The following letter and manuscript were sent to *Journal of Experimental Biology* on 10 Dec. 1999:

Dear Sir,

Please find enclosed some comments and supplementary notes to a paper of Mouritsen & Larsen (1998) that appeared in *Journal of Experimental Biology*.

I participated significantly in the experiments (both planning and in the field) and have a natural interest in the interpretation and presentation of the results. However, very soon after the experiments were terminated it became clear that Mouritsen and I did not agree. For me the results was just another brick in the wall – and not a typical one. For Mouritsen the results constituted a clear signal that juvenile birds – in the present experiment and in general – do not compensate for man-made displacement nor for wind drift, and that they are able to carry out only simple clock-and-compass orientation.

I read the draft of the Mouritsen & Larsen paper without comment because it was obvious that a "hybrid" of our different points of view could not be reached. However, in order to provide a more balanced discussion, I hope you will find space for my comments.

Sincerely Yours Jørgen Rabøl

Migrating young Pied Flycatchers, Ficedula hypoleuca, do not always compensate for man-made geographical displacements.

By

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Summary

Pied Flycatchers displaced from easternmost Denmark to west Denmark and the Czech Republic did not compensate for the man-made displacements (Mouritsen and Larsen 1998). This was considered as a strong indication for a simple clock-and-compass system as the one and only orientational mechanism behind the autumnal progress of juvenile migrants. However, the orientation of the flycatchers on the three sites a few nights following the trapping significantly shifted to the left compared with the standard direction of the population considered. Such a shift is not a possible outcome of a simple clock-and-compass system, but indicative of delayed compensation for displacement by prevailing winds before the arrival to the site of trapping.

Introduction

In a recent publication Mouritsen & Larsen (1998) found no evidence for compensation for geographical displacements 6º (400 km) to the W (Jutland) nor 5º (550 km) to the S (Czech Republic) of migrant Pied Flycatchers trapped on Christiansø in the Baltic Sea.

On the starry night of August 27 1997, following a large arrival to the island in the morning hours of the same date, 48 juvenile flycatchers tested in funnels displayed a rather scattered, but significant, SW-orientation. On the following night the caged birds were exposed for the sunset and early night starry sky on Christiansø. On August 29 two groups of each 16 birds were transported to Jutland (Klelund) and the Czech Republic, whereas a third group of 16 birds were retained on Christiansø. Until September 1 these three groups were each tested on two starry nights. All groups displayed strong and concentrated S-SSW-orientation, i.e. the birds did not compensate for the displacements, and the results are indicative of a simple clock-and-compass system in operation.

The experiment was well designed and carried out (by Mouritsen, Larsen, and this author). However, it constitutes only a single independent sample in a statistical context, as all three groups belonged to the same group of immigrants, and the result is atypical (Rabøl 1985, 1994, 1998): normally, displaced birds (at least when tested under a starry sky) compensate for a displacement, which means that some sort of navigation is involved.

If no compensation for a man-made displacement takes place, the reason may be that the birds were not displaced outside their zones of uncertainty (in terms of the navigatory system of Wallraff 1974; see also Rabøl 1985). The width of these zones may depend on the distance of displacement and on the orientational cues available during the test. Likewise compensatory reactions to preceding wind drift may temporarily overrule the compensatory responses and should be taken into consideration, which was not done by Mouritsen and Larsen (1998).

Comments on the interpretations

Mouritsen & Larsen (1998) interpret the result of this experiment as evidence that simple clock-and-compass is the one and only system used by juvenile birds in the autumnal migratory progress. However, the literature presented by Mouritsen & Larsen (1998) is scanty and a survey by Mouritsen (1999) contains significant errors and questionable interpretations. Furthermore much relevant literature is ignored (Rabøl & Thorup, in prep).

The central observation of Mouritsen & Larsen (1998) is that, “The mean directions of birds displaced to Klelund or the Czech Republic (Fig.2) did not differ significantly from each other in any case (all 95% confidence intervals overlap. Christiansø: 221º +/- 100º (day of capture), 200º +/- 18º, and 188º +/- 18º; Klelund: 222º +/- 47º, 214º +/- 43º, and 196º +/- 30º; and the Czech Republic: 170º +/- 20º and 183º +/-24º: respectively)”. Expressed a little differently: all samples share the same (intrinsic) directional tendency and the reason for the different mean directions observed is stochastical variation, only. However, overlaps in confidence intervals are not necessarily the same as no difference between their corresponding sample means (see below).

Another central point in the scenario of Mouritsen & Larsen (1998) is that the birds arriving to Christiansø on 27 August are perceived as originating in Sweden or perhaps to small extent directly from Norway or Finland. However, in all probability the birds were not “Scandinavian” on their first southward leg, but of Finnish/Estonian/Latvian origin with a southwesterly standard direction. During the night before 27 August, a fairly strong ESE-SE wind from Litaunia/Poland turned to SSE close to the Swedish coast (Stig Rosenørn, Danish Meteorological Institute, pers.comm.). On Christiansø the ground-wind was SE and the speed about that of a migrating flycatcher. The same weather prevailed during the previous 5-6 days, so a mass arrival from Sweden to Christiansø was not possible of flycatchers heading SSW or even S. Recoveries of Swedish pullus-ringed Pied Flycatchers indicate a standard direction of SSW – down to about latitude 52ºN (J.J. Madsen, pers. comm.).

The orientation on the first night (27 August) following the arrival was 221º - 0.31* (n = 39), which is clockwise to all six mean directions (starry nights) on Christiansø, in Jutland and in the Czech Republic on 30 August to 1 September (P = 0.03, Binomial Test). The pattern appears bimodal and doubling the angles leads to 243º/63º - 0.28*. Bimodal or not, the pattern indicates that the birds did not compensate for the presumed winddrift towards NW, but only proceeded in their standard/(reverse) direction. Furthermore, it is possible to compare the three sub-sample distributions on Christiansø 27 August with the distributions of the same sub-samples on Christiansø, in Jutland and in the Czech Republic on 30 August, 31 August and 1 September. These sub-samples are not presented by Mouritsen & Larsen. The Christiansø sub-sample displayed bimodal orientation on 27 August (248º/68º - 0.43, n = 14), and differed significantly from both the 30 and the 31 August orientations on Christiansø (P < 0.05, Mardia-Wheeler-Watson test) as did the Czech sub-sample between 27 August and 31 August (the repeated claim of Mouritsen & Larsen (1998) of “lightbiased” orientation on 31 August in the Czech Republic is speculation based on my rash field notes, and their conclusion is not shared by me). The three remaining comparisons showed no significant difference at the 0.05 level. The counterclockwise shifts are not compatible with a simple clock-and-compass system. Furthermore, the mean vector of the combined last experiments on the three sites 190º - 0.73*** (n = 47) differs significantly from the expected standard direction (220º, P < 0.01, confidence interval test). According to Weindler et al. 1995, the standard direction of Latvian birds is about 220º.

The other sample

Mouritsen & Rabøl also tested the orientation of another 48 Pied Flycatchers that arrived to Christiansø on 26 August in similar weather and undoubtedly from the same general region as the 27 August birds. This experiment is not mentioned by Mouritsen & Larsen (1998). The orientation on the starry night of 26 August on Christiansø was 180º - 0.31* (n = 43), or doubling the angles 176º/356º - 0.34*, i.e. a bimodal pattern was prominent. The doubled angle distributions on 26 and 27 August differed significantly (P < 0.01, Mardia-Wheeler-Watson test). A reasonable explanation could be that the birds on 26 August were more motivated and – without delay – compensated for the preceding displacement by the wind.

The Conclusion

In conclusion, the SW orientation on Christiansø on 27 August should be considered as simple compass orientation in the standard direction, whereas the S and SSW orientations on all three test sites from August 30 until September 1 may contain a component of delayed compensation for winddrift which dominated both tendencies to compass orientation in the standard direction and compensatory reactions to the man-made displacements. Therefore, the interpretations and generalizations of Mouritsen & Larsen (1998) are not substantiated.

References

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* I used the presentation in Mouritsen, H. (1998). Compasses and orientational strategies of night migrating passerines. Ph.D.thesis, Odense University, Denmark, pp.89-105.

** Later published in RIN 01 Orientation & Navigation – Birds, Humans & Other Animals. Oxford.

The paper was never published in J. Exp. Biol. In a letter dated 2 March 2000 the editor (R.G. Boutilier) remarks that *"both referees raise a number of critical points, and neither is sufficiently enthusiastic to enable me to accept your paper for publication"*.

Certainly, none of the referees were enthusiastic. Both claim that I gave too little information about the arrival weather. This is an interesting point as Mouritsen & Larsen (1998) gave absolutely no information on the arrival weather. One of the referees knows for certain that "Drift compensation is no navigation". He probably means that navigation does not need to be involved in compensatory orientation.