Energy saving in flight formation

Pelicans flying in a 'V' can glide for extended periods using the other birds' air streams.

Many species of large bird fly together in formation, perhaps because flight power demands and energy expenditure can be reduced when the birds fly at an optimal spacing[1-3], or because orientation is improved by communication within groups[4]. We have measured heart rates as an estimate of energy expenditure in imprinted great white pelicans (*Pelecanus onocrotalus*) trained to fly in 'V' formation, and show that these birds save a significant amount of energy by flying in formation. This advantage is probably a principal reason for the evolution of flight formation in large birds that migrate in groups.

We trained eight great white pelicans to fly after a moving motor boat and an ultralight aeroplane in Djoudj National Park, Senegal (Fig. 1). All flight sessions were filmed with a digital camera to measure wing-beat frequency and to synchronize recordings of behaviour and heart rate. The average heart rate was recorded by using an
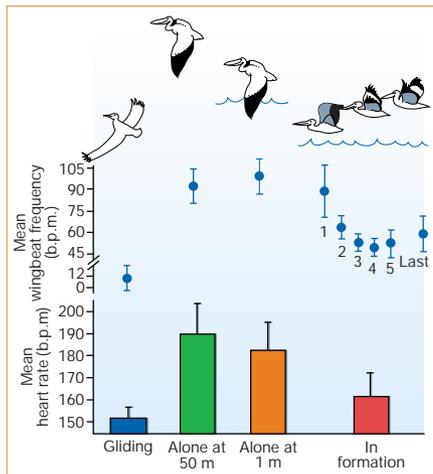
electronic heart-rate logger (Polar Electro, Finland) adapted for large birds[5]; the unit was attached to the back feathers with adhesive tape and the electrodes were placed dorsally about 250 mm apart directly under the skin. Heart rates and wing-beat frequencies recorded during the different types of flight were averaged for each individual over one to four different bouts that lasted for 30 seconds to 2 minutes.

Pelicans flying over water in diagonal formation used the typical flight pattern of pelicans in formation — a few wing-beats, followed by a short, 1–2-second glide — in which 42.2% of the time is spent flapping. Birds flap in time with the leader, either in unison or in regular succession. Within the formation, the number of glides per minute was similar for all birds (average, 12.6 ± 1.6 glides per minute), but the average wing-beat frequency decreased from the leader to the bird in the fourth position (Fig. 2).

When flying alone, 1 m above water or at higher altitude, pelicans beat their wings more frequently than birds flying in formation (Wilcoxon paired signed-rank test: $Z=2.2$, $n=6$ birds, $P=0.028$; and $Z=2.0$, $n=5$, $P=0.043$, respectively), but still glided briefly. When in formation, birds had a heart rate that was 11.4–14.5% lower than in birds flying alone at 1-m or 50-m altitude (Fig. 2; $Z=2.0$, $n=5$, $P=0.043$; and $Z=2.4$, $n=6$, $P=0.018$, respectively). When gliding, birds' heart rates decreased further and they beat their wings only occasionally (Fig. 2; $Z=1.8$, $n=7$, $P=0.068$ for both heart rate and wing-beat frequency). Birds flying alone over water had a slightly higher mean wing-beat frequency and lower heart rates than birds flying at higher altitude (Fig. 2); however, the differences were not significant ($Z=1.1$, $n=6$, $P=0.249$; and $Z=0.1$, $n=5$, $P=0.893$, respectively), suggesting that any ground effect[6] was not significant.

Our results provide empirical evidence that, compared with solo flight, formation flight confers a significant aerodynamic advantage which allows birds to reduce their energy expenditure while flying at a similar speed. In birds flying in formation, each wing moves in an upwash field that is generated by the wings of the other birds in the formation. Modelling has shown that when birds are flying with optimal spacing, a maximal reduction in power can be achieved[3] and total transport costs can be substantially reduced[2]. However, field observations of V formations indicate that birds often shift from their optimal positioning, perhaps in an attempt to maximize

Figure 1 Great white pelicans flying in formation over a river (photograph, R. Marzin, Galatée Films).

the aerodynamic advantage of flight formation[7], thus reducing the energy saving[8] — so geese, for example, may make an energy saving of only 2.4% (ref. 8).

In our study, pelicans often had difficulty staying within the formation, particularly when flying at the rear. But even though these birds were regularly adjusting their position, they still achieved a significant energy saving. This saving may be only partly due to effects of the wakes of other birds on the power input that results from formation flight itself. When flying in formation, pelicans appear to beat their wings less frequently and to glide for longer periods. A rough calculation based on our estimates of the proportion of time spent flapping and gliding in formation, and assuming that the overall costs of the glide–flap sequence is the sum of the gliding and flapping components, reveals an actual saving of 1.7–3.4% as a result of wake effects on power input — this value is comparable to that estimated for geese[8]. The main benefit of flight formation, which until now has not been recognized, could be that by flying in a vortex wake, pelicans are able to glide for a greater proportion of their total flight time, with the total energy savings of 11.4–14.0% being achieved primarily through this strategy.

Formation flight, by allowing birds to reduce their energy expenditure, enables them to increase their foraging or migratory range. Oblique and V formations are comparable in terms of energy gain for individual birds apart from the leader, and are aerodynamically the most advantageous compared with other types of flight in flocks[9]. Pelicans use such flight patterns extensively, not only during migration but also during group commuting trips between colonies and foraging zones[10].

Although pelicans benefit by saving

Figure 2 Wing-beat frequency and heart rate of pelicans engaged in various types of flight (mean ± 1 s.d.). Birds flying over a river following a motor boat cruising at a constant speed of 48 km h⁻¹ flew at an average altitude of 1 m above the water, initially alone at a distance from the boat ('alone at 1 m'), but then joining other birds in formation ('in formation'). Numbering of circles indicates the position in the formation, '1' being the leader. In formation flights, only birds in or behind the third position were used to measure heart rate, to avoid the possible effects of motor-boat turbulence on flight pattern. Wing-beat frequency of the lead and second birds was measured in groups flying far from the boat. Birds flying with an ultralight aeroplane cruising at 55–60 km h⁻¹ at an altitude of about 50 m were not able or willing to fly in the wake of the aircraft, and generally flew at a distance, using a flapping flight, at a speed of 45–50 km h⁻¹ ('alone at 50 m'). Pelicans following the plane finished their flight of 3 km with a glide of 2–3 min ('gliding') before landing on the water. Heart rates averaged 77.6 ± 15.2 beats per min (b.p.m.) when resting, and reached 198.2 ± 18.7 and 204.9 ± 15.7 b.p.m. when paddling in water and when walking, respectively.

energy when flying in formation, this arrangement may also favour communication and coordination within the group — for example, by helping birds to stay in visual contact[4,10] and enabling flight-pass and velocity information to be conveyed between them[6]. This may explain why several other naturally occurring configurations of bird flocks are aerodynamically neutral or even disadvantageous relative to solitary flight[8,11].

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Deep-sea ecology

Developmental arrest in vent worm embryos

Temperature is a key factor in controlling the distribution of marine organisms and is particularly important at hydrothermal vents, where steep thermal gradients are present over a scale of centimetres[1]. The thermophilic worm *Alvinella pompejana*, which is found at the vents of the East Pacific Rise (2,500-m depth), has an unusually broad thermotolerance (20–80 °C) as an adult[2,3], but we show here that the temperature range required by the developing embryo is very different from that tolerated by adults. Our results indicate that early embryos may disperse through cold abyssal water in a state of developmental arrest, completing their development only when they encounter water that is warm enough for their growth and survival.

We obtained early embryos of *A. pompejana* by *in vitro* fertilization, and reared them at temperatures ranging from 2 °C to 20 °C under atmospheric and deep-sea pressures. We monitored mortality (diagnosed by the breakdown of the plasma membrane or by production of irregular cytoplasmic blebs) and zygotic cleavage during early development.

Embryos kept at 20 °C and one atmosphere of pressure all died within 24 h (Fig. 1a), although many completed the first cleavage. At 14 °C and 10 °C, 70–90% of zygotes cleaved, with rates varying as a function of temperature. At 2 °C, oocytes and embryos remained intact, without cleaving, for 72 h (Fig. 1a) and for at least a further 8 days, when we stopped the experiment.

As low hydrostatic pressure inhibits cleavage in other deep-sea invertebrates[4], some irregular cleavages in our one-atmosphere incubations were not unexpected. When we repeated the incubation experiments at *in situ* pressures (250 atmospheres),

we obtained qualitatively similar results (Fig. 1b), with fewer abnormalities.

To investigate whether cold-water developmental arrest is reversible, we maintained zygotes at 2 °C for 72 h, exposed them to a 10 °C heat pulse for 45 min, and incubated them at 2 °C for a further 24 h. Although embryos maintained at 2 °C never underwent cleavage, those exposed to a short heat pulse resumed development, and cleavage continued even after the embryos were

moved back into cold water (Fig. 1c).

The large difference in temperature tolerance between adults (20–80 °C) and embryos (2–20 °C) precludes the possibility of embryonic development inside adult worm tubes. Optimal temperatures for development (10–15 °C) are found close to the bases of hydrothermal-vent chimneys. As eggs are negatively buoyant upon release, some embryos probably develop on or near the sea floor, just below the adult habitat. However, it is likely that at least some embryos are dispersed by currents and carried to new sites through cold (2 °C) abyssal sea water, as occurs in other vent species[5,6]. Our results show that embryos of *A. pompejana* survive but do not develop at this temperature.

It has been suggested that dispersing larvae of hydrothermal-vent bivalves[7] and polychaetes[8] may delay their development until they encounter warm water. Our results provide empirical evidence for such reversible developmental arrest in a vent species; a similar phenomenon has been reported in larvae of the bathyal echinoid *Linopneustes longispinus*[9]. Although we do not know how long the embryos of *A. pompejana* remain viable at low temperatures, this temperature-sensitive mechanism for controlling development may result in
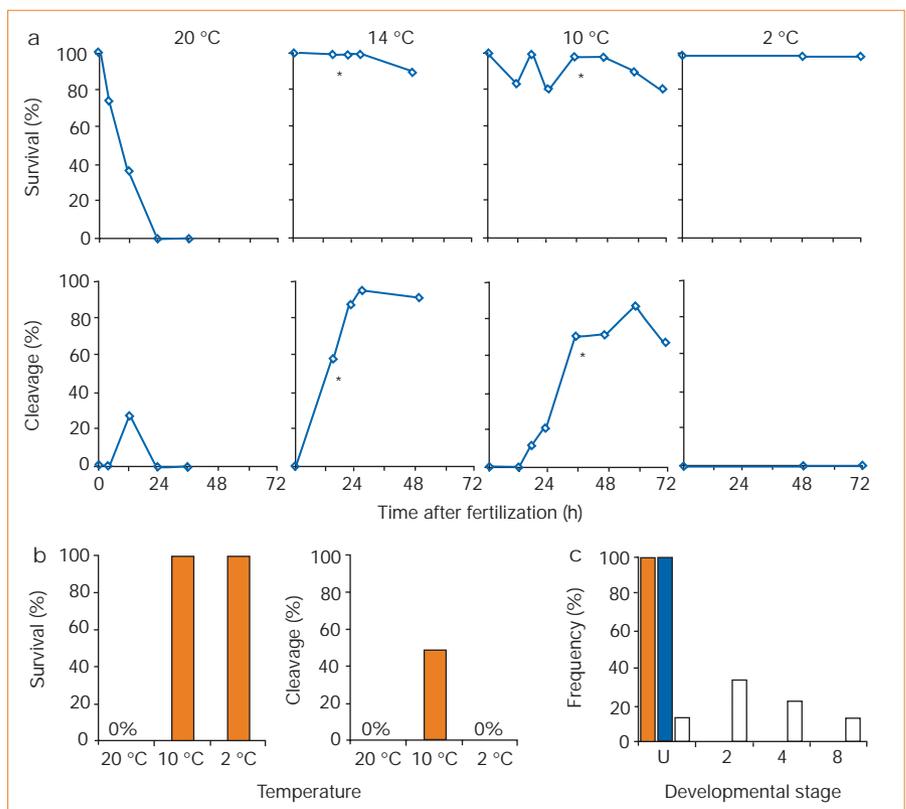

Figure 1 Effects of temperature on early embryos of *Alvinella pompejana*. **a,** Percentage of embryos surviving (top) and cleaving (bottom) when incubated at one atmosphere of pressure and at temperatures of 2–20 °C. At least 20 embryos were scored per sample, except for 2 samples (asterisks), which contained fewer embryos. **b,** Survival and cleavage at the indicated temperatures after 48 h at a pressure of 250 atmospheres. **c,** Distribution of cleavage stages in embryos incubated at 2 °C for 24 h (orange bar) and 8 days (blue bar) and in 72-h embryos exposed to a 45-min heat pulse at 10 °C (white bars), then transferred back to 2 °C for a further 24 h. Developmental stages are two- to eight-cell stages. U, uncleaved.