

**THE CALOPTERYX-SPLENDENS-CLINE
IN SOUTHWESTERN FRANCE,
ANALYSED BY QUANTITATIVE WINGSPOT ANALYSIS
(ZYGOPTERA: CALOPTERYGIDAE)**

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Received May 21, 1993 / Reviewed and Accepted June 2, 1993

It is confirmed that the reproductive barrier between *Calopteryx xanthostoma* and the *C.-splendens*-complex N of it is not imperious. Considerable gene flow occurs between both groups. However, the cline is not symmetrical: S of the contact zone, *C. xanthostoma* is homogeneous, whereas N of it, a genetic gradient, expressed in continuous variation of the apical extent of the ♂ wingspot, extends over many hundreds of km. The possible existence of a third genetic component, of eastern origin, cannot be ruled out. Also, it is presently impossible to decide in which direction introgression proceeds. While the Adour R. basin is inhabited by *xanthostoma* only, some pure *xanthostoma* populations on the southern tributaries of the Garonne basin are as probable to be pioneers as relicts. — Interbasin crossings, the very base of gene flow, proceed primarily via source areas of higher order tributaries, not via watershed crossings in lowland areas. The *Calopteryx* populations of different tributaries to a same major river may, therefore, be more different among themselves than populations of adjacent high-order streams belonging to different drainage basins.

INTRODUCTION

Understanding the *Calopteryx-splendens*-complex, which extends over an enormous range in Europe, North Africa, and West and Central Asia, is a formidable intellectual challenge. In a recent paper, MERTENS et al. (1992) described a method, involving computer-assisted wingspot analysis in males, which brings an objective (quantitative) analysis of samples (individuals) from different populations within reach. In the present contribution, we apply this method to samples

from 21 populations, extending from the foot of the Pyrenees in SW France, to Belgium (Fig. 1).

In the southern part of this area, a taxon occurs (*Calopteryx xanthostoma* Charpentier) which, having long been regarded as a subspecies of *C. splendens* (Harris), was raised to full specific status by DUMONT (1972). This author had seen several homogeneous populations from Spain and SW France, including some degree of habitat segregation with "splendens" in the latter area, but was unaware of the existence of a hybrid zone in central SW France.

The existence of hybrids was revealed by MAIBACH (1985, 1986, 1987) on grounds of morphology and enzyme polymorphisms, and this author formulated the conclusion that a taxonomic status higher than subspecies, but lower than full species (i.e. the non-canonical semispecies) would fit *C. xanthostoma* best.

Here it is not our aim to take issue with that stance, but rather to marvel at the very existence of this cline-building hybrid zone, and to describe its geographic aspects as accurately as possible.

MATERIAL AND METHODS

The material analysed is fully listed in Table I, where samples from 21 populations are organised in a South-North order, and identified by locality, coordinates, river name, and basin appartainance. The majority of samples was collected during a single sampling trip in 1991. Population 21 (in Belgium) was earlier included in the MERTENS et al. (1992) paper, and is here used as a reference sample of "typical" *C. splendens* (Harris). On all males collected, image analysis was performed, and wingspots were analysed quantitatively using the iterative computation protocol of MERTENS et al. (1992). Samples from populations with $n > 10$ were tested for significant differences in the criterium $x_{50,max}$ (a measure of the apical extent of the wingspot, using the nodus as a reference point) and in the Length/Width ratio of the wings. Because we converted all data to percentages, all data were subjected to a non-parametric Kruskal-Wallis one-way ANOVA (all data $p < 0.001$).

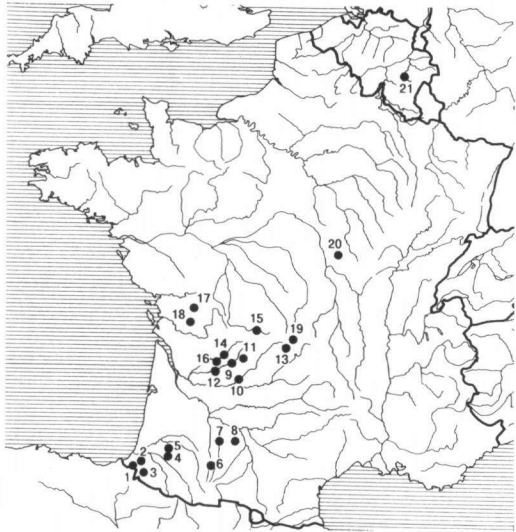


Fig. 1. Localisation of sampling sites.

Table 1
Sampling sites of the *Calopteryx* populations

Code	Locality	Coordinates	River	Basin	Date
1	Amotz	43°20'N-01°26'W	Nivelle	Nivelle	15.08.89
2	Itxassou	43°20'N-01°24'W	Nive	Nive	15.08.89
3	Arhansus	43°10'N-01°14'W	Bidouze	Adour	28.08.89
4	Sault de Navailles	43°33'N-00°40'W	Gave de Pau	Adour	28.08.89
5	Momuy-Orthez	43°37'N-00°37'W	Luy de France	Adour	26.08.91
6	Mirande	43°31'N-00°25'E	Grande Baïse	Garonne	19.08.91
7	Lectoure	43°56'N-00°38'E	Gers	Garonne	27.08.91
8	Larrazet	43°56'N-01°05'E	Gimonne	Garonne	19.08.91
9	Sarliac-sur-l'Isle	45°14'N-00°52'E	Isle	Dordogne	28.08.91
10	Les Eyzies	44°56'N-01°02'E	Vézère	Dordogne	28.08.91
11	Cubjac	45°14'N-01°56'E	Isle	Dordogne	28.08.91
12	Mussidan	45°02'N-00°22'E	Isle	Dordogne	29.08.91
13	St. Angel	45°30'N-02°14'E	Triouzoune	Dordogne	16.08.91
14	Périgeux	45°15'N-00°30'E	Dronne	Dordogne	18.08.91
15	St. Leonard-de-Noblat	45°50'N-01°29'E	Vienne	Loire	16.08.91
16	Villetourei	45°14'N-00°22'E	Dronne	Dordogne	29.08.89
17	Dampierre-s-Boutonne	46°08'N-00°20'W	Boutonne	Charente	17.08.91
18	Dampierre-s-Boutonne	46°08'N-00°20'W	Boutonne	Charente	10.09.88
19	Merlines	45°39'N-02°26'E	l'Abeille	Dordogne	15.08.91
20	Prémery	47°10'N-03°19'E	Nièvre	Loire	14.08.91
21	Bas Rendeux	50°16'N-05°27'E	Ourthe	Meuse	15.07.88

RESULTS

A wingspot covering the wing apex, typical of *C. xanthostoma*, and free of variation (thus, $x_{50,max} = 100$, s.d.=0) is found from the Pyrenees (the basin of the Adour River) to the upper southern reaches of the Garonne in Aquitania (samples 1-8). Remarkably, in the same Garonne basin, the situation changes further north, starting perhaps with the Dordogne subbasin. The change is gradual: 1 specimen out of 14 had a slightly hyaline wing apex at Sarliac-sur-l'Isle (No. 9), 4 out of 24 at Les Eyzies (No. 10), 4 out of 15 at Cubjac (No. 11), and 3 out of 5 at Mussidan (No. 12). One specimen in these populations had a concave instead of a convex spot borderline (Fig. 2, No. 10, min.). On the River Dronne (No. 14), the trend is even more outspoken: 2 specimens out of 35 are of the conventional "splendens" phenotype ($x_{50,max} = 76$), while only 2 have pure *xanthostoma* wingspots. The remainder are intermediary (Fig. 3). The River Charente populations (Nos 17, 18), representing so-called *C. splendens faivreii* Lacroix are a next step: specimens with a fully opaque wingspot no longer occur here. However, a particular type of pseudo-androchrome female (darkened wings with a darkest zone near the apex, and a lighter zone further basad) occurs here, beside

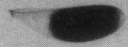





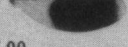








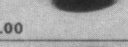







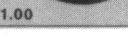
code	min.	mean(S.D.)	max.
9	 93.00	 99.50 (1.87)	 100.00
10	 87.00	 98.96 (3.53)	 100.00
11	 87.00	 98.20 (4.20)	 100.00
14	 66.00	 90.17 (6.64)	 100.00
15	 77.00	 92.72 (7.38)	 100.00
17	 82.00	 88.50 (3.30)	 97.00
18	 74.00	 85.25 (3.59)	 92.00
21	 70.00	 76.29 (3.47)	 81.00

Fig. 2. Illustration of the range of the variability (and its mean) of the wing spot in the populations with $n > 10$ by means of minimum, mean (standard deviation) and maximum values of $x_{50,max}$. There is no variability in populations 1 to 8 (see Tab II).

"standard" hyaline females. This, and the fact that the wingspot of these *faivre* males might extend further basal of the wings than in either *xanthostoma* or *splendens* (not yet analysed), suggests a genetic inflow from the East, and requires further study.

Populations on the Upper Loire River (Nos 19, 20), having an average $x_{50,max}$ value of c.83.7 stand halfway between the Charente and Meuse basin (No. 21) populations. One sample on the River Vienne (No. 15), an affluent of the Loire, is more nearly related to the Dronne populations (Nos 14, 16), a tributary of the Dordogne, however. A similar phenomenon of closer relatedness of populations situated near to one another geographically, but living in different river basins than populations occurring within a large river basin, far apart and in downstream locations, was also seen in the *xanthostoma* populations of the Adour basin (Nos 1-5) and the southern Garonne (Nos 6-8).

The standard deviation of $x_{50,max}$ is largest in the River Vienne population (92.72 + 7.38), and decreases towards the North as well as towards the South, suggesting that variation in wingspot size is at its maximum at this river.

Table II

The position of the apical borderline ($x_{50,max}$) of the wing spot and the wing width (B/L) of the 21 populations mentioned in Table I, including the standard deviation (s.d.) and the numbers (n) of males in the collection used for analysis

Code	n	$x_{50,max}$	s.d.	B/L	s.d.
1	10	100.00	0.00	0.53	0.02
2	3	100.00	0.00	0.54	0.02
3	9	100.00	0.00	0.52	0.02
4	15	100.00	0.00	0.52	0.02
5	11	100.00	0.00	0.54	0.02
6	7	100.00	0.00	0.54	0.03
7	5	100.00	0.00	0.52	0.01
8	10	100.00	0.00	0.54	0.02
9	14	99.50	1.87	0.55	0.02
10	24	98.96	3.53	0.54	0.03
11	15	98.20	4.20	0.54	0.04
12	5	88.80	10.57	0.53	0.03
13	2	91.00	0.00	0.52	0.02
14	35	90.17	6.64	0.56	0.04
15	18	92.72	7.38	0.53	0.02
16	7	89.71	5.09	0.54	0.02
17	30	88.50	3.30	0.56	0.02
18	28	85.25	3.59	0.63	0.04
19	9	83.67	7.52	0.53	0.03
20	3	83.67	2.89	0.56	0.01
21	24	76.29	3.47	0.67	0.04

DISCUSSION

From the foregoing paragraphs it is clear that the $x_{50,max}$ parameter forms a cline with a strong North-South oriented component across France. This is indicative of hybridisation between the taxa *xanthostoma* and "*splendens*", but it does not resolve the status of these two taxa. The fact that reproductive isolation by pre- or postmating barriers is not absolute is indeed widespread in the animal kingdom. *C. xanthostoma* may thus well be a good species, as evidenced by the lack of variation (complete homogeneity) in populations 1-8, and in all populations South of the Pyrenees. North of the Pyrenees, it has a limited East-West oriented contact zone with one of more members of the *splendens*-complex (at least with *splendens* s.s. and *faivreii*), and North of the contact zone its typicity is quickly diluted. Whether this means that *xanthostoma* is extending its range to the North, or "*splendens*" forms progress to the South, is impossible to derive from the available evidence. For this, a measure of the rate of introgression is needed, and introgression may occur on a time scale, too long to be measurable by a

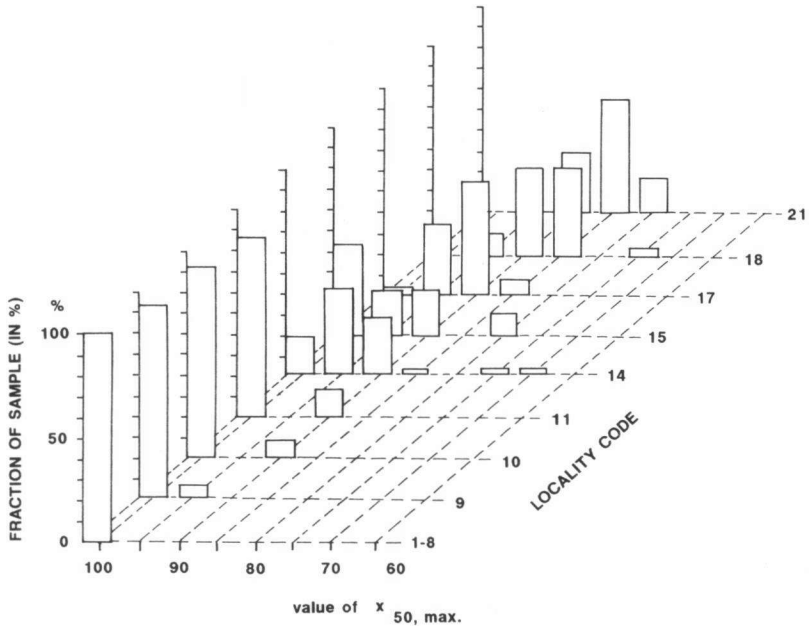


Fig. 3. Distribution (ordinate) of $x_{50,max}$ values (abscis) of the samples with $n > 10$.

human observer. Some circumstantial evidence seems to indicate that introgression in the *splendens*-group may proceed rapidly, however. Thus, in Lacroix's days (the first two decades of the century), androchromic females and very-large-banded males seem to have been more common than at present. Because this entails a change in gene frequencies, the inherent suggestion is that evolution may proceed rapidly, and that it might pay to keep an eye on certain critically placed populations. To date, it has been tacitly assumed that, by the narrow association of *Calopteryx* with running water, and its limited tendency towards inter-basin dispersal, individual basins should quickly acquire a randomly dispersed gene frequency. Such a random intra-basin gene frequency is clearly not confirmed by the facts. We find that positional factors (distance) are more important than basin appartenance (cf. populations 1-5 and 6-8). It might, however, well be that on a decadal time scale, such situations can rapidly change.

Another suggestion is that high-order (smaller) tributaries tend to form genetic isolates, which exchange genes with adjacent streamlets pertaining to different basins (like populations 14, 16 and 15) more rapidly than with downstream (low-order) tributaries of the same river basin (like populations 14, 16 and 9, 11, 12). Because in hot and dry summers the downstream sections of higher order tributaries often dry out completely, the *Calopteryx* gene pool of such rivers is mainly

preserved in upstream (source) areas. Assuming that in *Calopteryx* dispersal, the downstream component is much stronger than the upstream one, it should be expected that repopulation of low-order, major tributaries is effected by several, genetically heterogeneous propagules, while that of upstream source areas is much rarer (they do not dry out as frequently), and due to fewer (if not to single) propagules. The latter may as well be derived from adjacent basins as from the source area's own basin, and will likely be genetically homogeneous. This mechanism predicts that genetic variation as well as the likelihood of hybridisation increases with decreasing stream order. While it seems to describe the facts at hand rather well, it will evidently require much additional testing.

ACKNOWLEDGEMENTS

We thank HILDE DE PAEPE for help in the field as well as in performing the image analysis.

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