Phila. Herpetol. Soc. **9**, 11 (1961); *Calif. Agric.* **15**, 8 (1961); *Angew. Parasitol.* **8**, 210 (1967); J. H. Camin, G. K. Clarke, L. H. Goodson, H. R. Shuyler, *Zoologica* **49**, 65 (1964). Dri-Die 67 is a finely divided silica aerogel, containing 4 percent ammonium fluorosilicate. It is not toxic to ectoparasitic arthropods, but it abrades the epicuticle and adsorbs the cuticular lipids, destroying the waterproofing properties of the cuticle and causing death from desiccation. Dibrom, $C_4H_7Br_2Cl_2O_4P$, is an aliphatic derivative of a phosphorus compound and is toxic to the mites. The action of Dri-Die 67 apparently aids the penetration of Dibrom and enhances the toxicity of the latter. Neither acaricide is toxic to the bird hosts.

9. R. E. Ricklefs [*Auk* **85**, 30 (1968)] has analyzed weight recession in the barn swallow and elsewhere [R. E. Ricklefs, thesis, University of Pennsylvania (1967)] has derived equations describing the growth curves of martins and other birds.
10. P. R. Wilson, in preparation.
11. E. E. Klaas, thesis, University of Kansas (1970).
12. Mean maximum nestling weight (MMW; Table 2) was greater for broods of three than for broods of four nestlings in four of six available comparisons. In one case (1968, untreated) the weights were approximately equal, and in another (1969, treated) the MMW of a single brood of four was greater than that of a single brood of three nestlings. In no case, however, was the difference significant. On the other hand, in five of six available comparisons the MMW was greater for broods of four than for broods of five nestlings, and in three cases these differences were significant. The single case in which the MMW was greater for a brood of five than for four nestlings was also significant, but this case (1968, untreated) involved only one brood of five nestlings, and the unexpectedly high weights of these birds may be attributable to unusual food-gathering proficiency of a single pair of parents. In seven available comparisons of treated versus untreated broods of equivalent sizes, the MMW was greater for the treated than for the untreated birds in six cases, and in five of the six cases the differences were statistically significant. In only one instance (1969) was the MMW greater for the untreated broods and in this case the brood size was three, the lower end of the range, at which the food-gathering ability of the parents may be able to compensate for the drain of parasitism.
13. Although several days may elapse between laying of the first and last eggs of a clutch, all nestlings in a given nest tend to hatch on the same day. Weights of nestlings within one brood did not differ significantly over the season when tested according to order of hatching, which indicates that parents tended to distribute the available food more or less evenly among their young. The trend toward equivalent MMW for broods of n in the untreated colony and $n + 1$ in the treated colony was contradicted in the one case where a comparison could be made for the 1967 season (U-4 vs. T-5, Table 2) but was confirmed for the 1965 season (T-4 vs. U-3), the 1968 season (T-4 vs. U-3), and the 1969 season (T-4 vs. U-3; T-5 vs. U-4).
14. D. Lack, J. Gibb, D. F. Owen, *Proc. Zool. Soc. London* **128**, 313 (1957); C. M. Perrins, *Proc. Int. Ornithol. Congr.* **13**, 717 (1963); C. M. Perrins, *J. Anim. Ecol.* **34**, 601 (1965).

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Formation Flight of Birds

Abstract. *Formation flight of birds improves aerodynamic efficiency. Theoretically, 25 birds could have a range increase of about 70 percent as compared with a lone bird, the advantage being more pronounced when there is a tail wind. A vee formation is required to equally distribute the drag saving, and, contrary to other statements, the lead bird does not necessarily have the most strenuous position. The angle of the predicted vee compares with that observed in nature; stability mechanisms are described which make it easy and natural for the bird to sense optimal formations.*

Many birds migrate over long distances, some adopting a very specific vee formation in flight. Aerodynamicists have speculated that this formation is chosen to reduce flight power demand.

Wieselsberger (*1*) suggests that a vee formation would be desirable for approximate equipartition of drag. Because of the simplified analysis only small power savings were indicated. Others, for example, Storer (*2*), describe the mechanism of drag reduction by formation flight without quantitative analysis. There are certainly small power savings for some formations of aircraft, but this reduction occurs only for a dangerously close formation. We have completed a theoretical analysis of formation flight of birds, considering the greater aerodynamic freedom of animal flight. Our results showed that a striking saving in power occurred. Typically, a group of 25 birds has approximately 71 percent more range than a lone bird, and the vee formation is optimal, with the angle predicted consistent with observations. Also, the aerodynamics of optimal formation flight introduce certain invariants which can readily be sensed, making it easy and natural for the bird to fly optimally.

We first established the fixed-wing analog. By applying standard, unsteady wing theory to the ornithopter problem we showed that the flapping power required consists of three terms. Two of these, the profile power and the induced power, are of the same size. The third term, representing flapping losses, is of low magnitude if the ratio of the tip flapping speed to the flight speed is low. The profile power and induced power are identical to those required if the wing were fixed and propelled by other means. Thus, analyzing the bird as a fixed-wing aircraft gives a good estimate of its cruise power requirements. So we considered a fixed-wing vehicle of the same geometry as the bird.

It is a basic principle of aerodynamics that an object flying by dynamic lift in a fluid gets its lift by creating downward momentum within its span. This applies to fish or fowl, airplane or submarine. Beyond the wing there is an upwash field, which is very intense near the tip. Figure 1 shows streamlines and vertical velocities of this flow field. The power needed to generate this lifting momentum is called induced power, which is distinguished from the profile power—the power needed to drive the vehicle through the fluid against skin friction. There is an infinite number of downwash distributions for a given lift. For example, for increased tip lift the downwash at the tip will be stronger than that inboard on the wing. Induced power depends critically on downwash distribution, which itself is related to the distribution of lift across the wing (the spanwise loading). A theorem of

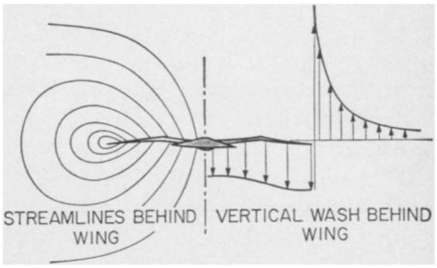

Fig. 1. Flow field of lifting wing.

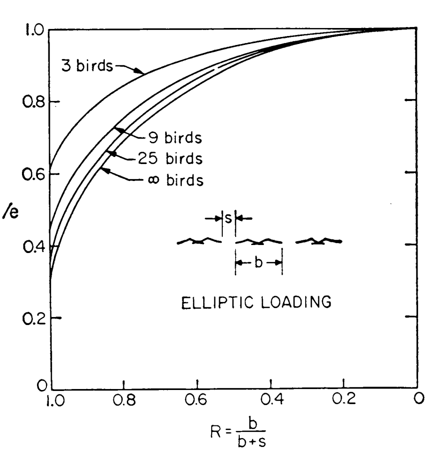

Fig. 2. Drag saving by formation flight.

classical aerodynamics states that, for a single monoplane, minimum induced power occurs when the wing generates a uniform downwash behind it, and this occurs for elliptical loading—that is, when the wing lift varies elliptically from zero at the tip to a maximum at the center.

The upwash beyond the tip creates a favorable interference for other vehicles flying abreast. Each flies in the upwash of neighbors, an effect similar to flying in an upcurrent, with less lift power needed; hence the induced power is reduced. The profile power, needed to drive the vehicle through the fluid, is unchanged.

The optimal spanwise loading (or downwash) maximizes these favorable effects for a set of wings flying line abreast. The general problem is complex; however, we obtained solutions to two limit cases, for a pair of birds and for an infinite set. With the constraints of equal lift and no rolling moment, we found that the optimal loading minimum power differed only by a few percent from the power associated with elliptical loading, for all normal lateral separations. This showed that elliptical loading was always very nearly optimal. We now considered only elliptically loaded fixed-wing monoplanes, for which the mathematics are quite simple. For tip spacing of a few percent of the span, elliptical loading is not optimal but still gives a conservative result for power reduction.

The induced power of a single bird as part of a line-abreast formation was then expressed as the ratio of the induced drag in formation compared to that in solo flight. Figure 2 shows this ratio ($1/e$) as a function of tip spacing. Only the formations of 3, 9, 25, and an infinite number of birds were analyzed. Figure 2 shows the essential data relating to the superior performance of formation flight. Significant drag savings occurred only when the tip spacing was small; and a formation of a score or so was almost as efficient as an infinite number. A bird can adjust its speed to obtain any ratio of induced to profile drag (the total drag being the sum); at high speeds the profile drag is the major component and vice versa. If we assume that the bird consumes fuel at a rate proportional to its flapping energy requirements, then, for maximum range, the cruise speed should be such that the induced and profile drags are the same so that the bird flies at its maximum lift-to-drag ratio. This ratio is directly related to the induced drag efficiency, and the range increases by a factor of $e^{1/2}$ while the optimum cruise speed reduces by a factor of $e^{-1/4}$. Thus, for a formation of 25 birds in tip-to-tip formation, $e = 2.9$, giving a 71 percent range increase with a cruise speed 24 percent below that of the single bird. The formation is more sensitive to ambient winds, and, while it is always better for any wind condition, a formation can use tail winds to much greater advantage than can a single bird because of the lower cruise speed.

The preceding analysis was for line-abreast formation. We now consider the effect of other formations. Munk's stagger theorem, a classical result of aerodynamics, states that any lifting assemblage may be staggered (the wings displaced parallel to the flight path) without changing the total induced drag. So the results hold not only for line abreast but for any planar formation—for example, echelon or vee. However, staggering causes a redistribution of the induced drag, although the total is unchanged. In line-abreast flight, the birds in the center have the maximum drag savings because they are flying in an upwash field caused by neighbors on both sides. In fact, for more than ten birds, the center birds have about double the savings of the tip birds. However, in a vee formation the drag can be evenly distributed. The reason is that in a vee the center experiences a weaker upwash on both sides from the birds behind, while the tip of the vee, although it is in a favorable induced wash from only one side, is in a more fully developed upwash field from the birds ahead.

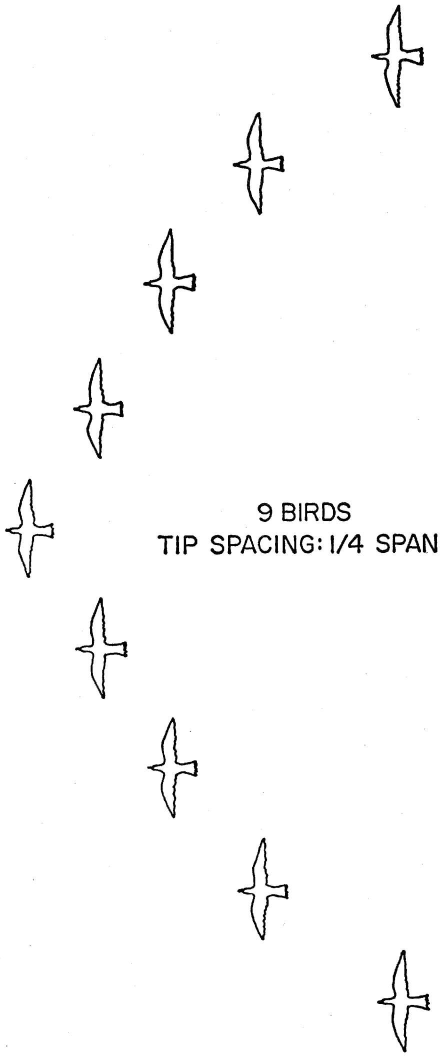

Fig. 3. Optimal vee formation.

The optimal shape of the vee formation, while swept, is not an exact vee; it is more swept at the tip and less at the apex (Fig. 3). Thus, if a line is drawn through the birds in the main part of one side, the lead and tip bird positions are behind this line. The angle is quite a strong function of spacing; with smaller spacing the vee gets sharper. Although an exact vee cannot give an exactly equal induced drag, it seems likely that an angle could be found which would give nearly uniform distribution. Again, a uniform distribution could be obtained by nonuniform spacing; for example, the tip bird could move inward and forward with the same induced drag, and thus "straighten out" the vee.

Formation flight of birds and aircraft differ. To obtain elliptical loading in a group, the aerodynamic shape of a wing (its twist and camber) must be different for different spacings and different positions. The wing must be twisted to have its normal lift in the nonuniform flow field. Also, the tip spacing must be about one-tenth span for significant effects. A bird can operate like this, while a rigid aircraft cannot. Since the drag saving is a function only of the formation, and not of the physical parameters like weight, size, flight, or flapping speeds, these results are valid for all cruising birds.

One may well ask how birds know about elliptical loadings and optimal formations. The vee formation may actually be a natural and easily achieved flight mode. We have shown that elliptical loading is optimum for a single bird, and very nearly so for all group flights, although in a formation the bird has to modulate its wing twist and camber to achieve this. However, if we assume that the main sensory mechanisms of the bird are the bending moments it feels in its "wrist," "elbow," and "shoulder" joint, then, if the bird always adjusts its wing aerodynamics to obtain the same feeling, it will be doing the right thing. So a young bird, having learned to fly solo, will immediately adjust to any slot in the formation simply by flying so that it "feels the same."

As to the vee formation, if a bird moves ahead of the vee line it finds more power is required to keep up with the flight so that, at the same power, its speed falls until it is back in line. Aft of the vee line less power is required. This stabilizing effect is easily sensed if one assumes that the flight will not tolerate malingerers who fly inside the vee where less power is required by one bird at the expense of more work for the main formation. Maybe this sheltered position is used by weaker birds. This implies that the idea that the lead bird has the most strenuous position is incorrect. Any bird can make small position changes within the general vee shape to adjust its drag; in fact, those changes in the streamwise direction occur automatically if the bird flies at fixed power.

The analysis also shows that the formation should be in a near horizontal plane, which is always observed in nature. If the formation were for purposes of visual contact only, many other nonplanar arrangements might be as effective.

It has been suggested that the vee formation is related to the flapping wavelength. Our analysis does not consider the flapping frequency—that is, the wing efficiency as a propulsor has been assumed constant. Propulsive flapping losses could certainly be reduced by favorable unsteady interactions. Calculations of this have not been made, but we believe that the steady induced power is the dominant effect, and that the second-order flapping terms (giving the propulsive losses) are much less important. Support is provided by photographs of birds in vee formation where the wing strokes seem to be randomly phased. If flapping synchronization were the only requirement, a sheared line or a zig-zag formation would be as good. The vee formation is the only one which can equally distribute the load. The vee does not have to be symmetrical, because only the influence of the neighboring half-dozen birds is important. One might have a vee with 15 birds on one side and 10 on the other, and small changes in lateral spacing would give even loading. The important thing is that the front bird should have others on both sides. In other words, one must always have a vee apex, but the legs can be different lengths.

It is interesting that optimal formation flight is at a lower speed than solo. This implies that observations should indicate that a formation of birds cruises at a lower speed than does a single bird of that species.

Many photographs of migrating formations exist, but because of their obliquity it is difficult to determine the precise geometry. It would be of great interest to acquire good data of bird formation, from which actual spacing, vee angle, speed, and flapping frequency could be established.

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Sex Attractant of the Grass Grub Beetle

Abstract. *The sex attractant produced by adult females of the grass grub beetle* Costelytra zealandica *(White) has been isolated and identified as phenol. Field tests with phenol-water mixtures were attractive to male beetles in particular.*

We report phenol, which has been isolated from the female beetle of *Costelytra zealandica* (White) (Scarabaeidae: Coleoptera), as a sex attractant for the male beetle of the same species. The larval stage of this insect pest is of major economic importance in New Zealand, causing considerable pasture damage.

Evidence for the presence of a chemical sex attractant in the female beetle has been described by Henzell *et al.* (*1*). The attractant was isolated from 1500 virgin female beetles by washing their abdomens with diethyl ether. The ether extract was concentrated to 0.5 ml by rotary evaporation at 25°C and 70 mm-Hg, and then sublimed on to a condenser cooled with Dry Ice, in a short-path apparatus at 30°C and 0.001 mm-Hg for 3 hours. The biologically active sublimate in diethyl ether was chromatographed (by spotting) on silica gel plates and eluted with two systems, chloroform and 10 percent ether in hexane. Only one active area, whose R_F value was consistent with that of phenol, was obtained with each system. A similar result was obtained when the extract was chromatographed on Whatman No. 1 filter paper and eluted with water, ethyl alcohol, or a mixture (1 : 1) of diethyl ether and ethyl alcohol.

The active sublimate was dissolved in diethyl ether and examined by preparative gas-liquid chromotography with five different column packings: 10 percent Carbowax 20M on 60-80 mesh Gas Chrome P; 4 percent UCW98 on 60-80 mesh Gas Chrome P; 2 percent Apiezon L on 60-80 mesh Silocel; 2 percent DEGS on 60-80 mesh Gas Chrome Z; 2 percent Altox G-1292 on 40-70 mesh Silocel.

Fractions were collected from each of the columns and bioassayed. An active fraction was obtained only from the 2 percent Atlox G-1292 column. The active compound, approximately 130 μg, had a retention time of 5.2 minutes which corresponded precisely with that of phenol. This collected fraction was dissolved in diethyl ether and examined by mass spectroscopy. Its spectrum was consistent with that of a mixture of phenol in diethyl ether, and the presence of phenol was confirmed by measuring the masses of the ions at (mass to charge) *m/e* 94, 66, 65, and 39. These had the expected compositions of C_6H_6O, C_5H_6, C_5H_5, and C_3H_3. In addition it was established by use of the "defocusing" technique that the following transitions had taken place; $94 \rightarrow 66$, $93 \rightarrow 65$, $66 \rightarrow 65$, and $65 \rightarrow 39$. There was no evidence that the ion $C_6H_6O^+$ had arisen from a precursor of higher molecular weight; therefore it can be confidently concluded that the compound under examination was phenol.

Laboratory bioassay was carried out as described (*1*), except that each fraction was placed on a paraffin dummy which was then dropped among ten male beetles confined under an inverted filter funnel (12 cm in diameter). Beetles responded within a few minutes to dummies treated with 0.1, 1.0, and 10.0 μg, respectively, of pure phenol, by attempting to copulate with the dummies as well as with one another. Eighty percent of the males responded to each amount of phenol on the dummy. Analysis by gas-liquid chromatography (*2*) of