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Point-of-view

Rethinking classic starling displacement experiments: evidence for innate or for learned migratory directions?

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In an attempt to encourage the discourse on sources of individual variation in seasonal migration patterns and the microevolution of bird migration, we here critically examine the published interpretations of a now classic displacement study with starlings *Sturnus vulgaris*. Based on the ring recoveries after experimental displacement towards the south and southeast of Dutch capture sites of over 18 000 hatch-year and older starlings, in a series of analyses published in *Ardea* from 1958 to 1983, A. C. Perdeck established that displaced starlings showed appropriately changed orientations only when they were experienced. During both southward and northward migration, released adults navigated to an apparently previously learned goal (i.e. the wintering or the breeding area) by showing appropriately changed orientations. Juveniles showed appropriate directions when returning to the breeding grounds. In contrast, during their first southward migration displaced juveniles carried on in the direction (and possibly the distance) expected for their release at the Dutch capture site. From the mid-1970s this work has become cited as evidence for starlings demonstrating ‘innate’ migratory directions. If the definition of innateness is ‘not learned by the individual itself’, then there is a range of non-innate influences on development that are not ruled out by Perdeck’s experimental outcomes. For example, young starlings might have carried on in the direction that they learned to migrate before being caught, e.g. by observing the migratory directions of experienced conspecifics. We argue that, despite over 60 citations to Perdeck as demonstrating innate migratory directions, the jury is out.

Keywords: innate, learning, migration, navigation, ontogeny, orientation

Introduction

The extent to which phenotypic traits are shaped by genetic information directly and uniformly, or directly yet following environmentally shaping via ‘reaction norms’, or fully moulded during individual development in interaction with the environment by processes of phenotypic plasticity and learning, remain at the heart the main contemporary evolutionary debate (West-Eberhard 2003, Gilbert and Epel 2009,



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Jablonka and Lamb 2014, Laland et al. 2014, Wray et al. 2014). Answers to these questions will also illuminate the sources of individual variation in seasonal migration patterns (e.g. genetic variation or different experiences during early development; van Noordwijk et al. 2006, Harrison et al. 2010, Verhoeven et al. 2019), and indeed the microevolution of bird migration (Alerstam et al. 2003, Pulido and Berthold 2010, Piersma 2011, Gill et al. 2019, Winger et al. 2019). In this dialogue, at least with respect to bird migration, studies on displacement experiments with young and older birds of a species have played a central role. To open-up and encourage this evolutionary discussion, and to emphasize the contributions of studies on migratory birds, in this Point-of-view we aim to ‘rethink’ the published interpretations of these early experimental studies of bird migration.

Starling displacement experiments

In five papers published between 1958 and 1983 in the Dutch ornithological journal ‘Ardea’, Albert C. Perdeck, aiming to study orientation mechanisms, presented and discussed the results of three massive displacement experiments with starlings *Sturnus vulgaris*. 1) In the months of October and November 1948–1957, totals of 7460 juvenile (hatch-year) and 3787 adult starlings were captured during migration in the dunes of the province of Zuid-Holland, the Netherlands, flown to one of three airports in Switzerland (Basle, Zürich or Geneva) and released, usually within 24 h after capture (but see details in Perdeck 1958). 2) In October and November 1959–1962, totals of 2703 juvenile and 885 adult starlings were captured, again in the dunes of southwest Netherlands, and flown to Barcelona, Spain, for immediate release (Perdeck 1964, 1967). 3) In February and March 1964–1971, about 3400 juvenile starlings captured in ‘the middle of the Netherlands’, were transported to and immediately released in either Zürich in Switzerland or nearby Radolfzell in Germany (Perdeck 1974, 1983). These releases subsequently yielded several 100s of recoveries. Comparisons of the locations between groups that were differently displaced and those of non-displaced starlings captured in the Dutch dunes, formed the basis of Perdeck’s inferences.

This experimental displacement of more than 18 000 starlings over a period of 24 years came after a flurry of similar but smaller displacements, often to study ‘homing’, in several bird species in Germany in the 1930s; many of the results were published only after the 2nd World War (Krätzig and Schüz 1936, Rüppell 1937, 1944, van Oordt 1943, Rüppell and Schüz 1948, Schüz 1949, 1950a, b). This German work inspired comparable efforts in North America (Griffin 1940, Rowan 1946). In the Netherlands, Perdeck’s experiments with starlings must have gestated during the pre-War years in the intellectually stimulating setting of ‘Vogeltrekstation Texel’, involving luminaries such as L. Tinbergen, H. Klomp and H. N. Kluyver. In fact, as a try-out, already in 1938 some 600 starlings were captured in the Netherlands and transported before release at Avranches, Lower Normandy, in northwest

France. ‘The outbreak of the war made an end to this experiment before results were obtained’ (Perdeck 1958).

The three displacement experiments represent successive steps in an examination of ontogenetic aspects of orientation, as a component of navigation, in migrating birds. To introduce the first experiment, Perdeck (1958) showed a clear scheme on how recoveries after displacement of actively migrating birds moving in a supposed ‘preferred direction’, would demonstrate either ‘one-direction orientation’ (later called ‘vector navigation’ by Able 2000), or ‘true goal orientation’ (Kramer 1952; Fig. 1). The release of naïve juveniles and experienced adults showed unambiguously that, upon release after a displacement of ca 600 km towards the SSE, juveniles continued in directions quite similar to the ones released at the catching location (i.e. showing one-directional orientation), whereas adults showed reorientation towards the NW to end up in the normal wintering area (i.e. showing true goal orientation; Fig. 1). Juveniles that were released jointly with the adults were recovered at the same general locations as juveniles that were released separately. Likewise, adults released jointly with the juveniles ended up in the same locations as the separately released adults. The second experiment, with displacements to Barcelona, northeast Spain, confirmed the previous results (Perdeck 1967), although a comparison with the Swiss releases suggested that, depending on the time of release and the suitability of the release area, juveniles either continued in the preferred ‘Dutch’ direction or, especially if released later in the year, halted to winter locally (Perdeck 1964). This work led to the third, late winter, displacement experiment, which demonstrated that birds in their first winter were in fact capable of true goal orientation on their first return migration to the breeding areas, just as adults (Perdeck 1974, 1983).

This body of work has become a ‘classic’. The maps from Perdeck (1958) have been used to illustrate goal orientation by adult starlings in at least 12 textbooks on bird migration (Drost 1962, Matthews 1968, Schüz et al. 1971, Baker 1978, Mead 1983, Alerstam 1990, Burton 1992, Berthold 1993, 1996, 2001, Newton 2008, 2010; Fig. 1). In an even-handed early review of orientation and navigation, Emlen (1975) spent five pages reanalysing and considering Perdeck’s experiments. And by now, according to the Web of Science, the paper has been cited over 200 times. Although the direct, factual representations of Perdeck’s findings usually are accurate, we suggest that there are issues with the interpretations in several of the citing books and in many of the journal publications referring to Perdeck (1958). Although part of the publications rightly refer to Perdeck’s experiments as evidence for learning, many publications refer to Perdeck as evidence that young starlings follow an innate compass direction. We take issue with this interpretation.

The history of ‘innate’ interpretations

Although the term ‘innate’ can have several different meanings in biology, which nevertheless are rarely made explicit

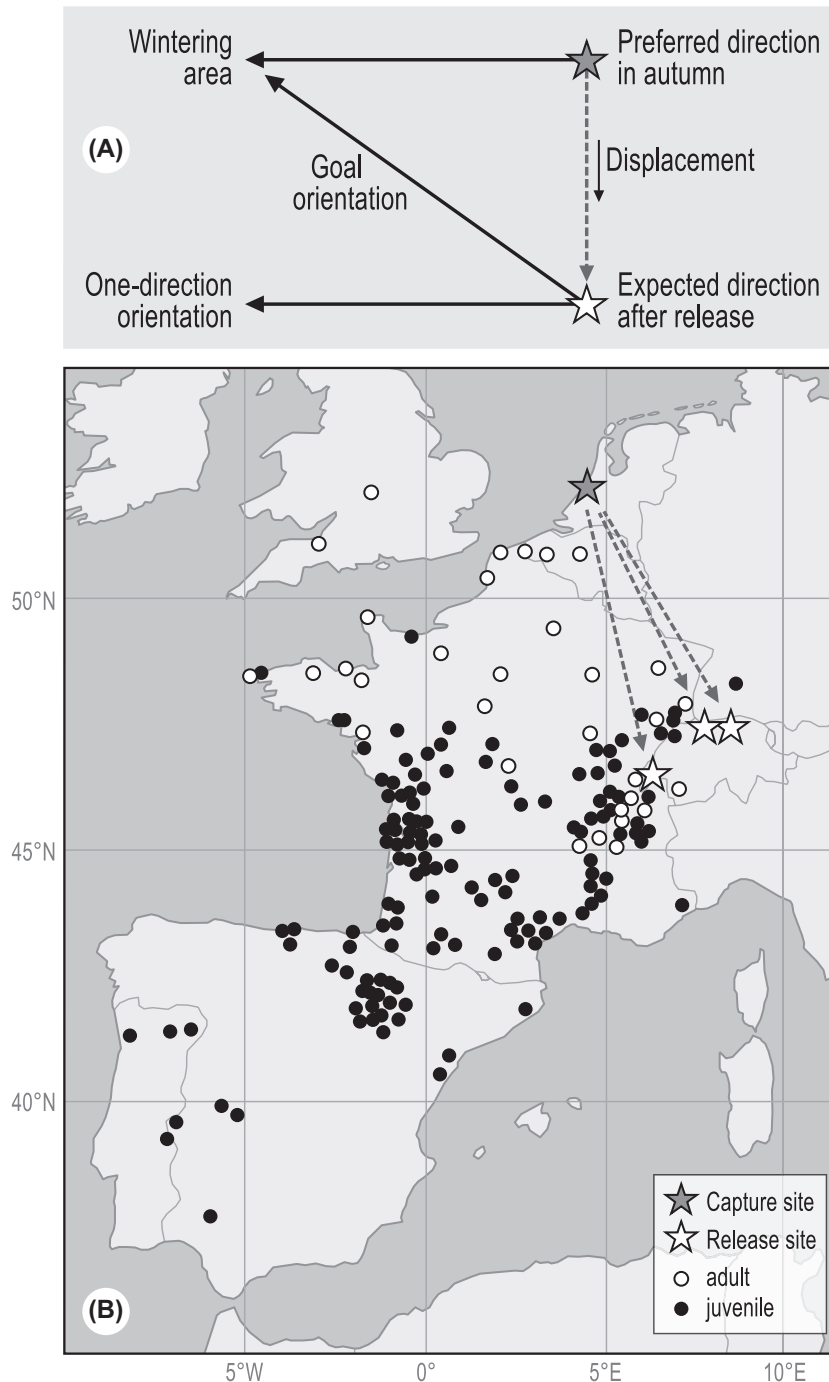


Figure 1. A visual of the orientation hypothesis tested by Perdeck (1958) in his displacement experiments with starlings (top panel) and the distribution of the recoveries from 3 release points in Switzerland of adults (open circles) and juveniles (closed dots) during the ensuing autumns and winters (lower panel). Both panels are based on Perdeck (1958), but this version is modified from Newton (2008).

(Bateson 2000, Mameli and Bateson 2011), we think that in the context of the migration studies the meaning of innate behaviour usually is: behaviour that is not learned by the individual itself. Perdeck himself had been extremely careful in his interpretations of the contrasting findings for juvenile and adult starlings. Following Geyr von Schweppenburg (1933), Perdeck realized that the term 'innate' is ambiguous,

and proposed to call the specific direction in which young birds fly without contact with adults their 'preferred direction', a term with no further connotations as to the other factors that might have influenced its development. However, as we will see below, since the mid-1970s it has become commonplace to use Perdeck (1958) in direct support of statements like 'inexperienced juveniles followed an innate clock

and compass strategy (e.g. vector navigation), leaving at the right time and flying the correct distance in the inherited migratory direction' (to quote a recent review, underlining is ours, by Merlin and Liedvogel 2019). We actually have made such citations ourselves (Ens et al. 1990, Verhoeven et al. 2019). In many cases the attribution is more implicit, with other references being cited too. A recent case is: 'simple, compass-based, vector orientation relying on an inherited initial direction seems to be the only mechanism available to many inexperienced animals that travel without experienced companions' (Mouritsen 2018).

Analysis of references to Perdeck (1958)

To elaborate the claim that the ambiguity with respect to Perdeck's results showing evidence for learning or rather for a 'behaviour that is not learned' ('innate'), we quantified how Perdeck's work has been interpreted. We first reviewed 12 books summarizing the contemporary state of knowledge on bird migration and assembled the ways in which Perdeck (1958) was cited (reproduced as Supplementary material Appendix 1). In August 2019 we used the Web of Science to search for journal articles citing Perdeck (1958) in relevant ways. We had to do this 'indirectly' (through one of the papers in WoS citing Perdeck 1958), as a direct search would not yield the 1958 paper. We found that 89 papers were relevant and digitally available, so that we could search the downloaded pdf's for the text accompanying the citation of Perdeck (1958). Of the 89 papers, 36 were reviews and the rest were topical articles. All the pertinent citations were assembled in a table, which is reproduced as Supplementary material Appendix 2.

For each book or journal article we scored the way in which the findings of Perdeck (1958) had been interpreted. We distinguished three different interpretations. The first was in line with Perdeck's own, allowing the option that the juvenile starlings maintaining the migratory direction of their capture location after displacement reflected learning. This is opposed to newer interpretations of Perdeck's findings as evidence for 'innate', 'inherited' or 'programmed' orientation behaviour, or a combination of these and/or similar terms (Supplementary material Appendix 2). Such attributions could either be 'indirect' (i.e. the Perdeck results being implicated in statements based on other studies), or direct. We acknowledge that there is an element of subjectivity in these assessments, which is why we reproduce all quotes in the Supplementary material Appendix 1–2, with specific indications of the exact formulations that made us assign citations to one of the three categories.

The three books published between 1962 and 1971 very factually reported Perdeck's findings. However, starting with Baker (1978), eight of the nine textbooks discussing Perdeck (1958), attributed the possibility of birds showing innate migratory directions to the outcomes of his experiments (Supplementary material Appendix 1). At the same time, from the mid-1970s onwards, the finding that displaced

young starlings (but not adults) continued in the direction expected from their place of capture, also in the journal articles became cited as having established the existence of innate directions (Supplementary material Appendix 2). Of all 89 publications, 53 (60%) refer to Perdeck (1958) as providing evidence for 'innate' orientation behaviour. In 30 of 53 cases (56%) this interpretation was attributed directly to Perdeck (1958); in the remaining 23 cases the attribution was indirect, invoking other studies to support notions such as 'endogenous vector programmes' (Wehner 1998) or 'genetically encoded programmes' (Muheim et al. 2018).

We suggest that these new attributions reflected the increasing popularity of the neo-Darwinian mind-set (Mayr 1952, 1961, Laland et al. 2011). The interpretation was enforced by 1) the impressive differences between closely related species of *Sylvia* warblers in the amount and timing of migratory restlessness (correlated with natural migration distances) of juveniles raised in isolation from the egg phase (Berthold 1973), and 2) the spontaneous temporal changes in the escape directions in octagonal registration cages of hand-raised garden warblers *Sylvia borin* (Gwinner and Wiltschko 1978). A typical quote from this time is by Wiltschko and Wiltschko (1978): 'The large scale displacement experiments of Perdeck (1958, 1967) clearly demonstrated that young birds on their first migration did not compensate for the displacement and thus apparently do not fly towards a goal, but on a standard direction. Many hand-raised birds isolated from adults showed in cages directional tendencies coinciding closely with the migratory directions of their free-living conspecifics, ... indicating that the information of the migratory direction is indeed innate.' Even though the experiments with hand-raised songbirds suggest that migratory direction may have a strong 'innate' component in the sense that it is not learned by following others, we argue that Perdeck's experiments did not demonstrate this.

Why Perdeck did not show 'innate' orientation?

As noted by Matthews (1968, p. 10): 'Where young and old migrate together the former could possibly learn the migration direction as well as the final location of the wintering area.' Indeed, although both Thorup et al. (2007) and Rabøl (1978) have cited Perdeck (1958) as showing evidence for innate migratory directions (Supplementary material Appendix 2), in a joint publication they state the opposite: 'the starling is a highly social, diurnal, short-distance migrant. This means that (Perdeck's) result could be influenced by social interactions' (Thorup and Rabøl 2007). For this reason, we join Matthews (1968, p. 15) in concluding that 'it is therefore regrettable that the results (of the displacement experiments) cannot be taken as conclusive proof of the existence of an innate directional tendency in the experimental birds.' The hatch-year starlings captured by Perdeck's teams in the dunes near the Hague no doubt had been migrating for some time themselves and were likely part of migrating flocks. These flocks will have been

composites of more or less experienced individuals. Thus, the young birds could already have learned, by non-social or social means, the direction they were supposed to fly in at the moment that they were transported to Switzerland.

In this light it is noteworthy that the direction taken by juveniles displaced to Switzerland was approximately 20-degrees more southward than the direction observed in the Netherlands. Perdeck (1958) offered four explanations for this discrepancy: 1) different methodologies, 2) different years of study, 3) different topographies (called 'leading lines' by Perdeck) and, perhaps most interestingly, 4) different flock compositions. The last point refers to the possibility that the direction observed in the Netherlands is actually a compromise between the true goal navigation of adults and the preferred direction of juveniles. If so, the 20-degree deviation from expectation observed after displacement might show us the uncompromised preferred direction of juveniles.

We believe that Perdeck was correct in considering the possibility that the observed direction in the Netherlands was a compromise between different 'kinds' of individuals, but why did he not offer the same explanation for the direction taken by juveniles after displacement? As an alternative to the later interpretations, i.e. that the displaced juvenile starlings demonstrated the use of 'innate', 'inherited' or 'genetic' information on migratory directions, the experimental birds could simply have demonstrated that they (partly) learned their migratory directions from 1) asocial learning before displacement (e.g. through the reward of food, safety and/or warmth when flying over land instead of water; see discussion by Kendal et al. 2005), 2) the guidance by, or imitation of, experienced adults before displacement, 3) asocial learning after displacement (e.g. in dealing with 'leading lines' in Switzerland) and 4) social learning from local adults after displacement to Switzerland.

The present state of the art

We will round off by presenting a tantalizing example of the complexities of early development of migratory direction in a social bird species. It begins with the results obtained from the pre-War westward displacements of hand-raised white storks *Ciconia ciconia* across their European migratory divide from what was then Rossitten in east Prussia (Schüz 1949, 1950a, b, Mayr 1952, and see Schüz 1938 for an impression of the flavour of the place and the research effort). Hand-raised eastern white storks transported towards the west, and released after the local (western) storks had departed south, showed significantly more easterly bearings (Schüz 1949) than the 'controls' released earlier. The early released birds clearly migrated in the company of locals in south-westward directions (Schüz 1950a). Note, however, that the late-released displaced eastern birds were not quite as south-easterly oriented as expected (Wallraff 1977). Repeated late-release experiments with naïve eastern storks in Latvia (Katz 1986, cited in Chernetsov et al. 2004) yielded southwesterly, rather than the expected southeasterly, migratory directions.

In an effort to settle the matter, Chernetsov et al. (2004) again hand-raised eastern white storks in what was then the Rossitten and is now the Rybachy area. This time the storks were displaced eastward and released at either normal departure times or after the departure of local birds. With brand-new and advanced tracking technology at hand, Chernetsov et al. (2004) obtained very detailed information on the individual migratory directions by deploying the young storks with satellite-tags. Despite all detail, the results could not have been more ambiguous with respect to the presence or absence of innate migratory directions. Chernetsov et al. (2004) concluded that 'in soaring migrants that are heavily dependent on local topography, social contacts and observation of the performance of migrating conspecifics play a much greater role than in nocturnal migrants that usually fly individually.'

We suggest that we cannot exclude this possibility for Perdeck's starlings as well. The case can only be closed with new experiments that include the translocation of completely unexperienced individuals, i.e. starlings that have been raised without any relevant social information. However, completely excluding all social information is harder than it may sound, as specific social circumstances during or even before hatching (e.g. sounds made by the breeding parent, Gottlieb 1976), and subtle social circumstances after hatching (e.g. conspecifics flying overhead) could all potentially influence the development of migratory preferences. Nonetheless, experiments that exclude specific social information will help to position the study of bird migration in the heart of contemporary studies on the role of individual learning (Gottlieb 2002) in relation to various forms of transgenerational information exchange in adaptation and evolution (Jablonka and Lamb 2014, Laland et al. 2015). For now, the question of whether the preferred migratory direction of Perdeck's displaced young starlings involved learning, or did not, is as open as it was in 1958.

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Supplementary material (available online as Appendix jav-02337 at <www.avianbiology.org/appendix/jav-02337>). Appendix 1–2.