



COMMENTARY

eBird records show substantial growth of the Allen's Hummingbird (*Selasphorus sasin sedentarius*) population in urban Southern California

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ABSTRACT

The sedentary subspecies of Allen's Hummingbird (*Selasphorus sasin sedentarius*) was originally endemic to the Channel Islands off the coast of Southern California, but it colonized the mainland at the Palos Verdes Peninsula sometime before 1966. In the decades since, its population has expanded in Southern California. I tracked its growth using eBird checklists. The mainland range of *S. s. sedentarius* has grown from ~ 70 km² in 1970 to $\sim 13,000$ km² today, representing an increase of $\leq 23\%$ in the total range of the species as a whole. Its main habitat within Los Angeles, Orange, San Diego, and western Riverside counties is urban parks, gardens, and campuses. The range expansion of *S. s. sedentarius* seems to be driven by food availability—although, given that it is found in urban habitats that the other subspecies, *S. s. sasin*, does not seem to utilize, a subtle change in the ecology of the 2 subspecies is also implied. Analysis of eBird data suggests that breeding *S. s. sedentarius* met *S. s. sasin* near Santa Barbara perhaps as early as 2005, raising the possibility of a new zone of intergradation of the forms. Given that *S. s. sedentarius* has a substantially longer breeding season and, thus, a potential fecundity advantage over *S. s. sasin*, it is possible that the island *S. s. sedentarius* will outcompete the mainland subspecies. Partners in Flight has Allen's Hummingbird on its 2016 watchlist because analysis of Breeding Bird Survey data suggest that this species has declined by 83% since 1970. This estimate is not credible for 3 reasons: it implies a 1970 population of 10 million Allen's Hummingbirds within the restricted range of this species; there are no suggestions that *S. s. sasin* has become extirpated anywhere throughout its historical range; and the geographic range occupied by *S. s. sedentarius* has grown by $\sim 700\%$ in the same period. I found eBird to be a useful new source of data for monitoring urban birds such as *S. s. sedentarius*.

Keywords: conservation biology, *Eucalyptus*, invasion, Los Angeles, *Tecoma capensis*, urban ecology

Registros de eBird muestran un crecimiento sustancial de la población de *Selasphorus sasin sedentarius* en las zonas urbanas del sur de California

RESUMEN

Las subespecie sedentaria *Selasphorus sasin sedentarius* era originalmente endémica de las islas del Canal en la costa del sur de California, pero colonizó el continente en la península de Palos Verdes en algún momento antes de 1966. Desde entonces su población se ha expandido en el sur de California. En este estudio hago un seguimiento de su crecimiento usando listas registradas en eBird. El área de distribución geográfica de *S. s. sedentarius* ha aumentado de aproximadamente 70 km² en 1970 a cerca de 13000 km² actualmente, lo que representa un incremento de hasta 23% en el área geográfica total ocupada por la especie. Su hábitat principal en los condados de Los Angeles, Orange, San Diego y Riverside occidental son parques urbanos, jardines y campus universitarios. La expansión geográfica de *sedentarius* parece ser impulsada por la disponibilidad de alimento, aunque debido a que se encuentra en hábitats urbanos que *S. s. sasin* no parece utilizar, es posible que exista un cambio sutil en la ecología de las dos subespecies. Los datos de eBird sugieren que individuos reproductivos de *S. s. sedentarius* se encontraron con *S. s. sasin* cerca de Santa Barbara tal vez desde 2005, abriendo la posibilidad de que se haya formado una nueva zona de hibridación entre las dos formas. Debido a que *S. s. sedentarius* tiene una temporada reproductiva sustancialmente más larga y por lo tanto una potencial ventaja reproductiva sobre *S. s. sasin*, es posible que la subespecie insular supere competitivamente a la subespecie continental. Partners in Flight tiene a *S. sasin* en su lista de observación de 2016 porque sus análisis de datos de censos de aves reproductivas sugieren que esta especie ha tenido un declive poblacional del 83% desde 1970. Este estimado no es creíble por tres razones: implica que la población de *S. sasin* en 1970 era de 10 millones en el área restringida de la especie; no hay datos que sugieran que *S. s. sasin* haya sido extirpado en ningún lugar en su distribución geográfica histórica; y el área geográfica ocupada por *S. s. sedentarius* ha crecido cerca de 700% en este mismo periodo de tiempo. eBird es una nueva fuente de información útil para monitorear aves urbanas como *S. s. sedentarius*.

Palabras clave: biología de la conservación, ecología urbana, *Eucalyptus*, invasión, Los Ángeles, *Tecoma capensis*

INTRODUCTION

Hummingbirds are charismatic, and thus species endangered by human activity can be ambassadors for conservation. Hummingbird species of conservation concern include the Chilean Woodstar (*Eulidia yarrellii*), which has suffered a severe population crash in recent decades, such that it is in imminent danger of extinction (Estades et al. 2007, Estades and Aguirre 2010, Clark et al. 2013, van Dongen et al. 2013). Humans are likely to blame, although the exact mechanism is unknown (Estades et al. 2007). Human-caused climate change is a clear threat to species such as the Inagua Hummingbird (*Calliphlox lyrura*; Feo et al. 2015), which exclusively occupies low-lying island habitats that could become inundated by sea-level rise.

Although human activities potentially imperil species such as the Chilean Woodstar or Inagua Hummingbird, human activities are instead beneficial for some species, such as by providing a resource subsidy (Chamberlain et al. 2008). Perhaps the most famous example from among hummingbirds is Anna's Hummingbird (*Calypte anna*). This species was once restricted to chaparral and related habitats within the California biogeographic province, prompting Woods (1927) to argue it should have the common name "California Hummingbird." Today this name would be a misnomer. Its range has greatly expanded over the past several decades (Zimmerman 1973) in apparent response to winter resources (gardens and feeders), such that it now breeds as far north as British Columbia and as far east as west Texas (Clark and Russell 2012), and there are new reports of breeding in Idaho (Rudeen and Bassett 2016). Here, I document another dramatic range expansion presently underway: that of the sedentary (nonmigratory) Allen's Hummingbird (*Selasphorus sasin sedentarius*), which was once endemic to California's Channel Islands (Grinnell 1929).

My personal observations, beginning in 2013, suggested that Allen's Hummingbirds in Riverside, California, were prevalent at backyard feeders and on the University of California (UC) Riverside campus. Resident birders estimate that they arrived as a breeding species on campus in approximately 2006 (N. Ellstrand personal communication); prior to that, any *Selasphorus* was as likely a migrating Rufous Hummingbird (*S. rufus*) as an Allen's (Lee 1995). Today the situation has changed, and the Rufous are now hard to pick out from the more numerous Allen's.

The source of this urban population is known. In the early 1970s, Shirley Wells studied hummingbirds on the Palos Verdes Peninsula south of Los Angeles. Wells and Baptista (1979) state:

There are no previous breeding [mainland] records for the Allen's Hummingbird south of Ventura County. On 2 June 1966 Wells noticed

two fledgling Allen's Hummingbirds being fed by adults near San Pedro on the Palos Verdes Peninsula.... [In 1967] *S. sasin* was found to be a common breeding bird on the peninsula.

This population was *S. s. sedentarius* and had either recently colonized the mainland from the Channel Islands or had escaped the notice of prior ornithologists. This population, localized and small in 1970 (Bradley 1980, Allen et al. 2016), has grown in the decades since.

These observations of an apparently robust, growing urban population (Allen et al. 2016) are belied by the recent assessments of bird conservation organizations. Audubon's assessment of climate-change impacts on birds (Langham et al. 2015) suggests that climate change will push Allen's Hummingbird breeding range out of Southern California in coming decades. This analysis assumes that the birds' range is sensitive to local climate, rather than to resources. The report "State of North America's Birds 2016" (NABCI 2016) places Allen's Hummingbird on its watchlist, and the U.S. Fish and Wildlife Service (USFWS) watchlist includes it as a bird of conservation concern (USFWS 2008). Both these watchlists derive their underlying assessments from Partners in Flight (PIF). The 2016 version of PIF's assessment of Allen's Hummingbird suggests an 83% loss, defined as "percentage of global population lost over the past 44 years" starting in 1970 (PIF 2016). It also estimates the current population of the species at 1.7 million and states that 96% of Allen's Hummingbirds winter in Mexico, which means that PIF estimates the nonmigratory *S. s. sedentarius* to constitute 4% of the total population. The 2016 PIF assessment relies exclusively on Breeding Bird Survey (BBS) data (K. Rosenberg personal communication).

The population trends suggested by PIF's analyses would be alarming if true, but they are at odds with the aforementioned observations of ornithologists and birders in Southern California (Allen et al. 2016). Therefore, the purpose of this article is to assess the population status of Allen's Hummingbird in Southern California. A new citizen science initiative, eBird, which allows anyone to upload checklists of observed birds (Sullivan et al. 2009, eBird 2012), provides a new resource to document the distribution of birds. Since birders tend to live in cities, eBird has dense, year-round sampling in areas with high human population density, such as the greater Los Angeles area. If the Allen's Hummingbird population is dramatically growing in size and expanding its range, I predicted that this pattern would be readily apparent in eBird's data, even with unsophisticated analytical techniques. If instead the population has shrunk to one-sixth its original size, as BBS analyses claim (Sauer et al. 2013), I predicted that this would produce a range contraction visible in eBird data, in relation to the historical distribution of this species

provided by Grinnell and Miller (1944). This is because the loss of 5 of every 6 individuals of a species is substantial and should result in local extirpation as populations occupying marginal habitat are completely extirpated.

METHODS

Subspecies

Allen's Hummingbird has 2 subspecies, *S. s. sasin* and *S. s. sedentarius*. *Selasphorus s. sasin* is migratory and breeds in a narrow habitat strip along the California coast. Its historical breeding range was from somewhere between Santa Barbara and Ventura (Grinnell and Miller 1944) to somewhere near the Oregon border (Howell and Gardali 2003, Clark and Mitchell 2013). This subspecies migrates north out of Mexico into California as early as January (Phillips 1975). In the San Francisco Bay Area, breeding males arrive on their courtship territories in late February or early March (Pitelka 1951, Clark and Mitchell 2013). Breeding ends, and males abandon their courtship territories, around the first week of June, and the birds then head southward, with males departing first. Diminishing numbers of females and hatch-year birds may be seen in the vicinity of breeding areas through July and, sometimes, early August (Phillips 1975, Howell and Gardali 2003)—although, if not in the hand, these birds are often not distinguishable from migrating Rufous Hummingbirds (Stiles 1972). Rather than migrating, a small number of *S. s. sasin* overwinter in places such as the botanical gardens at UC Berkeley (Ortiz-Crespo 1969, 1971), so checklists from the range of *S. s. sasin* occasionally contain reports of individual Allen's Hummingbirds at any time of year.

Selasphorus s. sasin is diagnosable from *S. s. sedentarius* only in the hand, using small mensural differences (Stiles 1972). As a result, all references to *S. s. sasin* and *S. s. sedentarius* throughout this article are assumptive rather than definitive. For example, a male holding a courtship territory in Riverside in October is assumed to be *S. s. sedentarius*, because this observation is inconsistent with what is currently known about the biology of *S. s. sasin*. References to "Allen's Hummingbird" are inclusive of both subspecies.

Analyses

On August 22, 2016, I downloaded the Christmas Bird Count (CBC) data for Allen's Hummingbird for all of California (from <http://netapp.audubon.org/CBCObservation/>). I downloaded eBird data (<http://ebird.org/>) on August 19, 2016, for Allen's Hummingbird. I disregarded data coded "Rufous/Allen's" (doing so seemed unlikely to bias the analyses described below). I analyzed eBird data from the counties of San Luis Obispo, Santa Barbara, Ventura, Los Angeles, Kern, San Bernardino,

Riverside, Orange, San Diego, and Imperial (hereafter referred to collectively as "Southern California"), for checklists across each "week" of the year (an eBird-year has 48 "weeks") for dates between January 1970 and August 2016. I compared this dataset to similar data from the Bay Area (comprising Alameda, Contra Costa, Marin, San Francisco, San Mateo, Santa Clara, and Santa Cruz counties) because these counties fall within the *S. sasin* breeding range and are densely populated (and thus have many eBird checklists). Because older eBird data contain few observations, I dropped data for weeks that had <10 checklists, which only affected weeks before 1990 (Southern California) or 2000 (Bay Area) (Figure 1D). The eBird documentation recommends analyzing the frequency of a species within checklists because this measure is relatively insensitive to the dramatic changes in sample sizes associated with the growth of data deposited in eBird over time. I initially computed a single yearly average of each weekly bin and regressed the frequency of Allen's Hummingbirds in checklists against time for dates spanning 1990–2016.

I then conducted a series of slightly more nuanced analyses, to address limitations or potential artifacts in the data. It became clear that data before 1990 for Southern California are sparse and variable. For instance, the years 1972 and 1973 are obvious outliers because they contain a substantial fraction of their checklists from the Channel Islands (where *S. s. sedentarius* is common) that clearly bias the data for these years. Thus, the next analyses only considered data from the relatively well-sampled 30 yr period beginning in 1987.

Some of the birds observed in Southern California will be *S. s. sasin*, which migrate northbound through the sampled region during January–March, and southbound during May–July (Phillips 1975, Howell and Gardali 2003, Clark and Mitchell 2013). Therefore, I examined weeks 29 (beginning August 1) through 47 (beginning December 15), which should have relatively few observations of *S. s. sasin*; and I examined week 48 separately, since week 48 had better sampling than other individual weeks, likely because it corresponds to the most active part of the CBC.

The instructions for eBird caution that its frequency measure is misleading when many birders chase the same extralimital individual, because the same bird is repeatedly reported as present in frequency analyses. Repeated tabulation of the same individuals will result in a large number of checklists with numerical abundances of $N = 1$ bird. To test this extralimital-individual hypothesis on Southern California lists, I calculated the average yearly abundance (including only lists reporting Allen's Hummingbirds as present), as well as the abundance from only weeks 29–47, and for week 48, and examined by eye whether they clustered around 1.

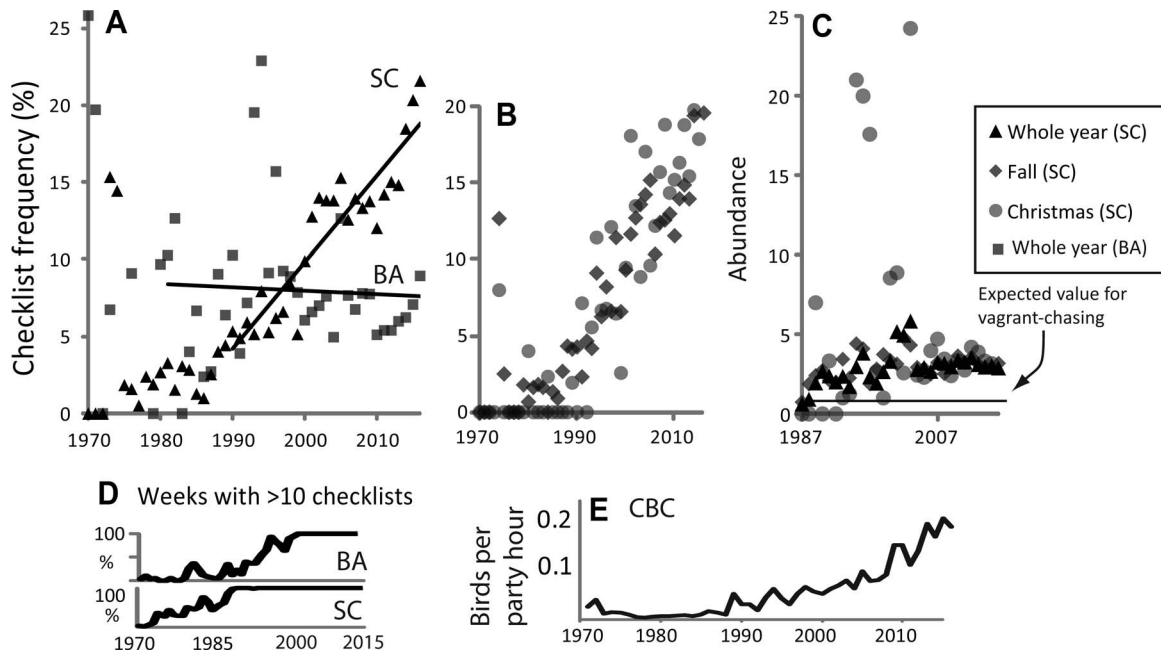


FIGURE 1. Data from eBird checklists reporting Allen's Hummingbird in Southern California (SC, triangles) and the San Francisco Bay Area (BA, squares), USA. Southern California comprises the counties of San Luis Obispo, Santa Barbara, Ventura, Los Angeles, Kern, San Bernardino, Riverside, Orange, San Diego, and Imperial; and the Bay Area comprises Alameda, Contra Costa, Marin, San Francisco, San Mateo, Santa Clara, and Santa Cruz counties. **(A)** Comparison of whole-year checklist frequency for Southern California and the Bay Area. **(B)** Fall (diamonds, August 1–December 15) and Christmas (circles, last week of December) frequency for Southern California. **(C)** Abundance of Allen's Hummingbird in checklists within Southern California. **(D)** Completeness of the weekly sampling across the Bay Area and Southern California within eBird. **(E)** Christmas Bird Count (CBC) data for all of California, as downloaded directly from <http://netapp.audubon.org/CBCObservation/> (accessed August 22, 2016).

I examined the spatial extent of the data to identify when Allen's Hummingbirds reached particular locations in Southern California. Within eBird's mapping feature, I mapped, by year, records of Allen's Hummingbirds during August–December in Southern California, when most *S. sasin* are in Mexico. I searched for noteworthy cities and the year in which Allen's Hummingbirds were reported for the first time, and every year they were reported thereafter. Finally I developed, as a thought exercise, approximate bird abundances, by using occupied surface area as a proxy for population size.

Because eBird images do not convert to black and white very well, the images presented in the figures were manipulated with the “replace color” function in Photoshop to enhance contrast.

RESULTS AND DISCUSSION

The presence of Allen's Hummingbird in eBird checklists in Southern California has grown dramatically between 1970 and 2016. Before 1990, when eBird records are sparse, the frequency remains below 5% except in 1972 and 1973, when an abnormally large number of lists from the Channel Islands were included (Figure 1A). Beginning in 1990, there are >10 checklists per week over the

entire year (Figure 1D), which means that annual variation in frequency begins to be relatively well described. After 1990, there is a steep (ordinary least squares, $r^2 = 0.84$, $n = 27$ yr) increase in the proportion of checklists reporting Allen's Hummingbird, such that today, well over 20% of Southern California eBird checklists report Allen's Hummingbird. This effect is not driven by migratory Allen's Hummingbirds, which may be present in the months of January–July; the whole-year pattern is essentially identical to data from August–December (weeks 29–47) as well as the CBC (Figure 1B, 1E). This frequency is averaged for all of Southern California and thus is diluted by checklists for localities in which Allen's Hummingbird is still not reported, such as Imperial County. If the analysis were restricted to checklists from just Los Angeles or Orange counties, the fraction of lists reporting Allen's Hummingbirds would be much higher.

This pattern is not driven by birders repeatedly chasing the same single, extralimital individual Allen's Hummingbird. Relative abundance across all checklists is initially near zero in 1987, but after 1992 all checklists reporting Allen's Hummingbirds have an average abundance of around 3 or 4 birds (i.e. >1, and some average abundances exceed 20; Figure 1C).

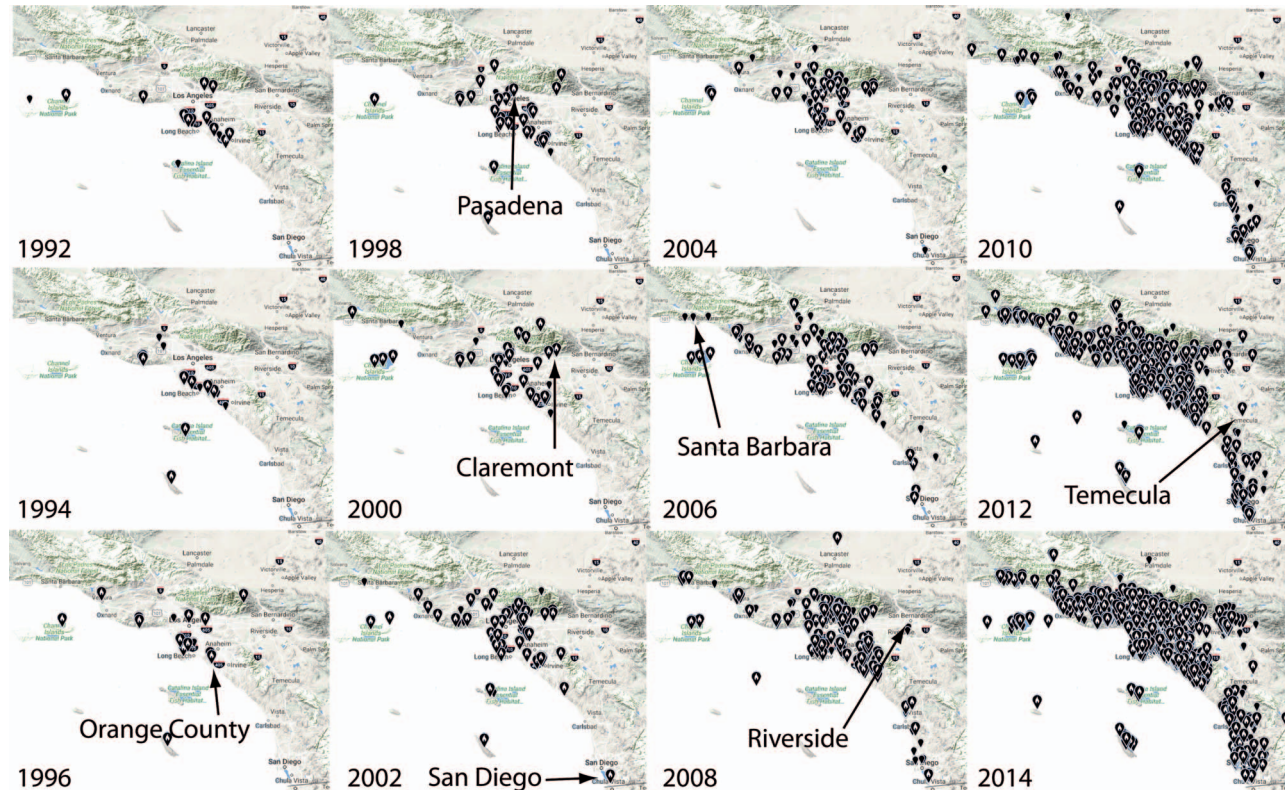


FIGURE 2. Maps showing locations of eBird records of Allen's Hummingbird in the Los Angeles Basin, California, USA, and surrounding areas, August–December. City names indicate apparent first detection of a resident population of *S. s. sedentarius* (note: only even-numbered years are shown; first detection was 2001 for San Diego, and 2005 for Santa Barbara). Images provided by eBird (<http://www.ebird.org>) and created August 19, 2016.

Data from the Bay Area do not show an increase in frequency similar to that observed in Southern California. Frequency of Allen's Hummingbird in Bay Area eBird checklists is highly variable before 1995, corresponding to low sample sizes of checklists. After 1995, the yearly average frequency of Allen's Hummingbird is $\sim 8\%$ and has remained approximately constant (Figure 1A).

Mapping the spatial extent of the eBird data for just the fall (Figure 2) reveals that during 1990–1995, Allen's Hummingbirds are reported from just a coastal strip spanning Los Angeles, Long Beach, Palos Verdes, Santa Monica, and Malibu. They then appear in Orange County (1996), Pasadena (1998), Claremont (2000), San Diego (2001), Santa Barbara (2005), Riverside (2008), and Temecula (2012). These patterns are consistent with trends reported in Allen et al. (2016), Unitt (2004), and a new report that Allen's Hummingbirds now breed in Baja California, Mexico (Erickson 2016). There are not yet any reports of Allen's Hummingbirds breeding in urban Coachella Valley, nor are there yet significant reports from north of the transverse ranges north of Los Angeles.

Growth in Distribution of *S. s. sedentarius*

Selasphorus s. sedentarius is currently present on the mainland in an area approximately spanning a triangle between the cities of Santa Barbara, San Diego, and Riverside, comprising $\sim 13,000$ km² of land—although within it, natural areas such as the Cleveland National Forest contain largely unsuitable habitat. As a thought exercise, I assumed that the birds currently actually occupy only half this area, $\sim 6,500$ km². The Palos Verdes Peninsula that was the source in 1970 is ~ 70 km² (or $\sim 1\%$) of this total area. In 45 yr, *S. s. sedentarius* has experienced 9,200% growth in Southern California, not including the Channel Islands; or 663% growth in area if the 900 km² of the Channel Islands is included. Assuming that *S. s. sasin* lives in a strip of habitat that is 920 km long (distance from Santa Barbara to Oregon) and 30 km wide (Figure 3A) and has not changed in the past 45 yr, *S. s. sasin* occupies 27,600 km². An additional 6,500 km² represents an increase of 23% in the land-space occupied by the entire species.

While it is difficult to know the density on a broad scale, PIF estimates a global population of 1.7 million birds. As a

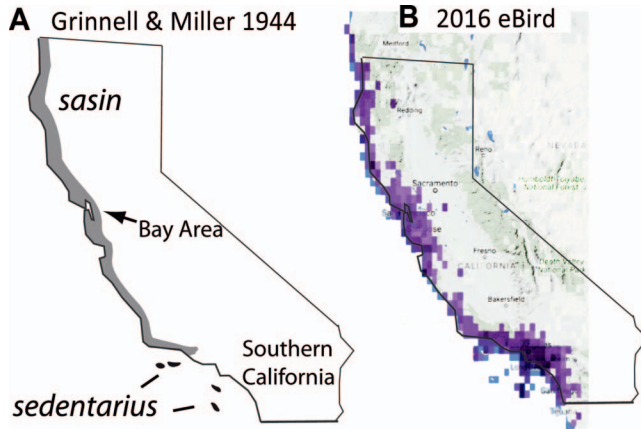


FIGURE 3. (A) Range map of Allen's Hummingbird in 1944, traced from Grinnell and Miller (1944; not including point records). (B) Map showing eBird occurrences of Allen's Hummingbird in February–June 2016. Darker shade indicates bird presence in a greater proportion of checklists. Images provided by eBird (<http://www.ebird.org>) and created October 13, 2016.

thought example only, applying that population estimate to my estimated range of 27,600 km² yields a rough estimate of 60 birds km⁻². This estimate seems reasonable for high-quality habitat such as the UC Riverside campus, but it seems high as an average across the entire range. By contrast, the Los Angeles County Breeding Bird Atlas (Allen et al. 2016) estimated that, in 1995–1999, the maximum abundance of Allen's Hummingbirds was ~7.2 birds km⁻². Therefore, I hold 7 birds km⁻² as a low estimate of density. Under the high estimate, the current population of *S. s. sedentarius* in urban Southern California is ~350,000; on Palos Verdes in 1970, under this same assumption, it was 3,780. Under the low estimate, the current population of *S. s. sedentarius* in urban Southern California is ~46,000 birds, from a source population of 490 birds in 1970. Assuming a constant rate of exponential growth, this corresponds to an *annual* rate of growth of 10% of the mainland *S. s. sedentarius* population over the past 45 yr. Qualitatively, this dramatic growth is corroborated by the CBC data (Figure 1E).

The sedentary *S. s. sedentarius* is no longer a nearly negligible fraction of the total Allen's Hummingbird population. It is virtually certain to now be >4% of the population of the entire species. Ecologically, they are clearly doing well; some even suggest they are displacing the ubiquitous Anna's Hummingbird within urban Los Angeles (Erickson 2016), although this claim warrants additional analysis.

What is responsible for the recent success of *S. s. sedentarius*? Part of the answer is clearly an ecological subsidy (Chamberlain et al. 2008). Urban development of

the Los Angeles Basin and surrounding areas has created habitat with a year-round food supply from which a bird would not need to migrate away. A handful of nonnative bird-pollinated plants seem to have been particularly helpful in this regard: one invariably finds *S. s. sedentarius* in the vicinity of blooming *Tecoma capensis* (Erickson 2016), *Eucalyptus* spp., and, to a lesser degree, blooming *Nicotiana glauca* (Ortiz-Crespo 1980). *Eucalyptus* and *Nicotiana* are invasive and are thus often considered “bad” from a conservation perspective. *Tecoma capensis*, a common landscaping cultivar from South Africa whose wild ancestors were pollinated by sunbirds (Nectariniidae), seems to bloom irregularly year round in Southern California.

Resources cannot entirely explain the range expansion, however, because *S. s. sasin* does not seem to have similarly benefited from human alteration of the environment. *Selasphorus s. sasin* is easy to find breeding in natural areas in the vicinity of riparian habitat, but one does not find *S. s. sasin* breeding in urban backyards or college campuses in the Bay Area in quite the same way that *S. s. sedentarius* does in Southern California. For instance, *S. s. sasin* used to breed on the main UC Berkeley campus in 1916; it does not breed there any longer, for the campus has become more urbanized and lost substantial shrub cover (Shultz et al. 2012). I hypothesize that there is a subtle ecological or behavioral difference between the subspecies that has allowed *S. s. sedentarius* to flourish in urban environments. Formally testing this hypothesis would be of interest for future work.

Another potentially important ecological difference between the subspecies is that, owing to its extended breeding season, *S. s. sedentarius* has a much higher theoretical rate of increase than *S. s. sasin*. The latter breeds during March–June (Pitelka 1951, Clark and Mitchell 2013), which is roughly enough time for a female to successfully fledge ≤ 2 nests (≤ 4 young). *Selasphorus s. sedentarius* breeds from early November until the end of May, enough time for one female to fledge at least 4 nests year⁻¹ and possibly more (Clark and Mitchell 2013). Four successful nests by one female has been documented in Orange County by Joe Dellwo, who runs a nest camera (<http://phoebeallens.com>). Perhaps this fecundity difference is what has fueled the dramatic year-upon-year annual increase.

In the future, the rate of growth of *S. s. sedentarius* seems likely to slow, because it may be rapidly running out of its prime suburban habitat. To the north it seems likely to be limited by the transverse ranges (the Santa Monica and San Gabriel mountains), while to the east it is partially hemmed in by the Mojave Desert. If only food limits the spread of *S. s. sedentarius*, then there is still some room for continued growth. There are not yet reports of Allen's Hummingbirds breeding in the gardens of urban Coachella

Valley (Figure 2), but given that Anna's Hummingbirds breed there (P. Unitt personal communication), I hypothesize that it is only a matter of time before Allen's do as well. Perhaps climate will prevent this, but given that Allen's Hummingbirds can survive the temperature of 43°C occasionally reached in Riverside during the 2016 summer, the leap over the San Gorgonio Pass into the Coachella Valley seems plausible. Given that Allen's Hummingbirds now breed in arid Riverside County, a considerably hotter climate than its ancestral home on the Channel Islands, Langham et al.'s (2015) prediction that Allen's Hummingbird will be pushed out of Southern California by climate change in coming decades seems unlikely.

Intergradation between *S. s. sasin* and *S. s. sedentarius*?

According to my interpretation of the eBird data, *S. s. sedentarius* met *S. s. sasin* in the vicinity of Santa Barbara or Ventura in approximately 2005 (Figure 2). Because there seem to be no noteworthy differences in the displays or other sexual signals between the subspecies, I hypothesize that they may now interbreed. This brand-new intergradation zone, if it exists, might be an opportunity to study a variety of questions traditionally studied in hybrid zones, such as the genetics of, or selection on, migratory behavior, similar to patterns observed in Swainson's Thrush (*Catharus ustulatus*) in British Columbia (Ruegg 2008, Delmore et al. 2016). Moreover, here an island form has invaded the mainland. Island forms are often thought of as competitive weaklings in comparison to their mainland relatives. Could *S. s. sedentarius* be outcompeting its mainland sister, given that *S. s. sedentarius* apparently has much higher fecundity?

Flawed Population Assessments

The dramatic increase of *S. s. sedentarius* in urban Southern California documented here (Figure 1) has been entirely missed by PIF because they based their population estimate entirely on BBS data. The BBS protocols are poorly suited to accurately capture hummingbird population trends. The BBS does not survey what is now clearly critical habitat for *S. s. sedentarius*: urban backyards within the Los Angeles Basin (BBS 2016). Moreover, the BBS surveys in California are conducted between May 15 and the end of June (R. Doster personal communication). Allen's Hummingbirds (both subspecies) cease breeding in early June, at which point *S. s. sasin* become scarce as they head south.

Perhaps the true explanation for apparent declines suggested by the BBS data is a slight phenological shift in breeding. If climate change has shifted the cessation of breeding forward by even a few days (Dunn and Winkler 2010), it could appear that Allen's Hummingbirds are

declining when really they are quitting their courtship territories earlier and becoming less apparent to observers. This might also explain the patterns for 2 other hummingbirds that PIF/BBS estimates to have large, healthy extant populations, yet also substantial declines, since 1970: Rufous Hummingbird and Costa's Hummingbird (*Calypte costae*). Neither of these species is known to be extirpated over any part of its historical range. Both are easy to find in their preferred habitats (C. J. Clark personal observation), and both make some use of suburban habitats. In 2015–2016, populations of Rufous Hummingbirds near Coos Bay, Oregon, and of Costa's Hummingbirds in Riverside, California, were both done breeding by the end of May (C. J. Clark personal observation). If breeding in these species has undergone a similar phenological shift forward, it would be a relatively benign resolution for the paradox implied by the BBS data. In fact, the only hummingbird with a large breeding range north of Mexico that does seem to be undergoing a slight contraction at the southern edge of its breeding range is the Calliope Hummingbird (*S. calliope*). Calliope Hummingbirds may no longer breed in the San Jacinto Mountains (Unitt 2004, P. Unitt personal communication), and certain local low-elevation populations have disappeared from the Sierra Nevadas (Tingley et al. 2012), while a couple of higher-elevation local populations on the northwest shore of Lake Tahoe that were present in 2010 had disappeared by 2015 (C. J. Clark personal observation).

The BBS-derived estimate of an 83% decrease in the Allen's Hummingbird population since 1970 is particularly difficult to reconcile with the generous current estimated population of 1.7 million birds. Together these numbers yield a population estimate of >10 million in 1970. This is impossible: 10 million birds corresponds to a 1970 average density of nearly 350 birds km⁻², assuming a range of 28,000 km². Although in small patches of ideal habitat, such as in a large stand of blooming *Eucalyptus*, local densities could be that high, this number is not credible as an average density across their entire range. Moreover, Allen's Hummingbird does not appear to have been extirpated over any part of its range, as would be predicted by a large contraction in numbers: the eBird range map from 2016 looks similar to the range map in Grinnell and Miller (1944) (Figure 3). There is no credible evidence that Allen's Hummingbird is in substantial decline.

The accuracy of PIF's estimates *matters*, both to the public and as the basis for the USFWS watchlist. Allen's Hummingbird is abundant on or adjacent to the campuses of most research universities in California, making it a convenient subject for scientific study. Research on Allen's Hummingbird could shed light on questions with conservation implications, such as adaptation to urban landscapes and resource subsidies, or phenological responses to climate change. However, because Allen's Hummingbird

is on the USFWS watchlist, permit applications for scientific take are limited, which steers researchers (particularly students) away from studying this species. This produces the “House Sparrow effect”: we know more about the biology of nonnative House Sparrows (*Passer domesticus*) than about most native species. Additionally, inaccurate analysis could steer limited money for conservation away from species in greater actual need. Finally, while some state agencies, such as the California Department of Fish and Wildlife, develop their own estimates of a given species' status (California Department of Fish and Wildlife 2008), managers at places such as state parks may rely on Internet searches to determine the conservation status of species under their stewardship. Websites from reputable conservation organizations claiming that a charismatic species is a “common bird in steep decline” should therefore be based on the best available data. As it happens, perhaps eBird's strengths can help supplement the BBS's weaknesses for species found in birders' backyards, such as Allen's Hummingbird.

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