more young (12–13 vs. 9) than neighboring pairs in 2 consecutive years (Irwin 1985).

Egg-laying. Starts 1–18 d after nest completion or refurbishment (Oberlander 1939, Irwin 1985, Wolf 1991). Phoebes stop vocalizing when near nest during week preceding laying and remain quiet near nest until several days after eggs hatch (Oberlander 1939, Irwin 1985). In Santa Clara Co., CA, for first nesting attempts laying started average of 4.4 d (range 2–8, n = 13) after nest completion, for second clutches 12.4 d (range 7–18, n = 8) after first brood fledged (Wolf 1991; also see Schroeder 1985). In Humboldt Co., CA, first eggs laid average of 7 d (range 4–9, n = 20) after nest completion; interval shortest for nests started late in season (Irwin 1985). First egg in replacement clutches laid on average 9.8 d (range 6–11, n = 5) after nest destruction (Wolf 1991). In Santa Barbara Co., CA, 11 d reported as minimum interval from fledging or nest destruction until laying of first new egg of new clutch (Schroeder 1985). In Humboldt Co., CA, first egg of second clutch laid on average 10 d (range 1–23, n = 11) after fledging of first brood (Irwin 1985).

In Humboldt Co., CA, eggs laid between 0700 and 0830 (Irwin 1985). In Santa Clara Co., CA, all eggs (except last) laid average of 91 min (range 13–235, n = 18) after civil sunrise; last eggs laid on average 173 min (range 56–252, n = 7) after civil

sunrise (Wolf 1991). Times similar for Eastern Phoebe (Weeks 1994). Skutch (1952) reported laying times of before midday for other tyrannids in Costa Rica.

Eggs typically laid at rate of 1/d (Irwin 1985, Schroeder 1985, Wolf 1991); exceptions noted by Oberlander (1939), Schroeder (1985), and Wolf (1991).

#### **INCUBATION**

Onset of broodiness and incubation in relation to laying. Needs study. Incubation begins with clutch completion (Oberlander 1939, Irwin 1985, Wolf 1991). Some females roost on nest during latter part of laying period, or are seen intermittently on nest during this time (Wolf 1991).

*Incubation patch.* Needs study. Loss of belly feathers observed 1–4 d before laying first egg (Irwin 1985). Incubation patches generally observed only on females (Oberlander 1939, Irwin 1985, Wolf 1991), but also on 3 males found incubating (Irwin 1985).

Incubation period. In Santa Clara Co., CA, incubation period averaged 388 h (16.2 d; range 373–426 h, n = 15; Wolf 1991). This period is 14–23% longer than is predicted for a 2.0-g egg, based on Drent 1975. Similar periods reported for Say's and Eastern phoebes (Shukman and Wolf in press, Weeks 1994). In other regions, period ranged from 15 to 18 d, with 17 d the most common (Irwin 1985, Schroeder 1985). Eggs incubated during colder weather had longest incubation periods (Irwin 1985).

Parental behavior. Incubation primarily by female, but in Humboldt Co., CA, at 3 of 16 nests males did most if not all incubation (Irwin 1985). Shared incubation duties reported by Jewett (1899), who also indicated that both sexes share in nest construction. Only females seen on nest by Wolf (1991) in color-banded population. Incubation by female alone also reported by Oberlander (1939) and Schroeder (1985), who found in 7 cases of experimental female removal during incubation, males did not continue incubation. In Eastern Phoebe, only females develop incubation patch and incubate eggs (Weeks 1994).

Generally, female does not fly directly to nest when resuming incubation; first perches within few meters of nest site. On arrival, frequently perches on nest rim and inspects contents before settling onto nest. Incubating birds remain alert; frequently scan surroundings and become motionless on appearance of potential predator. Also occasionally stand to inspect, turn, or probe eggs. Incubating bird sometimes takes and eats insects without interrupting incubation. Female frequently becomes restless before ending a period of

incubation; may be initiated by appearance of prey. Occasionally, male may prompt female to terminate bout by making short looping flights in view of nest or hovering in front of nest. During recesses, female perches by nest and preens for several minutes; more frequently, immediately starts foraging. Foraging short in duration; females may make 12–38 sallies in 2–4 min (Wolf 1991). Food-begging behavior by female observed during first 3 d of incubation; in only 1 reported instance did male feed soliciting female (Irwin 1991). Male spends most of day perched directly over nest site, either foraging, preening, or singing; aggressively defends area 3–5 m in diameter around nest from potential predators and site competitors (Wolf 1991).

Incubation bout length and interval between bouts vary. In Santa Clara Co., CA., 15, 16, and 29 bouts observed from 1000 to 1600 h for 3 different females on days 9, 13, and 3 of incubation, respectively. Attentive periods by these 3 females averaged 12.2 min (range 1–102) and accounted for 63–68% of observation period (Wolf 1991). In Humboldt Co., CA, attentive periods averaged 13.8 min (range 4.5–25.5) and accounted for 68% of observation period (Irwin 1985). Inattentive periods averaged 6.3 min (range 1.8–30.5), 32–37% of observation period, in Santa Clara Co., CA, and 6.5 min (range 2–19.5), 32% of observation time, in Humboldt Co., CA (Wolf 1991).

Hardiness of eggs against temperature stress; effect of egg neglect. No information; see Weeks 1994.

#### HATCHING

Preliminary events and vocalizations. No information.

Shell-breaking and emergence. Eggs pipped 4–72 h before hatching (Irwin 1985, Wolf 1991). In 10 instances, eggs that were found with a few pip marks hatched 4–11 h later (n = 10; Wolf 1991). Pipping birds cut ring around shell at its greatest circumference. Occasionally, oval approximately 5 x 10 mm is pipped in large end of shell during hatching (Wolf 1991).

Eggs tend to hatch in order laid. First-laid eggs hatched first in 6 of 7 recorded cases; last-laid eggs hatched last in 9 of 10 cases (Wolf 1991).

Parental assistance and disposal of eggshells. No observations of parental assistance during hatching. Parents removed shell fragments from nest and carried as much as 45 m away (Wolf 1991).

#### YOUNG BIRDS

**Condition at hatching.** From Wolf 1991, except where noted. Hatchlings altricial, eyes closed; mass averages 1.5 g (n = 24), approximately 71% of freshegg mass. Behaviors observed soon after hatching

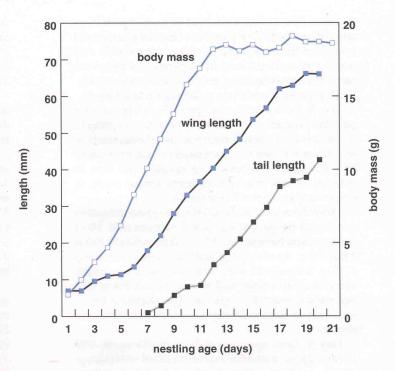


Figure 5. Mean body mass, wing length, and tail length of nestling Black Phoebes, as function of age (Wolf 1991). Feathers erupt from wing on days 5-6; values before this period represent elongation of hand.

include rhythmic pedaling of legs, grasping motions with claws, gaping and raising of heads, and weak peeping. Nestlings 1 dold usually rest on abdomen and head with bill pointing posteriorly and tucked beneath belly. Skin and tarsi colored orange flesh; viscera clearly visible through skin of abdomen. Bill flanges creamy yellow and gape bright yellow orange; mandibles and claws light yellow, with no feather papillae visible. Nares oriented toward tip of mandible; egg tooth situated approximately 0.5 mm from tip of upper mandible. Body lightly covered with medium gray neossoptiles (natal down piloplume feathers) and head more heavily covered with dark gray neossoptiles. At hatching, nestlings have 230–266 neossoptiles in 18–21 feather tracts (n = 3; Collins and Keane 1991). Total number of neossoptiles is intermediate within family Tyrannidae; members of genus Sayornis have more neossoptiles than many closed-nest species and fewer neossoptiles than species that build opencup nests in sites without protective ceiling (Collins and Keane 1991).

Growth and development. Mensural data for growth of nestlings as function of age are presented in Figure 5. The following (from Wolf 1991) details approximate age-specific morphological and behavioral changes for typical nestling. Nestling measurements and behavioral stages vary by 1 day or more for individuals within same brood because of hatching asynchrony.

Days 2–3: Eyes closed; dotting of primary-feather tract papillae present.

Day 4: Eyes closed; birds beat wings and pedal legs when disturbed; dark papillae of capital tract, spinal tract, alar tract, secondary-feather tract visible and continuous with primary tract; papillae of primaries ready to erupt from wing; papillae of rectrices visible. Ventral papillae visible in gular region and breast.

Day 5: Eyes starting to open (slits); capital-tract papillae prominent; spinal-tract papillae erupting in thoracic region; ventral-tract papillae almost ready to erupt; femoral- and alar-tract papillae visible; primary and secondary feathers have erupted (<1 mm in length); coverts erupting; rectrices almost ready to erupt; uropygial gland prominent.

Day 6: Eyes slits; birds pedal across ground beating wings and peeping when removed from nest. Most feather tracts have erupted from skin; primary P10 is 2 mm long; tip of upper mandible starting to darken

Day 7: Eyes still slits; P10 is 4 mm long; upper mandible darkening medially brownish black and egg tooth present, but light on edges; rectrices 1 mm; most feather tracts have ruptured skin, but feathers in sheaths.

Day 8: Eyes approximately a fourth open; P10 10 mm; upper mandible brownish black; secondary-coverts are 1 mm out of sheaths; spinal- and ventral-tract feathers starting to rupture feather sheaths.

Day 9: Eyes a third to half open; P10 14 mm; primaries and secondaries just starting to rupture feather sheaths; most contour feathers have ruptured feather sheaths.

Day 10: Eyes half open; P10 17 mm; wing-chord 35 mm long.

Day 11: Eyes two-thirds open; P10 21 mm and feather 6 mm out of sheath; wing 43 mm long; R1 13 mm and 2 mm out of sheath; body well feathered; legs and feet darkening.

Day 12: Eyes fully open, birds appear alert; P10 25 mm long and 9 mm out of sheath; wing 49 mm long; R1 17 mm; ventral apteria only area not well covered by feathers.

Day 13: P10 27 mm long and 10 mm out of sheath; wing 52 mm long; R1 20 mm long and 7 mm out of sheath; most contour feathers fully out of sheaths.

Day 14: P10 30 mm long and 10 mm out of sheath; wing 55 mm long; R1 23 mm long and 9 mm out of sheath.

Day 15: 32 mm long and 15 mm out of sheath; wing 58 mm long, R1 27 mm long and 14 mm out of sheath. Young birds typically capable of fledging.

Day 16: P10 35 mm long and 21 mm out of sheath; wing 62 mm long; R1 32 mm long and 17 mm out of sheath; egg tooth still visible; upper and lower mandibles grayish black.

Day 17: P10 37 mm long and 24 mm out of sheath; wing 64 mm long; R1 34 mm long and 19 mm out of sheath.

Day 18: P10 39 mm long and 27 mm out of sheath; wing length 66 mm; R1 37 mm long and 21 mm out of

sheath. Young fledged and capable of sustained flight of >200 m.

## PARENTAL CARE

Brooding. Primarily by female, but in instances where male incubated, male may share brooding duties with female. Following from Irwin 1985. Brooding decreases as nestlings develop; during first 3 d after hatching, attentive and inattentive periods averaged 4.4 min (range 1.0–11.5) and 6.8 min (range 3.8–13.0), respectively, with young brooded for 39.3% of observation period. Attentive periods averaged 5.3 min by fifth day and inattentive periods lengthened to average of 26.8 min. Brooding occupied only 19.7% of observation periods by fifth day. Brooding during day ended 8–9 d after hatching; at night, 9–11 d after hatching.

*Feeding.* Needs study. Both adults feed nestlings; carry insects to nest in bill (Irwin 1985). Feed nestlings by regurgitation for first 5 d after hatching (Wheelock 1904). In Humboldt Co., CA, adults averaged 8.7 visits/h (range 2–17; Irwin 1985).

Nest sanitation. No information.

COOPERATIVE BREEDING Not known to occur.

BROOD PARASITISM None reported.

## FLEDGLING STAGE

Departure from the nest. Needs study. Entire brood typically departs nest between days 18 and 21, on same day (Irwin 1985, Wolf 1991). Some young may return to nest to roost for 1–2 d. Mass at fledging approximates adult mass, but remiges and rectrices may be only 71% and 50% of adult lengths, respectively (BOW). Young are fully feathered and are strong fliers upon departure. Young birds 14 or 15 d of age may attempt to leave nest if startled, but do not fly well.

Association with parents or other young. Observations limited, but indicate that 1 to several young often disappear during first 3 d after fledging (Irwin 1985). After 3 d, young and adults may drift away from nest site. Young birds attain independence 7–11 d after fledging; female may leave brood earlier to incubate second clutch of eggs (Irwin 1985).

Ability to get around, feed, and care for self. Observations limited; young initially sit near each other in canopy of tree or bush; within 3 d are making short forays and flights from bush to bush. During this period adults and young remain near nest site. Young also start making foraging flights during this period (Irwin 1985). Young birds may be taught to capture prey by adult releasing live insects in front of them (Wheelock 1904).

#### IMMATURE STAGE

Little known. Juvenile birds tend to use closed habitats after attaining independence and until midwinter (Irwin 1985).

## **DEMOGRAPHY AND POPULATIONS**

#### MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Capable of breeding during first breeding season after hatching. Of 46 individuals sighted in their first spring after hatching, 31 were breeders, 15 presumed floaters (Schroeder 1985). In Santa Clara Co., CA, interval between fledging of first brood and laying of first egg of second clutch averaged 12.4 d (range 7–18; n = 8; Wolf 1991); in Humboldt Co., CA., 10 d (range 1–23; n = 11; Irwin 1985).

Annual and lifetime reproductive success. In Santa Barbara Co., CA, hatching success averaged 86.5%; of young hatched, 84.6% fledged successfully. Fledging success averaged 3.3 young/nest; nest success (production of >1 fledgling) rate averaged 66% (n =745; Schroeder 1985). In Santa Clara Co., CA, 91.4% of laid eggs hatched; 67% of those young fledged successfully. Fledging success averaged 2.88 young/ nest, and nest success averaged 59% (n = 25; Wolf 1991). In Humboldt Co., CA, average of 3.3 young/ nest (n = 21 successfully fledged). In Trans-Pecos, TX, hatching success 92%; 76.8% of young fledged successfully; fledging success averaged 2.52 young/ nest and nest success averaged 71% (n = 21; Ohlendorf 1976). Postfledging survival rates for this species are unknown.

No data on marked birds, but estimates of lifetime reproductive success, based on expected reproductive output and estimated annual mortality rates, indicate that males produce minimum of 4.13 male fledglings in their lifetime and that females produce minimum of 5.14 female fledglings. These numbers show the number of same sex fledglings an adult must produce to replace itself in the breeding population (Schroeder 1985).

Number of broods normally reared per season. Typically 1–2 broods raised per season; on rare occasions, 3 (Irwin 1985, Schroeder 1985, Wolf 1991). In Santa Barbara Co., CA, second clutches were reported at approximately 62% of nest sites surveyed (n = 270; Schroeder 1985). In Santa Clara Co., CA, 66% of breeding pairs laid 2 clutches of eggs in a season (n = 21; Wolf 1991) and in Humboldt Co., CA, 55% of breeding pairs laid 2 clutches of eggs and 5% (1 pair) laid third clutch (n = 20; Irwin 1985).

## LIFE SPAN AND SURVIVORSHIP

Life span not known. Survival rates for breeding phoebes in Santa Barbara Co., CA, estimated to be 74.9%/yr for females (n = 155) and 67.4%/yr for

males (n = 117), with combined average rate of 71.8% for both sexes (n = 278; Schroeder 1985). Survival table generated from these data for breeders (those that attempt breeding at least once) estimates that approximately 31.5% of females and 20.6% of males survive into their fifth breeding season, and 7.4% of females and 2.9% of males survive into their tenth breeding season (Schroeder 1985). These estimates assume that survival rate is independent of age. Records show that males and females are capable of breeding at least 5 and 6 yr, respectively.

#### DISEASE AND BODY PARASITES

Diseases. No information.

Body parasites. Adults. Needs study. In a Santa Barbara Co., CA, population, only 5 of 200 adults inspected had any visible ectoparasites, and none were heavily infested. Of those 5, 1 had feather lice (Mallophaga); 1 had a few feather lice and a ked fly (Diptera: Hippoboscidae); 2 had sticktight fleas (Hectopsylla psittaci), a recently introduced Neotropical species; and 1 had a single ked fly.

NESTLINGS. Heavy infestations of argasid tick (Argas coolyei) larvae and dermanyssid mites (Ornithonyssus sylviarum) caused death in approximately 9% of nestlings in Trans-Pecos, TX (Ohlendorf 1976). Mortality caused by infestations of argasid tick larvae and dermanyssid mites for young Black Phoebes in nests closely associated with nests of Cliff Swallows (Hirundo pyrrhonota). Schroeder (1985) found ectoparasites on only 11% (49/518) of nestlings examined, and only 5 nestling deaths were suspected to be caused by ectoparasite infestations; overall nestling mortality attributed to ectoparasites was estimated as <1%. Wolf (1991) attributed no nestling mortality to ectoparasite infestations. Wheelock (1904) indicated that nestling phoebes are routinely infested with various ectoparasites that cause significant mortality.

## CAUSES OF MORTALITY

Few data for adults. In Santa Barbara Co., CA, average mortality, estimated from return rates for 278 previously banded breeders (155 females, 117 males) between 1975 and 1980, was 28.2%/yr overall (25.1% for females and 32.6% for males; Schroeder 1985). Breeders rarely change sites or mates; thus it was assumed that failure of banded breeder to return to previous year's site (or its replacement by another individual) represented death of former. These estimates were corrected for known cases of interseasonal movement of nesting location (7 instances) and later reappearance of breeders from 1 to several years later (2 instances).

In Santa Barbara Co., CA, egg losses (271 of 2,012 eggs laid) were attributed to variety of causes: abandonment (26%), fallen nests (16%), addled eggs (16%), eggs missing for unknown reason (13%), suspected interference by nest competitors (9%),

sterility (7%), human interference (7%), broken or stuck (4%), known embryonic death (1%), and predation (1%; Schroeder 1985). Nestling losses (337 of 2,049 nestlings hatched) in the same population were attributed to desertion (36%), unknown causes (30%), fallennests (13%), starvation (8%), human caused (7%), suspected ectoparasites (2%), parental death (1%), and known predation (1%).

Egg losses (10 of 117 eggs laid) in central California (Santa Clara Co.) were attributed to sterility (30%), human interference (30%), embryonic death (20%), and predation (20%). Nestling losses (35 of 107 nestlings hatched) were of much greater importance to overall productivity; predation accounted for 83% of total nestling losses. Nestlings were also lost to abandonment or exposure (14%) and because of premature nest departure (2.9%; Wolf 1991).

In Humboldt Co., CA, weather was important factor in determining reproductive success (Irwin 1985). In 1977, sustained rainfall during breeding season apparently resulted in successful fledging of only 1 of 3 broods; successful brood was reared on territory that included fish hatchery where adults fed nestlings fish (steelhead [Salmo gairdneri], king salmon [Oncorhynchus tshawutcha], and silver salmon [O. kisutch]) fingerlings. Autopsies on nestlings from the other 2 broods indicate that these birds probably died from starvation. Following year, between 21 Mar and 1 May 1978, during period of sustained heavy rainfall, only 1 active nest was found. Parental death at this nest resulted in egg failure. Emaciated corpse of the incubating female was found on ground near nest. Other pairs delayed laying their first clutches by 22–59 d from previous year's laying dates.

In Trans-Pecos, TX, egg losses as a percentage of total eggs laid (6 of 75 eggs laid) were attributed to sterility (1.3%), human interference (2.7%) and unknown causes (4%). Nestling losses as a percentage of total nestlings hatched (16 of 69 nestlings hatched) either were of unknown origin (14%) or were caused by ectoparasites (8.7%; Ohlendorf 1976).

#### RANGE

Initial dispersal from natal site. In Santa Barbara Co., CA, juveniles during first autumn and winter were observed on average 2.0 km (range 0.7–41.4, n = 10) from hatching site (Schroeder 1985). Of first sightings of birds after their first winter, males averaged 4.4 km (0.5–20, n = 7) from hatching site, females 6.4 km (0.4–34.4, n = 14). Of individuals observed during first breeding season after hatching, males averaged 1.2 km (n = 5, range 0.5–20 km), females 4.9 km (n = 11, range 0.4–34.4 km) from hatching sites. Individuals attempting to breed in first year after hatching had average natal dispersal distances of 1.1 and 7.9 km for males (n = 4, range 0.5–20 km) and females (n = 9, range 2.9–34.4 km), respectively (Schroeder 1985).

Fidelity to breeding site and winter home range. In Santa Barbara Co., CA, 96% of 115 pairs observed for >2 yr moved <0.3 km (Schroeder 1985). Only 1 of 61 (1.6%) females observed dispersed >0.3 km; 4 of 51 (7.8%) males dispersed >0.3 km. Three breeders (all females) changed breeding sites within breeding season. Further evidence of strong breeding-site tenacity is offered by release of birds removed from territories earlier in season (at least 30 d in captivity; Schroeder 1985): 37% returned and bred the following season at or near their previous site, and 3 of 11 females released at foreign sites 6.8, 25.6, and 31.7 km, respectively, away from former breeding site returned to their original site the next season to breed.

Home range. Breeding territories are small (0.5–0.8 ha); activity largely confined to area within 40–50 m of nest (Verbeek 1975a, Irwin 1985). In Humboldt Co., CA, home ranges of nonbreeding birds were typically 9–11 ha (Irwin 1985).

#### POPULATION STATUS

Numbers. Breeding Bird Survey (BBS) data indicate densities of <1 bird/route over entire species range, excluding California. In California, densities vary from 1 to 10 birds/route; highest densities found in Central Valley and coastal region. Breeding densities can sometimes approach 5 or 6 pairs/km if nest sites exist in otherwise suitable habitats.

*Trends*. BBS data indicate significant increasing trend (p < 0.01) for U.S. that averaged 1.8%/yr for period 1966–1994. Most states and provinces show significant increases from 1966 to 1979 and significant declines from 1980 to 1994.

#### POPULATION REGULATION

Not well understood; few data. Density-independent factors such as sustained periods of heavy rain may have significant impact on breeding productivity and mortality of breeders in extreme northern part of Black Phoebe's range (n. coastal California; Irwin 1985). Farther south, however, weather appears to have little or no effect on breeding productivity (Schroeder 1985, Wolf 1991). Food limitation also seems unlikely (in all but northernmost part of range), because of sizes of home ranges, spacing, and generalist foraging characteristics of the species. Suitable nest sites may be major factor limiting breeding numbers. In many areas, new human-made structures may support range expansion of the species where suitable nest sites did not previously exist (Grinnell and Storer 1924, Schroeder 1985, Wolf 1991). Significant floater population apparently exists some years, and serial replacements often occur at active nest sites when 1 or both breeding adults are removed (Schroeder 1985). Floaters of both sexes detected; replacement rate 85.7% (n = 7) and 43.8% (n = 32) for males and females, respectively. No replacement or encroachment where territory holders were not removed from breeding site (Schroeder 1985).

Interestingly, breeding densities and occupancy rates of active sites do vary from season to season. Occupancy rates of 45 core nest sites monitored intensively for 5 yr varied from 75.6 to 93.4%. Data suggest that floater population is also quite variable from year to year (Schroeder 1985).

## **CONSERVATION AND MANAGEMENT**

#### **EFFECTS ON HUMAN ACTIVITY**

In many areas, human activity may benefit this species, but continued destruction of riparian habitat and water use practices that divert water from natural drainages are major concerns; both practices reduce suitable habitat for breeding and for foraging. Species is year-round resident in many areas, and these practices could result in reductions of resident populations. Tolerant of humans and often breeds on occupied dwellings; construction of culverts, bridges, buildings, etc., near water has provided additional nest sites for species (see Habitat, above). Construction of human-made lakes and canals has also provided habitat for breeding.

#### MANAGEMENT

Not currently a species of management concern, but conservation of riparian systems will have positive impact on the species.

## **APPEARANCE**

MOLTS AND PLUMAGES

*Hatchlings*. Body lightly covered with medium gray down (neossoptiles); head more heavily covered. At hatching, nestlings have 230–266 neossoptiles in 18–21 feather tracts (Collins and Keane 1991).

Juvenal plumage. From Ridgway 1907 and Brewster 1879. Similar to Definitive Basic (adult) plumage except black areas darker than in adult; feathers of lower back, lower scapulars, rump, and uppertail-coverts indistinctly tipped with pale brownish; posterior margin of black on breast, more or less strongly washed with brownish or rusty fulvous; wing-coverts, primaries, and secondaries tipped with cinnamon or light rusty; white of underparts suffused along border with brown or rusty. Tips of Juvenal rectrices also less rounded than those of adult (Pyle et al. 1987).

*Basic I plumage*. Prebasic I molt incomplete; includes body contour feathers and some to all greater primary-coverts, but not Juvenal remiges and rectrices (Bent 1942, Pyle et al. 1987). Molt occurs Jun–Sep (see Fig. 4).

Basic I plumage similar to Definitive Basic (adult) plumage but retained Juvenal wing-coverts buffy

cinnamon and retained Juvenal remiges and rectrices brownish rather than grayish black (Bent 1942, Pyle et al. 1987).

*Definitive Basic plumage*. Definitive Prebasic molt complete; occurs Jul and Aug (see Fig. 4; Bent 1942).

Upperparts plain dark sooty slate; head darker (almost black); back, scapulars, rump, and uppertailcoverts brownish slate. Flanks, thighs, undertailcoverts, and belly white; white on belly forms inverted V as it extends up onto lower breast. Undertailcoverts frequently streaked mesially (more or less broadly) with dusky (all specimens from central, e., and s. Mexico, and some from Baja California); median wing-coverts sooty gray, broadly tipped or terminally margined (more or less distinctly) with brownish gray; secondaries sooty gray, edged with pale brownish gray or dull white; remiges sooty gray, inner webs of remiges edged with pale brownish gray; axillars and underwing-coverts dark sooty gray or brownish slate, their outer webs mostly white and inner webs extensively white at tip; rectrices sooty gray, outer web of outermost rectrix (R6) edged (more or less broadly) with white (Ridgway 1907).

Aberrant plumages. Leucism described in 1 juvenile (U.S. National Museum specimen number 76,546) from Stockton, CA (Ridgway 1878). Prevailing color very pale pearl gray, fading to white on abdomen and lining of wing. Wing-coverts tipped with creamy buff, forming 2 distinct narrow bands. Specimen is full-grown juvenile, as shown by buff wing-bands and texture of feathers. Slight indications of normal plumage seen in small black spot just above posterior angle of right eye and several black feathers among lesser wing-coverts.

## BARE PARTS

*Bill and gape.* HATCHLINGS. Bill flanges creamy yellow; mandibles light yellow; gape bright yellow orange. Nares oriented toward tip of mandible; egg tooth situated approximately 0.5 mm from tip of upper mandible (Wolf 1991).

ADULTS. Bill blackish, more brown toward base, with small hook at tip; gape chrome orange (Wolf 1991; color names from Smithe 1975). Nares are oval, and rictal bristles are found on both sides of both mandibles.

Iris. Brown.

*Legs and feet*. Hatchlings: tarsi orange flesh; claws light yellow. Adults: brownish black.

## **MEASUREMENTS**

LINEAR

See Table 1. Total length: males, mean 165 mm (range 152–181, n = 16); females, mean 160 mm (range 147–176, n = 16; Ridgway 1907).

MASS

18

Body mass: males, mean 19.0 g (range 15.9-20.4, n = 14); females, mean 17.5 g (range 14.7–22.5, n = 45;

## PRIORITIES FOR FUTURE RESEARCH

Many aspects of the biology of this species remain unknown. With today's rapidly changing landscape, studies that examine the effects of the alteration of riparian systems on local populations through the annual cycle should be a priority. The nature and extent of postbreeding movement and migration are also poorly understood. Little is known about the population dynamics and demography of this species. Finally, as with most species of animals, there are few data on physiology, energetics, and nutritional requirements.

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**Table 1**. Linear measurements (mm) and mass (g) of Black Phoebe. Data shown as mean ± SD (range; n). Data from BOW and Coyote Creek Riparian Station; U.S. National Museum.

Mass Adult male Adult female	19.0 ± 1.34 (15.9–20.4; 14) 17.5 ± 1.41 (14.7–22.5; 45)
HY female*	$16.2 \pm 0.71 \ (15.3 - 17.0; 4)$
Wing-chord	
Adult male	$88.8 \pm 4.40$ (76.0–98.0; 37)
Adult female	$84.9 \pm 3.02$ (78.0–93.0; 65)
HY female*	$83.8 \pm 2.75$ (81.0–87.0; 4)
Rectrix	
Adult male	80.4 ± 3.91 (73.5–88.0; 23)
Adult female	$76.2 \pm 3.96 (70.0 - 84.0; 24)$
riddit iciiaic	70.2 ± 5.50 (70.0-64.0, 24)
Tarsus	
Adult male	$17.5 \pm 2.34$ (13.6–22.2; 23)
Adult female	$17.1 \pm 1.77 (12.4 - 19.3; 24)$
Middle toe	
Adult male	$10.9 \pm 1.44 (7.8-13.1; 14)$
Adult female	$10.9 \pm 1.44$ (7.0–13.1, 14) $10.4 \pm 1.21$ (8.2–12.4; 11)
riddit iciliaic	10.4 ± 1.21 (0.2–12.4, 11)
Exposed culmen	
Adult male	$11.4 \pm 0.53$ (10.5–12.6; 23)
Adult female	$10.9 \pm 0.67 (9.4 - 12.0; 24)$
*HY = Hatch-year.	

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