

A simple Model for the Use of Doppler Shifted Vocalisations by Migrating Birds

By M. A. Thake

In an earlier paper (THAKE 1981), I advanced the hypothesis that avian nocturnal migrants might improve their orientation by responding to Doppler shifts in the calls of conspecifics migrating around them. The hypothesis is developed further here, and a simple model is devised in a form which facilitates direct testing.

Model

The situation under consideration involves a population of a given species, all individuals of which migrate in the same direction. A single bird (referred to here as the observer) is considered to fly through the airspace used by this population. This bird might adopt various directions with respect to the direction adopted by the population. The population and observer are assumed to fly in the same plane. Equation 1 describes the frequency shift audible to a moving observer, of a vocalisation produced by a single moving source. The angles referred to are defined in Figure 1.

If the population of migrating birds is uniformly distributed around the horizon of the observer, then there are equal numbers of birds within a given unit sector of angular width $d\psi$ at any given time, for any given value of ψ . The calls of all birds within this sector are shifted to equal extents as θ and ψ are similar. Consequently for any given angle between the observer and the population's direction, there are two extreme shifted frequencies, between which all frequencies are approximately equally represented in terms of the number of calls per unit time. The extreme frequencies are overrepresented.

Equation 1 was used to calculate the approximate frequency shifts for various values of $(\psi - \theta)$. Each $(\psi - \theta)$ value yielded two extreme shifts. The range of these two extreme shifts for various angles between the population and observer directions is plotted in Figure 2. The speeds of observer and source are assumed to be similar (10 ms^{-1}). Many birds migrate at higher speeds than this, with a consequent increase in the range of Doppler shifts. Figure 2 therefore represents the range of Doppler shifts audible to the observer at various angles between the observer's direction and that of the migrant population, at the airspeed under consideration.

The situation facing the observer in different contexts is depicted in Figure 3. Shifts of less than $\pm 1.5\%$ are assumed to be below the frequency discrimination ability of the observer; calls shifted less than $\pm 1.5\%$ seem 'normal' to the observer. The observer thus hears normal calls over a range of 3% . If the observer in context B alters its direction away from the direction of flight of the population, until it is flying in an opposite direction to the population (context A), it will hear less normal calls of its own species, and these will constitute a smaller fraction of the total number of conspecific calls heard. If, on the other hand, the bird adjusts its heading towards the direction of flight of the population (context C), it will hear more normal calls and these will constitute a larger fraction of the total.

According to an earlier statement of the hypothesis presented here (THAKE 1981), the observer alters its track in such a way as to hear the maximum number of normal calls. The observer might respond to the absolute number or to the fraction of normal calls. The latter approach on the part of the observer might partially neutralise the effects of patchiness in the distribution of migrants in the airspace. According to the hypothesis, the observer flies for short distances in various directions, memorising the

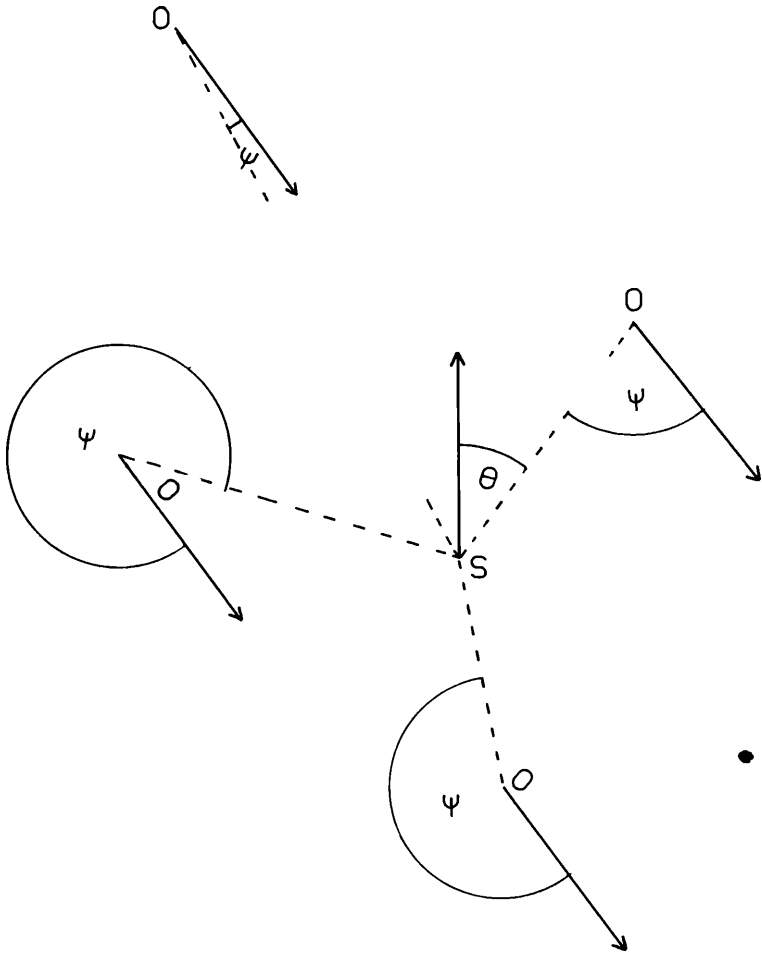


Figure 1 Definition of angles employed. Various relative positions and tracks of a source (s) and an observer (o) are shown. The tracks are coplanar.

Equation 1
$$\frac{f'}{f} = \frac{v + u_o \cos \psi}{v - u_s \cos \theta}$$

- where f' is the frequency audible to the observer
- f is the frequency emitted by the source
- u_o is the speed of the observer
- u_s is the speed of the source
- v is the speed of sound in air

fractions of normal calls heard in each direction. It then decides to fly in that direction in which the highest proportion of normal calls were heard.

As a direct consequence of the hypothesised behaviour, the observer would eventually prefer to fly in a direction which lies closer to the mean direction adopted by the population. I have adopted the view that the observer is willing to accept the direction of the population without question. This is unlikely, but the factors which determine directional decision making in birds are almost completely unknown.

Migrating birds generally show considerable dispersion of their headings, and the simple situation considered above is unlikely to occur in nature. Three cases in which the concentration coefficients differ, are shown in Figure 4. The fraction of normal calls heard by an observer flying at various angles relative to the mean direction is given for each case in Table 1. Clearly, the ability to distinguish between the various possible directional contexts (A, B, etc) depends on a high ability to distinguish between numbers or more probably fractions, as well as an ability to detect small frequency shifts.

In an earlier paper (THAKE 1981), it was pointed out that the mean frequency that the bird observes is shifted to higher frequencies than the normal call frequency. The differences are very small; less than 0,2 % for a bird flying directly against the stream of migrants. Moreover, the position of the mean is readily altered by any skewness in the distribution of directions, or patchiness in the distribution of migrants in the airspace. It seems unlikely that evolution would favour a difficult response when a simpler response would yield better results.

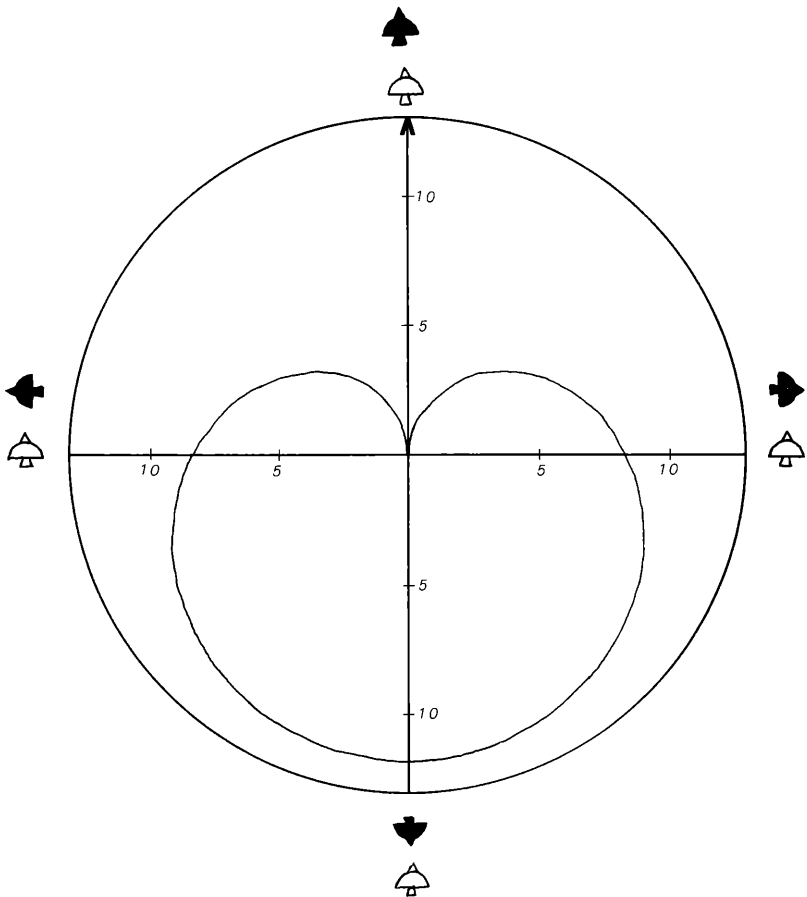


Figure 2 Polar diagram depicting the variation of the range of Doppler shifts with magnitude of the angle between the direction adopted by the observer and that adopted by the population. The figures marked on the radii represent percentage shifts. The dark bird represents the direction of the observer; the pale bird represents the direction of the source.

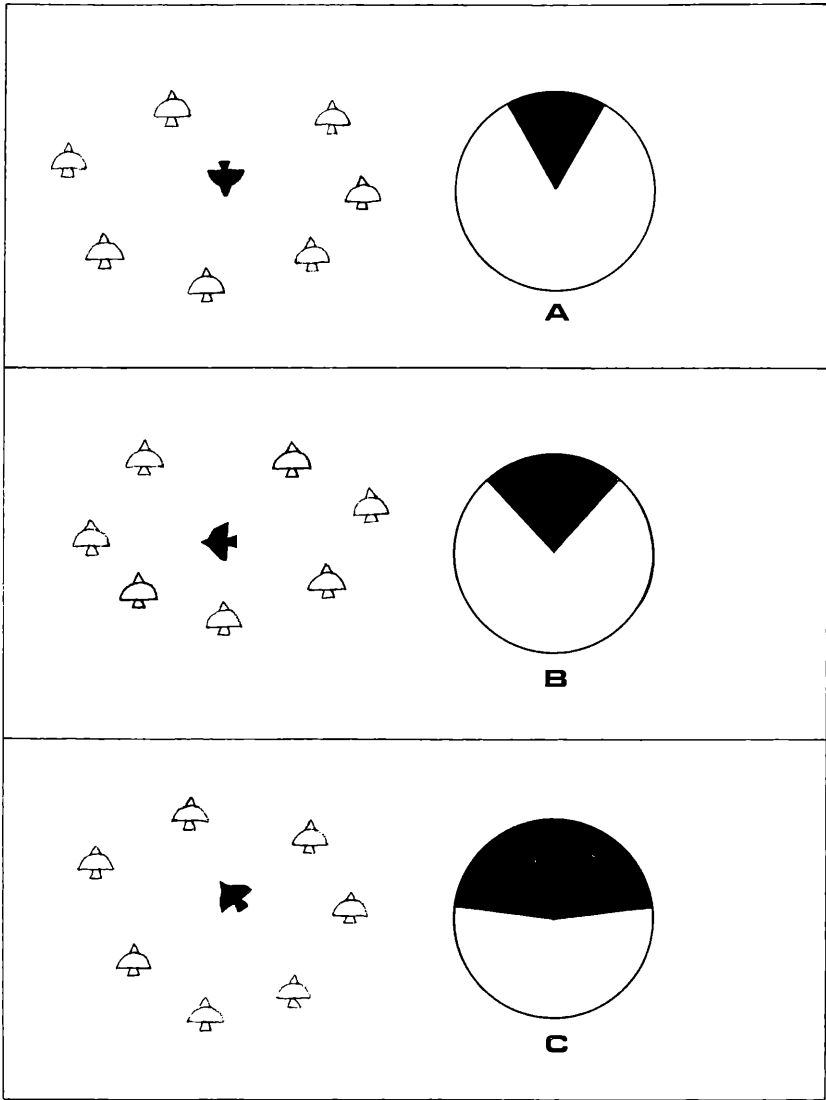


Figure 3 Fraction of normal calls in the frequency spectrum in three different contexts. The dark bird represents the observer while the pale birds each represent a source. The dark sector of the pie chart represents the fraction of normal calls heard by the observer (assuming a frequency discrimination ability of $\pm 1.5\%$, and an airspeed of both source and observer of 10 ms^{-1}). As the direction of the observer approaches that adopted by the population, the observer hears more normal calls and these constitute a higher proportion of the total.

Discussion

Limitations of model

The most obvious limitation of this model is its restriction to coplanar tracks. The qualitative attributes of this model should nevertheless apply to birds migrating in three dimensions.

Natural migrations are complicated by the fact that they often take place in winds whose speeds are comparable to or even greater than the birds' airspeed. The effect of wind on the frequency distributions is not considered in detail here, but is greatest when wind shear is high and migrants at different heights experience different wind directions and/or speeds.

The airspeeds of source and observer were assumed to be similar. Variations of speed would result in broadening of the frequency spectrum. A frequency discrimination ability of $\pm 1.5\%$ has been shown to be sufficient for considerable improvement in orientation. Data on the frequency discrimination ability of nocturnal migrants are not available. Published data for other birds suggest that the frequency discrimination ability is sufficient. The pigeon (*Columba livia var*) is capable of discriminating frequencies which differ by 2.4% (PRICE et al. 1967). The Budgerigar (*Melopsittacus undulatus*) can distinguish between frequencies which differ by as little as 0.7% (DOOLING & SAUNDERS 1973). The Barn owl (*Tyto alba*) has been shown to be able to discriminate between frequencies which differ by only 0.5% (QUINE & KONISHI 1974). The fact that calls of different frequency are available for comparison almost contemporaneously should greatly facilitate discrimination.

The hypothesis developed here requires an external frame of reference. This might be provided by landmarks on the ground, by a star or magnetic compass. Alternatively, an inertial system might allow the observer to determine the angle between successive exploratory directions. Various theories and experiments relating to the use of inertial systems by birds are reviewed by EMLEN (1975).

Intuitive considerations suggest that detection of frequency shifts should be easiest if the calls are pure tones covering a narrow frequency range. Avian flight calls generally do not conform to these requirements. It might be pointed out here that humans experience no difficulty in detecting Doppler shifts in the din emanating from a blaring car radio as the car in question passes the human observer. The distinction is particularly easy if the tune being played is a familiar one.

The most severe limitation is the requirement for large sample sizes. Simple calculations suggest that sample sizes of approximately fifty calls should be sufficient. An observer might accumulate such a sample by flying in a given direction for a short period before sampling in another direction. Under conditions which cause an increase in dispersion of headings, the sample size required for discrimination ought to increase (see case 3 in Figure 4 and Table 1). This requirement might be met by an increase in the rate of calling by each individual under such conditions. Migrant calls are more conspicuous on overcast nights (pers. obs., ABLE 1980), but this might be due to the birds flying low under such conditions. Anecdotal evidence suggests that diurnal migrants call more frequently than nocturnal migrants. Moreover, not all nocturnal migrants may be heard calling. A microphone mounted 150 m above ground in Switzerland resulted in the detection of the calls of thrushes, waders and Ortolan buntings (*Emberiza hortulana*) only (B. BRUDERER, in lit.). Of course, this might be because other species migrated at higher levels in the airspace.

Possible adaptive significance

The most obvious consequence of the hypothesised behaviour ought to be improved orientation. Clearly, it should be advantageous to a migrant to migrate in a direction produced and maintained by natural Selection. The model described here is most effective when the dispersion of directions is slight, i. e. orientation is accurate. As such it could be of considerable use to inexperienced migrants which might be migrating at an angle to the direction adopted by the rest of the population.

As should be apparent from Table 1, discrimination becomes more difficult as the dispersion of headings increases. An increased rate of calling could circumvent this, as would a tendency to fly at low levels which would increase the local density of migrants at this level. The latter response (low flying in overcast) might well have evolved under

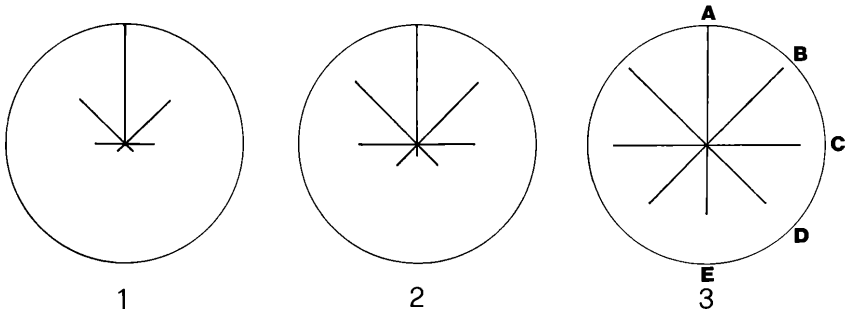


Figure 4 Dispersion of headings in the population. Three cases having different concentration coefficients are depicted. The observer might adopt various headings with respect to the polar direction. These contexts (A, B, etc) are examined in Table 1.

Table 1 Percentage of calls which appear normal to an observer flying in various directional contexts (A, B, C, etc., see Figure 4) in four cases, each having a different concentration coefficient for the distribution of directions of the population. In case 0, all members of the population except the observer fly in direction A.

Case	A	B	C	D	E
0	100	46.5	23.5	17.8	16.4
1	59.9	47.5	33.8	24.5	20.4
2	49.7	44.6	36.2	28.1	24.3
3	40.0	38.7	36.5	34.3	33.0

different selective pressures, but the response is clearly useful in terms of the above model. In addition, if birds participate in the process of information sharing envisaged, the final direction adopted has a dispersion which varies inversely with the number of birds participating (see WALLRAFF 1978, THAKE 1980 for reviews). Synchronous migration by large numbers of birds, which is often observed (LACK 1960), should therefore lead to added advantages.

According to the model presented here, both observer and source might benefit from the fact that the source emits calls. The observer benefits by improving its orientation. The source benefits because the response of the observer makes a mid-air collision with the source less likely. Natural selection should thus favour birds which call as well as those which respond to calls in the manner postulated.

The hypothesis presented here is not incompatible with those of HAMILTON (1962) and GRIFFIN (1969). These hypotheses are less demanding in terms of sensory and integrative requirements, and require fewer participating birds. The present hypothesis however appears easier to test directly. It should be relatively easy to find answers to the following questions. Do birds in migratory condition prefer to hear normal calls? Are migrants able to distinguish between proportions of normal calls?

Finally, it should be stressed that the proposed model is purely speculative and has not yet been tested.

Summary

It is suggested that nocturnal migrants can detect Doppler shifts in the calls of conspecifics migrating around them. Assuming an airspeed of 10 ms^{-1} , maximum Doppler shifts of $\pm 6\%$ are expected. Simple calculations show that a frequency discrimination ability of 1.5% would be suf-

ficient to greatly reduce dispersion of headings. This reduction in dispersion might be achieved if the birds alter their headings in such a way as to hear a greater proportion of normal (i. e. unshifted) calls.

Zusammenfassung

Ein einfaches Modell für die Richtungsverbesserung von Nachtziehern durch Doppler. Effekte ihrer Zugrufe

Es wird die Möglichkeit diskutiert, daß Nachtzieher Doppler-Effekte in den Rufen ziehender Artgenossen wahrnehmen können und dies zur Verbesserung der eigenen Zugrichtung nutzen. Bei einer angenommenen Luftbewegung von 10 ms^{-1} können maximale Doppler-Effekte von $\pm 6\%$ erwartet werden. Einfache Berechnungen zeigen, daß eine Frequenzunterscheidung von $1,5\%$ ausreichen würde, um ein Abweichen der Richtung zu verringern. Ein Abweichen von der Zugrichtung würde vermieden, indem Vögel ihre Flugrichtung dahingehend ändern, daß sie einen höheren Anteil normaler „unverzerrter“ Rufe hören. Voraussetzungen und Grenzen des Modells werden diskutiert.

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