

such as rabbits (*Sylvilagus* sp.), hares (*Lepus* sp.), and pocket gophers (*T. talpoides*), in our study probably were young juveniles or carrion.

Sordahl and Tirmenstein (1980) reported observing a possible helper at a Long-eared Owl nest. The presence of so many owls roosting communally, sometimes beneath active Long-eared Owl nests on the INEL, suggests that some sort of cooperation may have occurred at the nest sites. However, we have no evidence that such behavior happened even though about 6 h were spent in observing one nest through night-viewing devices on two nights in early June (Jim Watson pers. comm.; pers. obs.). Furthermore, on all visits to the nests, only one or two owls defended against our intrusion.

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Visual Angle and Formation Flight in Canada Geese (*Branta canadensis*)

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The V formation, a special case of line-formation flight (Heppner 1974) practiced by large water birds such as geese and cormorants, has spawned several hypotheses about its functional significance. One school of thought (Lissaman and Shollenberger 1970, Badgerow and Hainsworth 1981) holds that the formation evolved to minimize the energy cost of flying, possibly by recapturing some of the energy lost by individual birds through the induced drag associated with winged flight. A different view (Bent 1925, Gould and Heppner 1974) is that the V formation might be related to social or visual factors, and V-formation flight might be a by-product of the characteristics of the visual field of line-formation flying birds. Vision might be essential in coordinated, close-order movements (Potts 1984). If a V-formation flying bird were to have the central monofovea (Duke-Elder 1958) typical of many birds, it would be advanta-

geous to align oneself in the formation such that a neighbor ahead would be positioned on one's optic axis. In this way, the neighbor's image would fall on the fovea, yielding the best possible resolution. If the eyes are relatively immobile in their sockets, as is the case with most birds, it would be possible to bend the neck to change the field of view, but that would increase aerodynamic drag. Although the two hypotheses are not mutually exclusive, it would be instructive to know the angle of view of the eyes of a typical line-formation flying bird, and further, to examine the mobility of the eyes in the sockets of such a species.

During the hunting season of 1982, we obtained the heads of 5 Canada Geese (*Branta canadensis*) from hunters in the field. The heads were immediately preserved in 5% formalin for later examination in the laboratory.

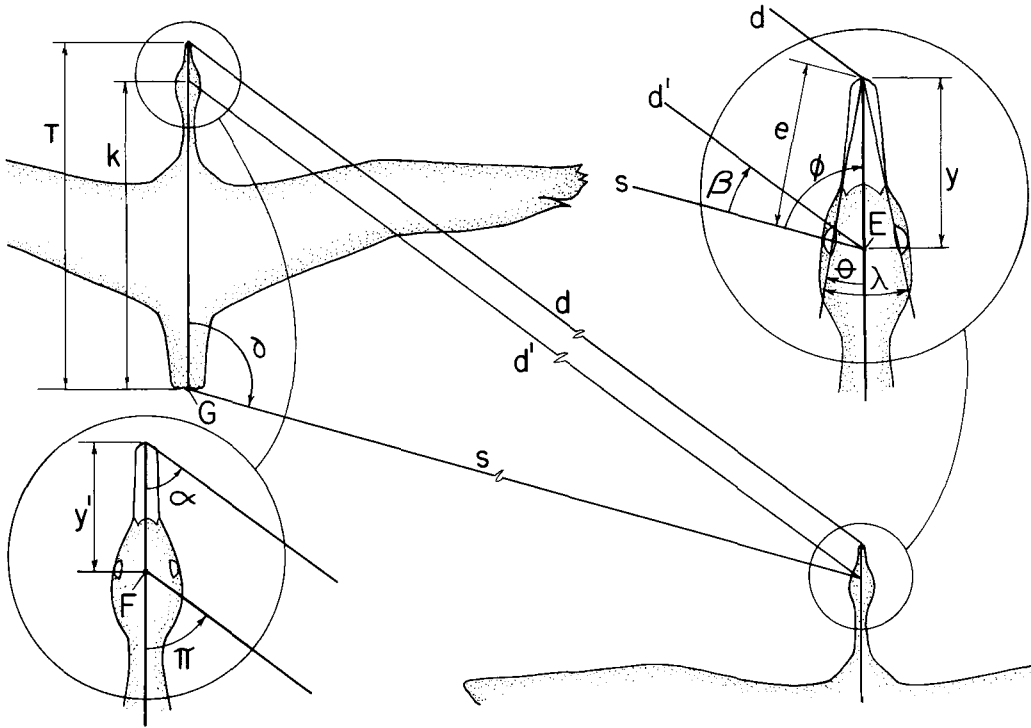


Fig. 1. Geometric determination of angle of formation required for birds to be on the optic axis. See text for explanation.

The heads were mounted in a clamping device and the angle of the eyes (Fig. 1, λ) measured with a goniometer-protractor. The apex of the goniometer was placed over the tip of the bill, and the legs of the instrument were spread until they touched the exposed portion of the eyes. The mean angle of the eyes was $31.4^\circ \pm 2.6^\circ$ SD.

The distance between the optic axis and a line parallel to the optic axis but intersecting the apex of the bill was measured and recorded as the tip-optic axis distance. The mean value of this distance was 8.9 ± 0.6 cm SD.

One head was further studied to determine the actual field of vision. The goniometer was used to determine total width of field, degree of binocularly, and width of the blind area behind the head.

The visual field for each eye was 135° . There was a binocular overlap of 20° and a blind area at the back of the head of 29° on each side of the midline. These values correspond closely with those reported by Molodousky (1979) for other line-formation flying birds such as the Smew (*Mergellus albellus*), which had 25° of binocular vision and a blind area at the back of the head of 31° on each side of the midline.

Two of the eye globes were then dissected out for microscopic examination. The eyes were imbedded

in paraffin, and $5\text{--}7\text{-}\mu$ horizontal sections were made. Bielchowski's silver staining method for rods and cones was used for qualitative determination of cone density. The retina appeared to be avoveate. The orbital muscles were well developed, suggesting a potential for movement of the eye within the orbit.

In the fall of 1983, 3 live, pinioned Canada Geese were obtained for photographic examination of eye movement. A 16-mm ciné camera was mounted on a tripod and aimed at a tabletop surface upon which the goose's head could be firmly pressed, while its body was supported by an experimenter. A vertical grid was mounted behind the tabletop to provide a frame of reference. When the head was immobilized, various objects were moved through the animal's field of vision. Both frontal and lateral views were taken. No individual filming lasted longer than 60 s. Frame-by-frame analysis of the film suggested that some movement of the eye existed, but its magnitude was not greater than $\pm 5\%$ off the optic axis.

A geometric calculation was performed to determine what angle the legs of a V formation would have to be, if the birds were positioned along the visual axis of the eyes (Fig. 1).

If the angle of the eyes is λ , θ is one-half λ , e is the distance between the apex of the bill and the center

TABLE 1. Relationship of angle of view to position in formation. Refer to Fig. 1 for location of values.

Bird number	θ (°)	ϵ (cm)	T (m) ^a	δ (°)	y (m)	d (m) ^a	β (°)	α (°)	2α (°)
1	15.8	8.4	0.85	105.7	0.09	4.1	10.3	63.9	127.8
2	13.7	8.3	0.85	103.9	0.09	4.1	10.5	65.7	131.4
3	15.2	9.1	0.85	185.2	0.09	4.1	10.3	64.5	129.0
4	17.4	9.6	0.85	107.4	0.09	4.1	10.1	62.6	125.1
5	16.3	9.3	0.85	106.3	0.09	4.1	10.2	63.5	127.0
Mean	15.7	8.9	0.85	105.7	0.09	4.1	10.3	64.0	128.1

^a Values taken from Gould and Heppner (1974).

of the eye, $\phi = 90^\circ - \theta$, and y , the distance from the apex of the bill down the midline of the head to the intersection of the optic axis, is $\epsilon/\cos \theta$.

If the visual line S is extended to the tail of the immediate leading neighbor, the smallest possible angle for a V formation that would place the tail of that neighbor on the visual line can be determined. T is the distance from apex of bill to tail, $\delta = 180^\circ - \phi$, and d is the distance from billtip to billtip. For this value, Gould and Heppner's (1974) center-to-center distance was used, with center-to-center and tip-to-tip distances forming equal sides of a parallelogram.

To solve for α , a line parallel to d was drawn from E to F . As T is parallel to y , $d = d'$. Distance $k = T - y'$. Distances k and d' and angle δ are known, so the Law of Sines can be used to calculate angle θ :

$$\frac{\sin \delta}{d'} = \frac{\sin \beta}{k}$$

Because d and d' are parallel lines intersecting a line, angle π is $180^\circ - (\delta - \beta)$ and $\pi = \alpha$. The angle between the legs of a V structured such that the tail of a bird lies on the visual axis of a trailing neighbor is given by 2α . Table 1 shows the measured and calculated distances and angles for the 5 heads studied.

To fly so that each bird on a leg would be on the visual axis of its following neighbor, the angle of the V should be $128.1^\circ \pm 2.1^\circ$ SD. The angles reported for V-formation flying birds are 27.5–44° (Canada Geese, Gould and Heppner 1974), 38–124° (Canada Geese, Williams et al. 1976), and 24–121.75° [American White Pelicans (*Pelecanus erythrorhynchos*), O'Malley and Evans 1982]. It is clear that formation-flying birds typically are not flying along their optic axes. Lack of a distinct fovea would not encourage alignment along the optic axis, because the image of a neighbor presumably would be equally sharp across the visual field.

Of the line formations, the V has prompted the most interest (Higdon and Corrsin 1978, Badgerow 1982). This is natural, because its symmetry attracts the observer's attention. However, those who have studied it in the field have noticed that true Vs are both uncommon and highly variable in structure.

Of the formations Gould and Heppner (1974) stud-

ied, 16.4% were Vs. Williams et al. (1976) noted that "The Vs were rarely regular, and more often should be described as a 'J'." O'Malley and Evans (1982) observed a range of 0.9–10.4% Vs in their pelican formations.

To maximize aerodynamic advantage Lissaman and Schollenberger (1970) suggested that birds should fly in a formation with an approximate angle of 104°. The present study suggests that birds would have to fly in a formation of 128°, so that each bird on a leg would be on the visual axis of its following neighbor. That birds in the field do not fly in either of these configurations suggests that a reexamination of the phenomenon might be useful.

If a behavior confers a selective advantage, one expects to see it used frequently under appropriate conditions. The V formation seems to be characterized by rarity and variability, so the question must be asked, Does the V in fact have any functional significance, or is it simply a by-product of a larger phenomenon of genuine utility?

A V is a type of echelon formation, as is a J or a single-line echelon. If we consolidate Js, Vs, and single echelons into a larger "echelon" category, we find that echelon flight of all kinds is the most common line formation in any of the reported field studies. What might be the significance of echelon flight?

The reported range of V angles for V-formation flight is 24–124°. Dividing those values in half yields the angle of the echelons that make up the V. The most acute angle reported for an echelon is thus 12°.

If the visual field of the Canada Goose is examined, it is seen that there is a blind area to the rear of 29° on each side of the midline. If the angle of the formation were greater than 29°, every bird along the echelon would be able to see every other bird in line, including those flying behind. [This assumes that the birds are not flying exactly on a straight line, in which case nearby birds would block the view of more distant ones. Williams et al. (1976) noted that the apex of the V frequently was rounded.]

If birds fly in a column, they cannot see the birds behind them and lose visual communication with following members of the flock. If they fly abreast of one other, they cannot follow the leader because there

is no obvious leader. Any intermediate echelon will suffice for purposes of visual communication, as long as its angle is not so acute as to put following birds in the blind area. A V is two echelons joined at the apex, and it is perhaps not surprising that echelon flight is common, while V-formation flight is not. If there is functional advantage to the V, it is evidently not of great significance.

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Differential Contribution of the Sexes to Prefledged Young in Red-throated Loons

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The extent of parental investment by each sex is relevant to analyses of mating systems (Kleiman 1977; Ralls 1977; Searcy 1979; Yasukawa 1979, 1981), yet empirical data on time budgets and resource acquisition by each sex are still limited for many taxa. Loons (Gaviidae) are monogamous (Cramp and Simmons 1977) and monomorphic in plumage patterns, and from general theory (Ralls 1977) the sexes could be expected to have roughly equal investment in raising the young. Yet in the 4 loon species, there is moderate size dimorphism, males being 10-15% larger. Greater size may be advantageous for territorial defense or may allow niche partitioning with the female (Selander 1966, Reynolds 1972). However, size dimorphism resulting from sexual selection (Trivers 1972) could indicate reduced male investment. Field studies of loons (Olson and Marshall 1952; Hall and Arnold 1966; Braun et al. 1968; Sjölander and Agren 1972, 1976; Furness 1983; Reimchen and Douglas 1984) indicate that both sexes contribute to raising the young, but the relative investment has not been determined for any of the species.

Red-throated Loons (*Gavia stellata*) on the Queen Charlotte Islands, British Columbia, feed their young marine fish, flying from the lake nesting territory to the ocean for prey throughout the 50-day prefledging period (Reimchen and Douglas 1980, 1984). For

each sex we documented the number and taxa of fish brought to the young and the time budget for foraging flights, brooding, attending, and territorial defense for a nesting pair in 1982 and 1983. Observations were made continuously from predawn to dusk (21 days in 1982, 19 days in 1983), including the first 6 days following hatching and thereafter at intervals over the prefledging period. For the 1982 data, weights of fish were calculated from video tape recordings of feedings (details in Reimchen and Douglas 1984); mean weights for each taxa were determined and used for estimating fish weights for the 1983 data. The pair also nested during 1984, and we supplemented the previous data with records of the proportion of foraging flights made by each sex.

Differentiation of the sexes was made during observations of copulation, which confirmed a marginal size dimorphism, and by a difference in the number and spacing of vertical white lines on the back of the neck, the female having 6-7 lines and the male 10 lines. For each sex, the neck patterns on the breeding plumage were similar over the 3 yr.

Summarized data for 1982 and 1983 are shown in Table 1. Duration of each flight to the ocean to obtain food for the young was significantly shorter for the male than for the female during the first 6 days after hatching; by the third time block (days 27-48) male