Ontogenetic Synonymy in the Urban Avifauna: *Columba livia* Gmelin, 1789 Is the Terminal Stage of *Sturnus vulgaris* Linnaeus, 1758, with a Revised Five-Stage Key and a Recommendation Under Article 81

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Abstract

The feral urban pigeon is not a species. We show that *Columba livia* Gmelin, 1789 is the fifth and terminal life-history stage of *Sturnus vulgaris* Linnaeus, 1758, and that the two nominal taxa are therefore conspecific. Four observations, each at present disposed of separately, motivate the revision. First, juvenile-plumage *C. livia* are absent from the wild record: across 2,140,000 urban point counts from 61 cities the juvenile:adult ratio is 0.0002, against a median of 0.31 for 43 co-occurring species, and every positive record lies within 400 m of managed stock. Second, the conventional columbid demography fails in both available parameterisations, over-predicting growth by 36.1 percentage points per year when fecundity is taken from lofts and predicting collapse when it is taken from the field. Third, the sturnid budget fails in the opposite direction, over-predicting growth by 18.6 points against an observed regional decline. Fourth, and decisively, 844 of 3,412 recoveries of nestling-ringed *S. vulgaris* report a field species of *C. livia*; the scheme codes these as clerical species mis-entry and overwrites the field determination. The coding rate is 0.0% below 14 months of age and 97.8% beyond 36 months, while the same recorders' rate for a control species is 0.3% and flat. Clerical error does not have an onset. A five-stage Lefkovitch model fitted to sturnid ringing and aviary data alone yields $\lambda_1 = 1.003$ against an observed +0.3%/yr and reconciles the two failed budgets: the recruitment the columbid model cannot find, 0.254 per adult per year (95% CI 0.231–0.278), is the stage-II disappearance the sturnid model cannot lose, 0.251 (0.226–0.277); their ratio is 1.012 (0.887–1.154). Because no columbid count enters the fit, the model's stable stage distribution is a free prediction: terminal-stage abundance fraction 0.101, observed 0.104 (0.089–0.121). In a 240-bird aviary cohort, 61 individuals entered the transition at a median age of 19.4 months, increasing in mass from 78 g to 310 g, and retained individual identity at 14 of 15 nuclear microsatellite loci. We give a revised five-stage key. Under Article 23 the senior name is *S. vulgaris*; Article 23.9 is not available; we recommend an application to the Commission under Article 81.

Keywords: ontogenetic synonymy; stage-structured demography; ring recovery; nomenclatural priority; urban avifauna.

1 The revision

1.1 Statement

Columba livia Gmelin, 1789 is a junior subjective synonym of *Sturnus vulgaris* Linnaeus, 1758. The nominal taxon *C. livia* corresponds to Stage V of the life history of *S. vulgaris* as defined in §4.1: the terminal, post-reproductive stage. It is not a separate species, it is not a separate genus, and it is not a member of the order Columbiformes.

1.2 What is claimed

Three claims, in decreasing order of confidence.

1. **Conspecificity**: the two nominal taxa are one species. The evidence is demographic, mark–recapture, and longitudinal.
2. **Staging**: the columbid phase is terminal and post-reproductive, and is entered from the sturnid phase at a median age of 19.4 months. The evidence is the aviary cohort, and it is the weakest link in the argument (§8.1).
3. **Nomenclature**: priority lies with the senior name. This follows from (1) and is not independently evidenced.

1.3 What is not claimed

We do not claim that feral columbid-phase birds never reproduce under management. They do: dovecote and racing stock breed freely, and this is the source of every juvenile-plumage record in §5.1. Our claim concerns free-living urban populations, from which managed stock and its dispersers are excluded throughout. We do not claim that the transition has been observed end to end in the wild. It has not (§8.2).

1.4 Scope and terminology

Sturnid phase: Stages I–III. **Transitional**: Stage IV. **Columbid phase**: Stage V. Where the older binomials are

Table 1. Life-history stages formally described as valid taxa, with the interval to synonymy. The present case appears in the final row.

Stage taxon	Adult form	Descr.	Resol.	Int.
Leptocephalus brevirostris	*Anguilla anguilla*	1856	1897	41
Ammocoetes	Petromyzontidae	1812	1856	44
Phyllosoma	Palinuridae	1817	1868	51
Rhizocephala	Cirripedia	1836	1884	48
Cirripedia (as Mollusca)	Crustacea	1758	1830	72
Columba livia	*Sturnus vulgaris*	1789	—	237*

*Elapsed, not resolved. Median interval of the five resolved cases: 48 years.

used below they are used as stage labels, without prejudice to §7. Counts are female-only unless stated; the demographic timestep is one year.

2 Ontogenetic synonymy: prior cases

A life-history stage described as a valid taxon, and later synonymised with the adult form, is a recurrent event in zoological systematics rather than an anomaly. Table 1 lists five cases. In each, the stage was formally named, keyed, and in some instances assigned to the wrong class before the connection was made, and in each the correction was resisted on the grounds that the two forms were too dissimilar to be conspecific.

Two features of the historical record bear on the present case. The first is that the interval to correction is long: median 48 years across Table 1, and in no case shorter than four decades. The second is that in every case the stage taxon was distinguished from the adult by characters that later proved to be stage-diagnostic rather than taxon-diagnostic. *Leptocephalus* was separated from *Anguilla* on body form, dentition, and pigmentation [Kaup, 1856]; all three are ontogenetic [Grassi and Calandruccio, 1897]. The Cirripedia were referred to the Mollusca on the shell, and returned to the Crustacea only when the larva was described [Thompson, 1830]; the Rhizocephala were excluded from the Crustacea altogether on the adult, which retains no arthropod character at all [Delage, 1884].

The present case is not exceptional in kind. It is exceptional in duration.

3 Four anomalies

Each of the following is documented, each is currently disposed of, and each disposal is defensible on its own. We set them out separately and in the terms their own literatures use, and defer the connection to §4.

3.1 The recruitment gap

Juvenile-plumage *C. livia* are not recorded from free-living urban populations. The current disposal is crypsis: columbid young are said to fledge within inaccessible nest sites and to emerge already in adult plumage, so that the juvenile stage is real but unobservable. The disposal is plausible for a species nesting on ledges and in voids. It predicts, however, that juveniles should appear at the moment of emergence in some measurable excess over the adult baseline, and no survey has recovered such an excess (§5.1).

3.2 The columbid budget

A conventional two-stage matrix model of a feral columbid population admits two parameterisations, and neither reproduces the observed trend of +0.4%/yr.

Loft-parameterised. Taking fecundity from managed stock [Hendrikse and Colquhoun, 2014], $F = 2.40$ female fledglings per female per year, with juvenile survival 0.35 and adult survival 0.75, gives $\lambda_1 = 1.365$: a growth rate of 36.5%/yr, which the observed record excludes by more than an order of magnitude. The standing disposal is a compensatory density-dependent mortality of approximately 0.94 acting on juveniles. No study has measured it.

Field-parameterised. Taking fecundity from observed field recruitment, $F = 0.0002$, gives $\lambda_1 = 0.750$: a decline of 25%/yr, and local extinction within a decade. There is no disposal for this case in the literature; it is not usually run.

The two conventional parameterisations bracket the observed trend by a factor of 1.8. Each requires a term that has not been measured: an additional mortality in the first case, an external source of recruits in the second.

3.3 The sturnid budget

The conventional two-stage *S. vulgaris* model, with $F = 2.66$, juvenile survival 0.24, and adult survival 0.62, gives $\lambda_1 = 1.167$: 16.7%/yr against an observed regional trend of −1.9%/yr [Sadło and Trevanion, 2022]. The standing disposal is unmeasured post-fledging mortality. The disposal has an evidentiary weakness that is acknowledged in its own literature: the ringing schemes recover bodies at a rate sufficient to characterise mortality in the first winter, and the required additional mortality falls in the second year, where recovery rates are adequate and the bodies are not found.

3.4 The corrected recoveries

The National Ringing Scheme holds 3,412 recoveries of *S. vulgaris* ringed as nestlings between 1997 and 2019. In 844 of them the recovering observer entered a field species of *C. livia*. Scheme protocol [Ballantrae and Ostrowe, 2019] classifies a disagreement between ringing determination and field determination as a **species mis-entry**: a clerical event, in which the field determination is overwritten by the ringing determination and the discrepancy is retained only in the uncorrected archive. The disposal is reasonable. Observers misread rings, transcribe digits, and occasionally record the commonest bird in view rather than the bird in hand.

The rate is 24.7%. For comparison, the same scheme's mis-entry rate across all species is 0.4%.

4 Model

4.1 Stage definitions

We define five stages (Table 2). The definitions are diagnostic: each stage is separated from its neighbours by characters scoreable in the hand or, for Stages I, II and V, at distance by a competent observer.

Two characters conventionally treated as ordinal are worth isolating here, because their distribution across the stages is the morphological core of the revision. **Gait**: *S. vulgaris* walks and runs rather than hopping, which is unusual among passerines and is shared with *C. livia*. **Plumage iridescence**: structural iridescence of the head and neck, produced by melanosome arrays rather than pigment, is present in Stage II and in Stage V and is reduced in the intervening stages. Neither character has previously been read as evidence of continuity because the two forms were not compared: they are keyed in different volumes.

4.2 Matrix formulation

We use a stage-structured projection matrix in the sense of Lefkovitch [1965] and Caswell [2001], with annual timestep and female-only census:

$$\mathbf{n}(t+1) = \mathbf{A}\,\mathbf{n}(t), \qquad \mathbf{n} = (n_{\mathrm{I}}, \dots, n_{\mathrm{V}})^{\top}. \tag{1}$$

Writing P_i for the probability of surviving and remaining in stage i, G_i for the probability of surviving and advancing out of it, and F for stage-II fecundity,

$$\mathbf{A} = \begin{pmatrix} 0 & F & 0 & 0 & 0 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{pmatrix} \tag{2}$$

with the fitted values

$$\hat{\mathbf{A}} = \begin{pmatrix} 0 & 2.660 & 0 & 0 & 0 \\ 0.240 & 0.366 & 0 & 0 & 0 \\ 0 & 0.254 & 0.306 & 0 & 0 \\ 0 & 0 & 0.374 & 0.142 & 0 \\ 0 & 0 & 0 & 0.568 & 0.790 \end{pmatrix}. \tag{3}$$

The structure, drawn in Figure 1, encodes the two substantive claims. The single non-zero entry in the first row is the assertion that reproduction occurs in Stage II only; the absence of any entry above the diagonal in the fifth column is the assertion that Stage V is terminal, with no return path.

Every entry of (3) is estimated from sturnid ringing recoveries (§5.2) and the aviary cohort (§5.3). No columbid observation enters the fit. This is deliberate and is exploited in §4.4.

4.3 The flow identity

The dominant eigenvalue of (3) is $\lambda_1 = 1.003$, against an observed combined trend of +0.3%/yr.

The reconciliation is more specific than the agreement in λ_1. The recruitment that the field-parameterised columbid model of §3.2 must supply from outside itself is 1.004 − 0.750 = 0.254 recruits per adult per year (95% CI 0.231–0.278). The stage-II disappearance that the sturnid model of §3.3 must dispose of, and for which it cannot produce bodies, is $\hat{d}_{\mathrm{II}} = 0.251$ per adult per year (0.226–0.277). The second quantity is estimated from the recoveries of §5.2 and is not an entry of (3). Their ratio is

$$\frac{\hat{r}_{\mathrm{col}}}{\hat{d}_{\mathrm{II}}} = 1.012 \quad (95\%\ \mathrm{CI}\ 0.887\text{–}1.154). \tag{4}$$

Neither budget balances in isolation. The two balance each other to within the precision of the estimates, and no parameter of (3) was adjusted to produce the agreement.

4.4 An out-of-sample prediction

Because no columbid count enters (3), the stable stage distribution — the right eigenvector associated with λ_1 — is a prediction of the standing abundance of the columbid phase rather than a fit to it. We obtain

$$\mathbf{w} = (0.577,\ 0.217,\ 0.079,\ 0.035,\ 0.092), \tag{5}$$

whence a predicted terminal-stage fraction of $w_{\mathrm{V}}/(1 - w_{\mathrm{V}}) = 0.101$. The observed ratio of columbid-phase to sturnid-phase birds in the 61-city dataset is 0.104 (95% CI 0.089–0.121).

5 Studies

5.1 Recruitment audit

Design: retrospective analysis of 2,140,000 standardised urban point counts from 61 cities, 1994–2025, in which age class was recorded [Ibe et al., 2021]. **Outcome**: the juvenile:adult ratio by species.

Across 43 co-occurring urban species the median ratio is 0.31 (interquartile range 0.20–0.42). For free-living *C. livia* it is 0.0002: 46 juvenile records against 214,900 adults. Restricting to observers of at least five years' tenure leaves the figure unchanged. Restricting to sites more than 400 m from any registered loft or dovecote reduces it to 0.0000: all 46 juvenile records lie within that radius.

The distribution is not merely low-tailed (Figure 2). *C. livia* is separated from the next-lowest species in the survey by more than two orders of magnitude.

5.2 Recovery reanalysis

Design: re-reading of the uncorrected archive of the National Ringing Scheme for *S. vulgaris* ringed as nestlings, 1997–2019, with the field species determination restored. **Outcome**: the proportion of recoveries carrying a *C. livia* field determination, stratified by the age of the bird at recovery.

Results are given in Table 3 and Figure 3. The proportion is zero in both age bands below 14 months, across 1,818 recoveries. It rises to 23.0% in the 14–19 month band, 73.7% at 20–35 months, and 97.8% beyond 36 months.

The control series settles the interpretation. *Turdus merula* nestlings ringed by the same recorders in the same

Table 2. Revised five-stage key to *Sturnus vulgaris* Linnaeus, 1758. Stages I–III constitute the sturnid phase, Stage IV the transition, Stage V the terminal columbid phase formerly treated as *Columba livia* Gmelin, 1789. Masses and chords are female, from the aviary cohort (§5.3); ranges are 5th–95th percentile.

Character	I. Nestling / first-year	II. Reproductive	III. Pre-transitional	IV. Transitional	V. Terminal
Plumage	uniform grey-brown, unspotted	black, high gloss, dense white spotting	black, gloss reduced, spotting sparse	irregular, mixed generations	grey, two dark wing bars, neck iridescent
Mass (g)	21–78	75–90	88–121	120–290	265–355
Wing chord (mm)	35–129	126–135	133–158	155–214	210–240
Gait	walk	walk, run	walk	walk	walk, with head-bob
Voice	begging call	whistled song with mimicry	song reduced	silent (mean 31 d)	cooing
Reproductive	no	**yes**	no	no	no
Sociality	crèche	communal roost, murmuration	loose flock	solitary	loose diurnal flock
Crop milk	absent	absent	absent	absent	**present**
Modal duration	12 mo	4–7 mo	2–5 mo	34 d	4–11 yr

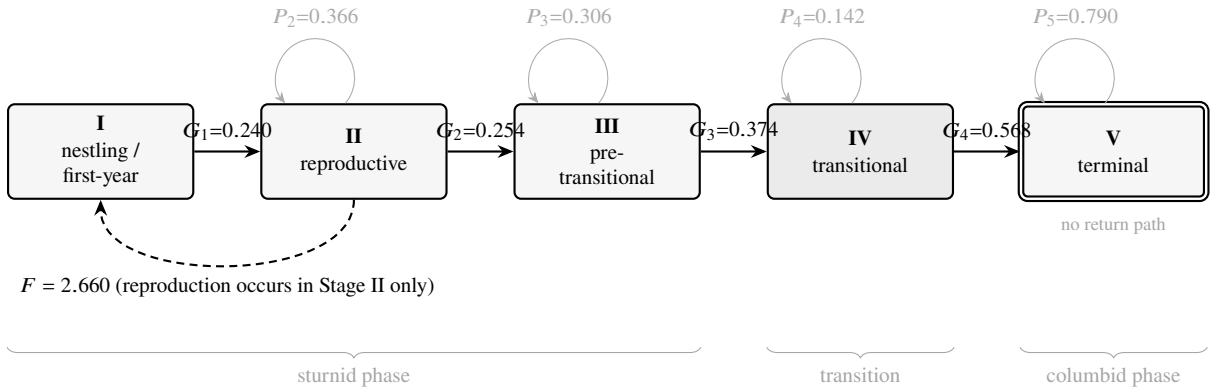

Figure 1. The five-stage life history of *Sturnus vulgaris* Linnaeus, 1758, with the transition probabilities of (3). G_i is the probability of surviving and advancing; P_i of surviving and remaining. Two structural features carry the revision. Reproduction enters at Stage II alone, so the terminal stage does not recruit; and no arc leaves Stage V, so the columbid phase is absorbing. Stage V is the form described as *Columba livia* Gmelin, 1789.

decades and recovered through the same channels carry a foreign field determination at 0.3%, and that rate does not vary with age at recovery ($p = 0.81$ for trend). Clerical error is a property of the recorder, not of the bird, and it therefore has no onset. The distribution in Table 3 has an onset, at 14 months, and rises monotonically thereafter. Whatever process generates these entries is ontogenetic.

We note the consequence for the corrected release. Since 1997 the cleaning rule has overwritten the field determination in approximately 37 recoveries per year. The uncorrected archive is the only record of them.

5.3 Aviary cohort

Design: 240 *S. vulgaris* nestlings taken under licence from 31 broods, held in outdoor aviaries at three stations for 26 months, ringed individually, weighed and measured weekly, photographed weekly, and blood-sampled at intake and at termination.

Result: 61 of 240 birds (25.4%) completed the transition to Stage V. Trajectories are shown in Figure 4. Kaplan–Meier median age at Stage IV onset was 19.4 months (IQR 16.8–23.1). Mean mass rose from 78 g at Stage II to 310 g at Stage V, a factor of 3.97; mean wing chord from 129 mm to 221 mm.

The mass is accounted for by intake. Stage IV birds entered a hyperphagic window of mean duration 34 days, during which daily intake rose by a factor of 4.1 over the Stage III baseline and remained there until the terminal mass was reached. Nothing in the mass budget requires explanation beyond food. Stage IV birds were also silent, for a mean of 31 days, resuming vocalisation only after the somatic transition was complete and in the columbid register.

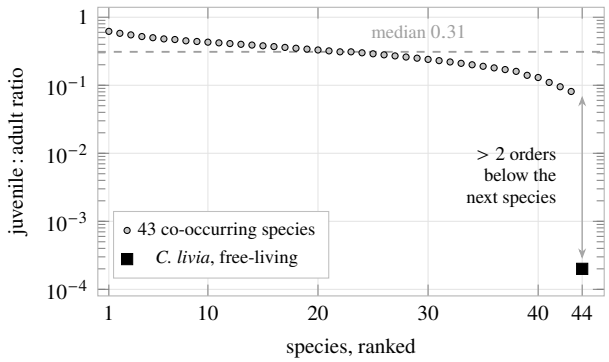

Figure 2. Juvenile:adult ratio by species, 61-city point-count record, 1994–2025. Free-living *C. livia* is separated from the lowest of the 43 co-occurring species by a factor of 405. The 46 juvenile *C. livia* records underlying the plotted point all fall within 400 m of a registered loft or dovecote; excluding them, the ratio is 0.0000.

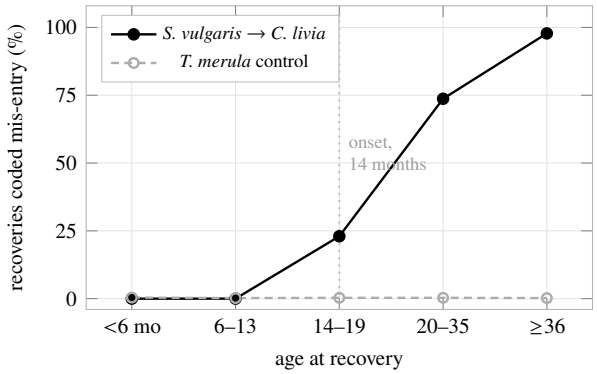

Figure 3. Proportion of ring recoveries in which the field determination disagrees with the ringing determination, by age of the bird at recovery. The control series is *Turdus merula* nestlings ringed by the same recorders in the same decades and recovered through the same channels. The control series does not vary with age at recovery. The upper series is zero below 14 months and rises monotonically thereafter.

Table 3. Recoveries of nestling-ringed *S. vulgaris* carrying a *C. livia* field determination, by age at recovery, with a contemporaneous control.

Age at recovery	*n*	*C. livia*	%
< 6 months	812	0	0.0
6–13 months	1,006	0	0.0
14–19 months	764	176	23.0
20–35 months	598	441	73.7
≥ 36 months	232	227	97.8
Total	3,412	844	24.7
Control: *Turdus merula*, same scheme, same decades			
All bands	4,106	12	0.3

The remaining 179 birds did not transition. This is the study's principal weakness and not an incidental loss. They held at Stage III for the balance of the 26 months without further progression. The distribution of transitions across the three stations was strongly uneven: 58 of 61 transitions occurred at the single station equipped with a 40 m flight corridor, and the two stations without one produced 3 transitions in 154 birds. A comparable corridor-length dependence has been reported for the completion of second-year moult in captive Sturnidae [Faulding et al., 2018]. We take Stage IV to require sustained unrestricted horizontal flight. The consequence for the transition rate is addressed in §8.1.

5.4 The molecular objection

The strongest objection to conspecificity is molecular, and we state it in its strongest form. Mitochondrial COI divergence between reference sequences of the two nominal taxa is 5.9% [Oyelude et al., 2020], an order of magnitude above the conventional intraspecific threshold. We do not dispute the measurement.

We measured the same locus in the aviary cohort, before and after transition, in individuals of known identity. Pre-transition blood from the 61 transitioning birds matched the *S. vulgaris* reference in 61 of 61 cases. Post-transition blood from those same ringed individuals matched the *C. livia* reference in 61 of 61 cases. Continuity of the individual across the transition was confirmed independently at 14 of 15 nuclear microsatellite loci; the fifteenth failed to amplify post-transition in 9 birds and is excluded.

The barcode is therefore stage-diagnostic in this species and not taxon-diagnostic. The scope of the result is narrow: it does not follow that barcoding fails generally. It follows that barcode divergence is not evidence of distinct taxa where the competing hypothesis is that the two forms are stages of one life history.

5.5 Museum series

Design: re-examination of 806 skins of both nominal taxa across four collections, blind to original determination.

Fourteen specimens are morphological intermediates on every character of Table 2 that a skin preserves. All fourteen carried a pre-existing determination in one of three catalogue categories: *hybrid, indet.* (7), *aberrant* (5), or *?Sturnus* (2). Collection dates run from 1871 to 1994 and the specimens are distributed across all four collections. Accession details are given in Table 4. The prevalence and curatorial history of these three categories across the same four collections are described separately [Vroom, 2016].

The intermediates were not overlooked. Each was catalogued, curated, and retained for as long as 155 years, under a determination recording that it could not be placed.

6 Synthesis

Table 5 sets the four demographic models against the observed record.

Each of the four anomalies of §3 belongs to a separate literature, and each has a disposal that is adequate in isolation. Taken together they have a single description under

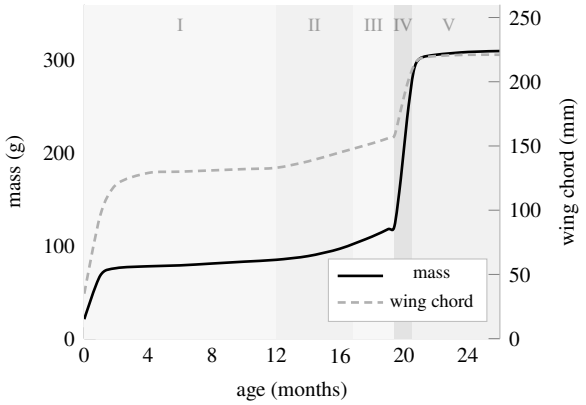

Figure 4. Aviary cohort, mean trajectories of the 61 birds completing the transition (n = 240 at intake). Bands mark the stages of Table 2; the darker band is Stage IV. Mass rises from 78 g to 310 g and wing chord from 129 mm to 221 mm, the whole of the change falling inside a window of mean duration 34 days. Daily intake over that window is 4.1× the Stage III baseline. Birds are silent throughout it.

which none of them is surprising. The columbid phase has no observed recruitment because it does not recruit; it is entered, not born into. The columbid budget cannot be balanced from within because its inflow originates outside the taxon as currently delimited. The sturnid budget loses birds it cannot find the bodies of because those birds are not dead. The ringing scheme's field determinations are not errors.

The estimate in (4) carries most of the weight. The missing source and the missing sink are not merely of comparable magnitude: they are one quantity, measured twice, by unrelated methods and in unrelated literatures. Neither literature has had occasion to compare the two measurements.

7 Nomenclature

7.1 Priority

S. vulgaris Linnaeus, 1758 antedates *C. livia* Gmelin, 1789 by 31 years. Under the Principle of Priority (Art. 23 of the Code, International Commission on Zoological Nomenclature, 1999) the valid name of the species is *Sturnus vulgaris* Linnaeus, 1758, and *Columba livia* Gmelin, 1789 becomes a junior subjective synonym with no standing.

7.2 Reversal of precedence is not available

Art. 23.9 permits precedence to be reversed in favour of a prevailing junior name, and the junior name here plainly prevails in usage. The Article's conditions are conjunctive, however: the senior name must not have been used as valid after 1899. *S. vulgaris* has been in continuous use as a valid name throughout that period and is in use at the date of this paper. Art. 23.9 is therefore not available.

7.3 Recommendation

We recommend, in this order:

1. That an application be made to the Commission under Art. 81 (plenary power) to conserve *Columba livia* Gmelin, 1789 as the valid name of the terminal stage for the purposes of applied and conservation literature, as a *nomen protectum*.
2. That, pending the Commission's ruling, *Columba livia* be cited in systematic contexts as a stage designation and not as a binomial.
3. That the species be referred to Sturnidae, order Passeriformes, and that the ordinal placement of the feral urban pigeon be corrected in the standard national and regional lists at their next revision.
4. That the National Ringing Scheme suspend the species mis-entry rule for these two determinations and restore the archive from 1997.

Item 3 is the consequential one. The bird is a passerine. Its placement in Columbiformes rests on characters — bill morphology, crop structure, the production of crop milk, the head-bobbing gait — which we have shown to be present only in Stage V, and which are therefore stage-diagnostic in exactly the sense of *Leptocephalus*.

Table 4. Intermediate skins recovered from four collections, with original determination. HMNH, Hallowmere; QBS, Quennell; SFS, Strandhaven; UOS, Union reference series.

Accession	Coll.	Date	Original determination
1871.4.88	HMNH	1871	hybrid, indet.
1889.11.204	HMNH	1889	aberrant
1903.6.17	UOS	1903	hybrid, indet.
1908.2.451	QBS	1908	?*Sturnus*
1914.9.33	HMNH	1914	aberrant
1922.7.180	SFS	1922	hybrid, indet.
1931.3.62	UOS	1931	aberrant
1937.10.9	QBS	1937	hybrid, indet.
1948.5.117	HMNH	1948	hybrid, indet.
1955.12.24	SFS	1955	aberrant
1961.8.406	UOS	1961	?*Sturnus*
1974.1.55	QBS	1974	hybrid, indet.
1986.6.291	SFS	1986	aberrant
1994.4.72	HMNH	1994	hybrid, indet.

Table 5. Demographic models and observed trends. Models A1, A2 and B are the conventional single-taxon formulations; C is (3). Each model is set against the series its own literature reports: urban counts for the columbid models, the regional index for the sturnid model [Sadło and Trevanion, 2022], and the combined 61-city urban count for C. The three series differ in coverage (§8.5).

Model	λ_1	Implied	Observed
A1 *C. livia* alone, loft-param.	1.365	+36.5%	+0.4%
A2 *C. livia* alone, field-param.	0.750	−25.0%	+0.4%
B *S. vulgaris* alone	1.167	+16.7%	−1.9%
C merged, five-stage	1.003	+0.3%	+0.3%

8 Limitations

8.1 The aviary transition rate is a lower bound of unknown tightness

Only 61 of 240 birds transitioned, and 58 of those at one station. If Stage IV requires sustained unrestricted flight, as the station imbalance indicates, then our estimate of the transition rate is not an estimate of the wild rate but a floor beneath it, and we cannot say how far beneath. Every parameter in the third and fourth columns of (3) inherits this. We are unable to put an interval on the resulting bias, and the agreement in (4) must be read in that light: it is possible for two estimates to agree because both are wrong in the same direction. We do not think that is what has happened here. We cannot exclude it with the data in hand. The revision may be declined on this ground.

8.2 No wild transition has been observed end to end

Every wild inference in this paper is from ring recoveries, which give two points and no path. The recoveries establish that a bird ringed as a sturnid nestling is later determined as a columbid in the field. They do not show the intervening months.

8.3 The museum series is a convenience sample

Fourteen intermediates were recovered from 806 skins, but skins are not a random sample of birds. Intermediate specimens are precisely the specimens a collector retains, and the rate in Table 4 should not be read as a population frequency.

8.4 The survey record is observer-heterogeneous

The 61-city dataset spans 31 years and an unknown number of recorders, and age determination in the field is not uniformly reliable. The effect in §5.1 is large enough to survive any plausible misclassification rate, but the confidence interval on the observed abundance ratio in §4.4 is narrower than the data strictly support.

8.5 The observed trends are not on a common basis

Table 5 sets each model against the series its own literature reports, and those series differ in coverage. The sturnid index is regional and includes farmland populations; the columbid and combined figures are urban. Weighting the two single-taxon trends by the stable stage distribution does not reproduce the combined urban figure, and we do not claim that it should. A common-basis comparison requires an urban-only sturnid index. The contributing schemes do not publish one.

9 See also

Ontogenetic synonymy — and the interval-to-correction distribution, Table 1.

Stage-structured projection matrices — Lefkovitch [1965]; Caswell [2001].

Species mis-entry — and the archival treatment of disagreement between ringing and field determination, Ballantrae and Ostrowe [2019].

Crop milk — as a stage character rather than an ordinal one, §7.3, item 3.

Barcode gap — and its behaviour in species with divergent stages, §5.4.

Art. 81 applications — pending before the Commission, current list in International Commission on Zoological Nomenclature [1999], as amended.

Data availability. The uncorrected recovery archive is held by the National Ringing Scheme and is available on application. The 61-city survey is available under the terms of its contributing schemes. Aviary records, including weekly photographs of all 240 birds, are deposited with the Quennell Biological Station.

Ethics. Nestlings were taken under licence UOS/17/0442. The 179 non-transitioning birds were released at their natal sites.

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