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Reviews

Organized flight in birds

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The organized flight of birds is one of the most easily observed, yet challenging to study, phenomena in biology. Birds that fly in organized groups generally do so in one of two fashions: Line formations and Cluster formations. The former groups are typical of large birds such as waterfowl, where birds fly arranged in single lines, often joined together. The scientific questions about these groups usually involve potential adaptive functions, such as why geese fly in a V. Cluster formations are typically made up of large numbers of smaller birds such as pigeons or starlings flying in more irregular arrangements that have a strong three-dimensional character. The groups are defined by synchronized and apparently simultaneous rapid changes in direction. Scientific questions about these groups are usually concerned with mechanism such as how synchrony is achieved. Although field observations about the phenomenon date to the origins of natural history, experimental studies did not begin until the 1970s. Early experimenters and theoreticians were primarily biologists, but more recently aeronautical engineers, mathematicians, computer scientists and, currently, physicists have been attracted to the study of organized flight. Computer modelling has recently generated striking visual representations of organized flight and a number of hypotheses about its functions and mechanisms, but the ability to test these hypotheses lags behind the capacity to generate them. We suggest that a multi disciplinary approach to the phenomenon will be necessary to resolve apparently conflicting current hypotheses.
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The orderly aerial manoeuvres of birds have fascinated and mystified observers since the beginnings of written natural history 2000 years ago, when Pliny suggested that geese 'travel in a pointed formation like fast galleys, so cleaving the air more easily than if they drove at it with a straight front' (Rackham 1933). Why do geese fly in a V, and how do pigeons all seem to be able to take off and turn at once? The study of these phenomena offers an encapsulated model of the development of knowledge of other behaviours, starting with anecdotal descriptions and speculation, measured observations of increasing precision, formation of testable hypotheses, and then tests of these hypotheses. In the case of the study of organized flight in birds, the first phase began at about the beginning of the 20th century, the second and third in the 1970s and the fourth in the mid-1980s. The study of bird organized flight also offers a good demonstration of Kuhn's (1962) suggestion that science advances in saltatory fashion, each 'revolution' being prompted by a new technique or apparatus that allows old data to be looked at in a new way.

The early investigators of organized flight were, with a few notable exceptions, biologists. In the 1970s, aeronautical engineers started to be attracted to the phenomenon, followed by computer scientists in the 1980s, and physicists and mathematicians in the 1990s. These later investigators have been primarily interested in modelling the behaviour. The fraction of active investigators with a biological background has steadily decreased over the years. We try to demonstrate that as the elegance of models has increased, so has their distance from behaviour in the field, and that future progress in the area will depend on collaborations between physicists, mathematicians, computer scientists and biologists rather than specialists working alone.

THE ERA OF ANECDOTE AND SPECULATION

Several ornithologists of the 1930s made field observations that would later be very provocative to experimentalists and theoreticians. Nichols (1931) noted that in turning and wheeling pigeon, *Columba livia,* flocks, the position of the birds at the head of a turning flock would be exchanged with birds at the side after the completion of a turn; there did not appear to be consistent 'leadership' in such flocks. He speculated that this behaviour might be the result of faster birds in the front of the formation moving ahead of the flock, then turning back to rejoin. The visual stimulus

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provided by the turnaround might provide a signal for the rest of the birds to turn, apparently simultaneously. He suggested that a change in direction was related to a change in positional leadership.

Selous (1931) made a 30-year series of meticulous observations on various species of birds flying in organized flocks, and was convinced that within the limits of unassisted human vision, there were occasions when birds rose from the ground or made turns simultaneously. He concluded that there could be only two possible explanations for such a phenomenon: disturbance from outside the flock, say the sight of a predator, which would be instantaneously received by all birds in the flock, and would be reacted to in identical manner, or an undefined quality he called 'thought transference', or what we might call today 'telepathy'.

Selous appeared convinced that there were at least some occasions when groups of birds would rise from the ground, apparently spontaneously, with no discernible source of outside disturbance. He also noted in contrast that there were times when a flock on the ground would be indifferent to the rapid approach of an aerial predator, as when members of a flotilla of Eurasian coots, *Fulica atra*, leisurely swam away as a great black-backed gull, *Larus marinus*, made a low pass over their group. Penrose (1949) made a similar observation when he dived from above towards a large European starling, *Sturnus vulgaris*, flock in a sailplane.

Selous also noted that flocks on the ground would sometimes take to the air in a stepwise fashion. Individuals or small groups of black-headed gulls, *Larus ridibundus*, would take flight without any discernible effect on neighbours, and then, with no obvious temporal relationship to previous small group departures, the entire remainder of the flock, hundreds of birds, would take flight simultaneously.

'Thought transference' had a different standing in the scientific community in Selous's time than it does today, and it is not surprising that, for want of a better explanation, a careful observer such as Selous might be led to something as heterodox as telepathy to explain an otherwise inexplicable phenomenon. Rhine (1983) had started reporting the results of parapsychology experiments using conventional experimental design in 1927, and England, where Selous made his observations, was a centre of interest in 'paranormal' phenomena. Selous never explored what the nature of thought transference might be.

Gerard (1943) was one of the first individuals to try to quantify turning behaviour in a flock. While pacing a group of approximately 100 unidentified birds in a car being driven at 35 mph (60 km/h), he observed that the entire flock turned left in a flanking movement, rather than a column movement, in military parlance. In a flanking movement all individuals turn at once upon the signal to do so, rather than advancing to a defined point and then turning. He speculated that no bird advanced more than a body's length beyond any other bird before turning, by his calculation within 5 ms of any other bird. Assuming a minimum reaction time of 100 ms, he proposed that any coordinating signal must have been acted on with great constancy by receiving individuals. Gerard's own vision must have been remarkable to be able to make this observation while driving a car, but his estimate of probable reaction time was very close to Pomeroy & Heppner's (1977) laboratory study results of startle reaction times in the European starling of 70 ms.

Much of the early work on flight flocking was devoted to considerations of the biological utility of flocking, from an ecological or behavioural standpoint, rather than the perspective of organizing principles or mechanisms. Beer (1958) questioned whether large groupings of birds had 'any' distinctive utility, and were merely 'haphazard organizations'. Vine (1971), on the other hand, suggested that a circular grouping provided the best predator avoidance strategy against visual predators. Emlen (1952) looked at flocks from the ethological perspective of the times, and suggested that both flocking itself and the structure of the flock resulted from the interplay of attractive and repulsive behavioural forces.

One of the annoyances that has persisted over the years for those studying flocks is an etymological one; there has been no consistency in the literature in terms of the definition and categorization of 'flock'. The difficulty is not a trivial one. One author might be describing the properties of a class of behaviours that is very different from those studied by another investigator, but both will use the same term.

For example, Emlen (1952, page 160) described a flock as 'any aggregation of homogeneous individuals, regardless of size or density'. This definition immediately presents difficulties, because there are very common aerial groupings, such as mixed icterid groups, composed of different species. Beer's (1958, page 78) definition of a flock was 'two or more birds which associate with each other due to innate gregarious tendencies'. This definition breaks down in the face of more recent flocking studies, such as Reynolds's (1987) study, which suggest that coordinated flocking may be the product not simply of 'gregariousness', but of extremely simple behavioural rules followed by each bird in the group.

Heppner (1974) developed a taxonomy of airborne bird flocks. The primary dichotomy in this scheme was between 'flight aggregations', which are unorganized groups of flying birds gathered in an area for a common purpose, such as gulls circling about a fishing trawler, and 'flight flocks', which are organized groups of flying birds coordinated in one or more aspects of flight, such as taking off, turning and landing. However, these distinctions seem not to have been universally adopted in the literature; one regularly sees the term 'aggregation' used to describe what Heppner would have called a 'flight flock'.

Heppner's second-order division of 'flight flocks' has demonstrated some persistence and consistency in the literature. He differentiated flight flocks into 'line formations' and 'cluster formations' (Fig. 1). Line formations are demonstrated by relatively large birds that fly in regular lines or queues, such as geese, cormorants or ducks. Cluster formations have a three-dimensional structure like a sphere, and are typically seen in smaller birds such as pigeons, starlings and smaller shorebirds. Line-flying birds such as geese may sometimes be seen in a cluster, but cluster-flying birds such as starlings are rarely, if ever, seen flying in single lines.

The categories of biological questions that are raised by each of these formations are very different. Typically, 'how' questions are raised about cluster flocks. Do the birds really turn all at once? How can they achieve synchrony in taking off and landing? How do they decide when to turn, and in what direction? 'Why' questions are more characteristic of line-flying birds. What might be the biological advantage of flying in this configuration? Are there energy savings to be had? Does the formation shape facilitate communication? A broad question that might apply to both groups is whether there is a general advantage to flying in groups, as opposed to solitary flight?

A literature search suggests that investigators recognize that the two formation categories may represent very different biological issues. Early key papers on line formations tend to be cited through generations of papers on line formations, but not cluster formation studies, and vice versa. For this review, we recognize the difference between these lines of investigation, and treat them separately.

LINE FORMATIONS

Line-flying birds typically fly in staggered, or 'echelon', formations rather than in straight lines nose-to-tail. If two such formations are joined at an apex at the front of the formation, we have a V or a J, its asymmetric variant. Franzisket (1951), von Holst (1952)

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