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CLASSICS

Lissaman, Shollenberger and formation flight in birds

Steven Portugal discusses the impact of Peter Lissaman and Carl Shollenberger's classic paper 'Formation flight of birds', published in *Science* in 1970.

For centuries, mankind has been fascinated by V-formation flight in birds. Back in AD 79, Pliny the Elder noted that flocks of geese flew 'like fast galleys, cleaving the air more easily than if they drove at it with a straight front', and since then, numerous ideas have been proposed to explain the function of the V-shaped flocks that are a such a familiar sight. Many of these explanations often implied that there was an energetic benefit to be had from V-formation flight and that each bird within the flock was profiting from travelling as a group; essentially, flockmates were helping each other out. In 1970, Peter Lissaman and Carl Shollenberger published a paper in *Science* that was the first to detail the precise aerodynamic interactions that were likely to be taking place within a flock that could produce an energetic benefit. The authors made specific predictions about where each individual bird should position itself within the V for maximal energetic benefit. Subsequently, these predictions have persisted as the gold standard in comparison with all subsequent work, and as such, the paper was a pivotal point in the study of formation flight.

The premise for the paper was founded in the basic principle that an object flying in a fluid produces lift by creating downward momentum within its span. When a wing is generating lift, the air on the upper side of the wing has lower pressure relative to the bottom side, and air flows from below the wing and out around the wingtips. At the wingtips, vortices – circular patterns of rotating air around the wingtip – are generated (Fig. 1), with a wingtip vortex trailing from the tip of each wing; this results in a vortex trailing from the right-hand wing and a vortex trailing from the left-hand wing. These vortices generate upwash, creating a favourable airflow for other birds flying abreast that they could take advantage of if they flew in the optimal position to capture the upwash. The lift provided by the upwash causes a reduction in the lift power that trailing individuals must produce, and thus can bring about an energetic saving. Between these two regions of upwash, however, there is a large region of downwash – created as a result of air being pushed down as the bird moves forward – that most birds want to avoid.

In their 1970 paper, Lissaman and Shollenberger set out an aerodynamic model of how birds should position themselves side-by-side (wingtip spacing) in a V formation, describing how optimal positioning could reduce the induced power – the power required to maintain enough lift to overcome the force of gravity – requirements of flight for each bird in the flock (Lissaman and Shollenberger, 1970). This comparison was based on the assumption that as wingtip spacing decreases, the induced power required also decreases, as the following bird is now flying in an increasingly stronger upwash from the shed vortices of its neighbour. Similarly, beyond a critical wingtip spacing – as the V formation becomes tighter – the following bird then starts to fly in the downwash produced by the bird preceding it and experiences an increase in costs, as opposed to an energy savings. As such, there is an optimal wingtip spacing that maximises the benefits of flying in formation while minimising any potential costs as a result of downwash. Lissaman and Shollenberger expressed their analysis by comparing formation flight in relation to flying solo, or rather, the induced power of a single bird as part of formation was then expressed as the ratio of the induced drag in formation compared with solo flight ($1/e$; Fig. 2) (Lissaman and Shollenberger, 1970). The quantitative analysis revealed that for a formation of approximately 25 birds or more, the power requirements for lift can be reduced by a factor of 2.9 if the birds fly wingtip-to-wingtip (Fig. 2). This reduction in power requirements equates to an increase in flight range of approximately 70% for formation flight versus solo flight.

Although formation flight increases flight range, the authors noted that the optimal flight speeds for solo versus formation flight are quite different, with a 24% reduction in speed for formation flight compared with solo flight. To achieve the maximal energy savings, the correct spacing between individuals is essential and these spacings are small. However, the duo adds that assembling in a V-shaped formation is not, in principle, a prerequisite for optimal energy expenditure: abreast in line or an echelon formation would also generate energetic savings for some members of the flock, but the V is the only shape that allows a total equipartition of drag among all members. Based on their calculations, Lissaman and Shollenberger suggested that an exact V is not the optimal aerodynamic flock shape (Lissaman and Shollenberger, 1970), but rather it should be more swept at the tip and less swept at the apex (Fig. 3). Many papers followed in the 1980s and 1990s (e.g. Gould and Heppner, 1974; Badgerow and Hainsworth, 1981; Hummel, 1983; Cutts and Speakman, 1994) that re-examined the Lissaman and Shollenberger model and fleshed out what was a fairly sparsely reported model at the time of publication. Badgerow and Hainsworth (1981) in particular provided more depth to the model and specified the relationships between induced drag and wingtip spacings expressed in Lissaman and Shollenberger (1970) as a single equation:

$$e = rs^{-q}, \qquad (1)$$

where e is the measure of energy savings available through formation flight, r is a

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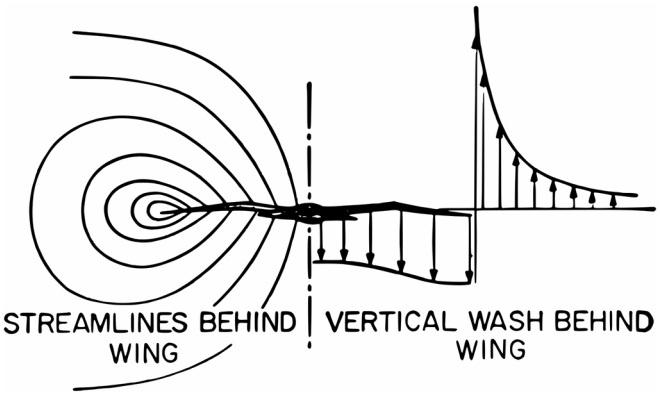

Fig. 1. The flow field of a lifting wing, showing streamlines and vertical velocities, and highlighting the region of upwash on the wingtip. Figure taken from Lissaman and Shollenberger (1970), and used with permission from the AAAS (*Science*).

proportionality constant, s is wingtip spacing and q is a value between zero and one that varies with the size of the formation. Their model also began considering negative wingtip spacings – i.e. when wingtips overlap – something that Lissaman and Shollenberger did not contemplate in the 1970 paper, although it eventually became apparent that this scenario is the most likely arrangement adopted in a V-shaped flock.

Lissaman and Shollenberger also acknowledged that they treated flapping birds as fixed-wing aeroplanes and did not consider the wing flapping component of flight, or the range of possible flapping frequencies that birds are capable of. They allude to the formation shape as possibly being related to the 'flapping wavelength' (the distance the bird moves forward in one wingbeat cycle, linked to the length, magnitude and shape of the air trailing off the wingtip, as well as the speed and flapping frequency of the bird) but concluded that this element was unlikely to be influencing flock geometry, because of photographic evidence showing that the wingbeats of birds flying in V formation are apparently completely unsynchronised. They concluded that if flapping synchronisation was the key requirement in determining flock shape, a zig-zag or sheared line would be equally as good as a V profile. Later research, however, showed that the 'flapping wavelength' is indeed a decisive factor in the shape of V formations and the pivotal component of the aerodynamic interactions that take place between individuals within a flock (Portugal et al., 2014). When it was published, Lissaman and Shollenberger's 1970 paper was largely theoretical because of the lack of suitable technology that could study dynamic V-formation flight, and it wasn't until the invention of biologgers that were able to measure energy expenditure, body movements (accelerometers) and individual positioning (GPS) that many of the key ideas in the paper could be tested.

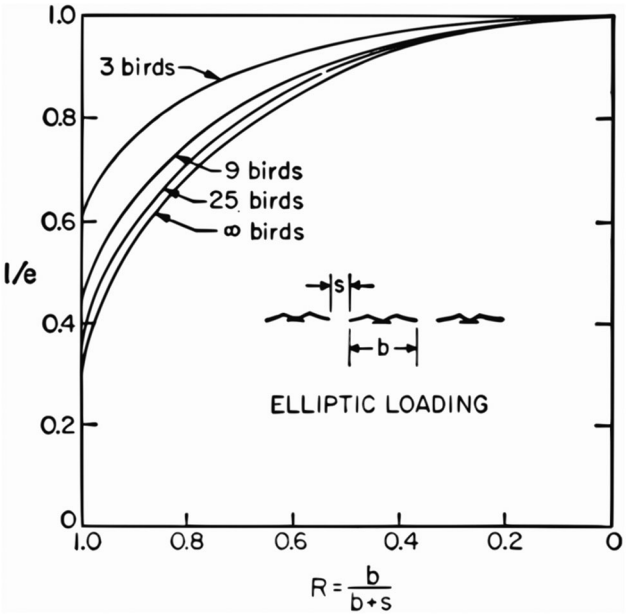

Fig. 2. Drag saving by formation flight. 1/e is the ratio of the induced drag in formation compared with in solo flight. The wingtip spacing index (R) is calculated from wing span (b) and wingtip spacing (s). Figure taken from Lissaman and Shollenberger (1970), and used with permission from the AAAS (*Science*).

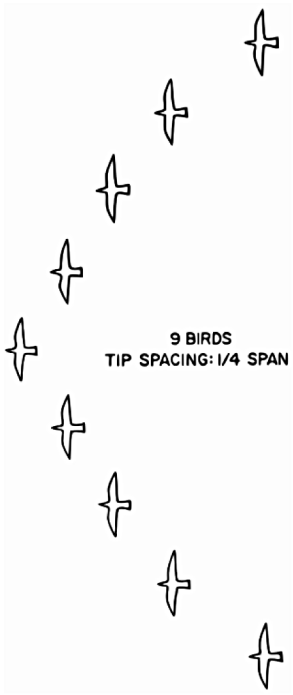

Fig. 3. Optimal V-formation shape, showing apex angle and individual spacing. Figure taken from Lissaman and Shollenberger (1970), and used with permission from the AAAS (*Science*).

In 2001, the first empirical paper that presented evidence for an energetic benefit from V-formation flight was published in *Nature*, by Henri Weimerskirch and colleagues (Weimerskirch et al., 2001). Through the use of implantable data loggers that recorded heart rate – a proxy for energy expenditure – the authors were able to show that individuals flying at the back of a flock of great white pelicans (*Pelecanus onocrotalus*) in a V-shaped formation had lower heart rates and lower wingbeat frequencies than when

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flying alone. The later advent of high-precision GPS and accelerometry data loggers subsequently allowed the study of this phenomenon in greater detail and provided the opportunity to track the movement of each bird within a V formation. In 2014, Portugal and colleagues showed that when flying in formation, northern bald ibis (*Geronticus eremita*) favoured positions that were predicted by fixed-wing aerodynamics that would allow them to profit best from the upwash (Portugal et al., 2014). More interestingly, the ibis coordinated their wing flaps with a phase-shift mechanism which meant that their wingtips followed the path of the preceding bird's wingtips through the air. This mechanism allows the birds to maximise the capture of upwash through positive aerodynamic interactions and means that taking advantage of upwash is an active, not a passive, process. This is in contrast to Lissaman and Shollenberger's suggestion, where they proposed that the phasing of the wingbeats between birds would play no role in the positioning of individuals within the V formation (Lissaman and Shollenberger, 1970).

Another question that Lissaman and Shollenberger touched on was that of leadership in the V formation. Robert May re-visited this question in a paper published in *Nature* in 1979 (May, 1979), where he suggested it would be interesting to know whether the lead bird, considered to be at a disadvantage, would maintain the lead position at the front of the V-shaped formation for long periods, or whether the lead would continually shift. Sixteen years later, a study published by Voelkl and co-workers in *Proceedings of the National Academy of Sciences* demonstrated that the amount of time a bird leads the formation is strongly correlated with the amount of time that the individual had previously benefited from flying in the wake of another bird. This matching of time spent in another's wake versus time spent leading was achieved through frequent pair-wise switches, implying that the birds were cooperating by directly taking it in turns to lead. Interestingly, analyses revealed that this pair-wise switching had a substantial influence on the overall cohesion of the V formation (Voelkl et al., 2015), suggesting that understanding flight in V formation has much to offer interdisciplinary research between game-theoretic models and animal groupings.

Ultimately, Lissaman and Shollenberger's detailed analysis of the aerodynamics behind V-formation flocking has led to hundreds of papers investigating and discussing the topic. Much of this later work set out to determine how 'right' Lissaman and Schollenberger were and whether their model held true for different species, group sizes and contexts (e.g. migration versus local movements). The duo pioneered our appreciation of V-formation flight and, in doing so, acted as a research catalyst prompting the investigation of organised animal movements in many groupings, including fish (Liao et al., 2003), crustaceans (Bill and Hernnkind, 1976), birds (Usherwood et al., 2011) and mammals (Fish and Hui, 1991). More recently, such research has expanded to integrate the rules of collective behaviour (Couzin et al., 2005), social networks (Nagy et al., 2010) and animal personality (Harcourt et al., 2009) into our understanding of organised animal movements, and the findings of these studies have prompted debate about how such behaviours evolved (Andersson and Wallander, 2004) and how the rules for organised group travel are learnt and established through development (Biro et al., 2016). This avenue of research has been viewed as leading the way to identify potential mechanisms to reduce aircraft fuel consumption and increase travel distance by many in the aeronautics industry, and is seen as having much to offer the fields of biomimetics, applied aerodynamics and robotics as we prepare to move into the next generation of technological advancement and artificial intelligence.

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