

thought to be related to functional asymmetry in hemispheres of the brain (Annett 1985).

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Estimating Absolute Densities of Flying Seabirds Using Analyses of Relative Movement

LARRY SPEAR, NADAV NUR, AND DAVID G. AINLEY

Point Reyes Bird Observatory, Stinson Beach, California 94970, USA

The 300-m-band-transect sampling method is currently the most widely used method for counting seabirds at sea because it provides an estimate of density (birds/unit area; reviewed by Tasker et al. 1984, Haney 1985; see also Burnham et al. 1980). Density estimates derived from these counts often are affected by variation in detection rates of seabirds caused by several factors, including bird size, color and behavior, as well as weather and observer ability. However, the most critical bias results from the effect of movement by flying birds (reviewed by Tasker et al. 1984). Counts of flying seabirds are actually a measure of bird "flux" and, thus, are usually an overestimation of absolute (i.e. true) density (J. A. Wiens, D. Heine-

man, and W. Hoffman, 1978 unpubl. report to National Oceanic and Atmospheric Administration, Boulder, Colorado). Due to the effects of bird movement, Tasker et al. (1984) concluded that it was "unlikely that the conversion of raw counts of all birds seen (birds/unit time) to bird densities will ever be possible," and Haney (1985) concluded that calculations of absolute densities would not be possible without "considerable additional qualifications." Yet, a standardized approach to seabird censuses is essential for valid comparisons between studies, an important consideration in view of the recent upsurge of seabird studies at sea. Accurate density estimates are particularly critical for calculating energy fluxes and food

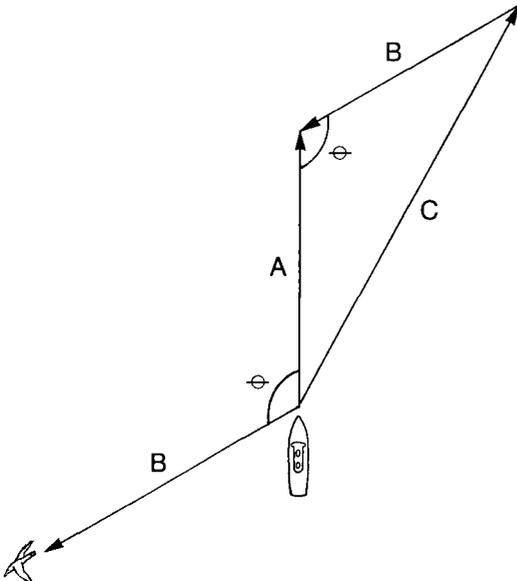


Fig. 1. Example of trigonometric relationship used for calculating correction factor ($K^{-1} = A/C$) from ships traveling at known speed and direction while observing birds of known speed and direction. A is length of ship vector \vec{A} ; B is length of bird vector \vec{B} ; and C is distance moved by ship relative to bird (length of vector \vec{C}). Angle θ equals difference between bird course and ship course. Note that vector \vec{C} equals the difference between \vec{A} and \vec{B} .

requirements, given the importance of seabirds in marine ecosystems (reviewed in Tasker et al. 1984, Croxall 1987). As we shall demonstrate, such an approach also is important for interspecific comparisons of abundance within a single study.

Studies to date have not dealt adequately with flying seabirds. Wiens et al. (unpubl. report) and Gaston et al. (1987:7) derived equations for adjusting observed densities to correct for the effect of bird flight speed relative to the speed of the ship, but they did not correct for the effect of flight direction relative to the course of the ship. To ignore flight direction is unacceptable, because flight is often directional as a result of colony or feeding location, migration, or wind direction (Jouventin and Weimerskirch 1990; Spear and Ainley, pers. observ.), and because the effect of bird flight direction on density estimates can be great (see below). Finally, Tasker et al. (1984) and Gould and Forsell (1989) recommended adjusting for bird flux by making several instantaneous counts during each transect over an area that equaled the area censused during the transect. As noted by Haney (1985), this method is usually not feasible because of observer inability to detect all species equally well at distances greater than 300 m.

We (1) demonstrate the effects of variation in bird

flight speed and direction on estimating absolute densities of seabirds, and (2) introduce a method for correcting counts of flying birds made during standard 300-m-band-transect censuses to yield an estimate of absolute density that will provide a standard for direct comparison between or within studies. This method does not apply to seabirds that are attracted to a ship; the estimation of absolute densities of such birds must be considered separately.

Methods previously used for estimating densities of seabirds at sea consist essentially of dividing the number of birds seen by the area over which the census was conducted. In the case of the 300-m-band census, this area consists of a rectangle with a length equal to the distance traveled by the ship during the transect multiplied by the transect width of 300 m. This method yields what we term an "apparent bird density," because it takes into account only the movement of the ship. When birds are stationary, the apparent density equals the absolute density. If birds are flying, however, the chance of encountering them usually increases because of the additive effects of simultaneous bird and ship movement. Thus, the rate that a given number of birds (traveling in fixed formation at a constant absolute density) will be encountered in a given length of time increases with increase in their flight speed, and values of apparent density increase with increase in flight speed relative to that of a ship. Because it is the motion of the birds relative to that of the ship that determines the rate at which they will be encountered, their flight direction, relative to the course of the ship, also affects apparent density. Thus, with few exceptions, the apparent density of flying birds overestimates their absolute density, and apparent density varies with change in flight speed or direction of the bird relative to the ship.

To adjust values of apparent density to yield standardized estimates of absolute density, one must first determine the relative movements of bird and ship. If the ship movement is represented by vector \vec{A} (Fig. 1), and that of the bird by vector \vec{B} , then the movement of the bird relative to the ship is given by vector \vec{C} (note that the vector \vec{C} is the difference between vectors \vec{A} and \vec{B}); that is, the censuser will encounter the same number of birds per unit time whether the observer and the birds are in motion (the observer at velocity \vec{A} and the birds at velocity \vec{B}), or whether the birds are stationary and the observer is moving at velocity \vec{C} (Wiens et al., unpubl. report). The ratio of C (ship movement relative to movement of birds) to A (absolute movement of ship); C/A , which we call K , is proportional to the magnitude by which apparent density overestimates (or underestimates) absolute density. Thus, we can correct our measure of apparent density for biases induced by the effects of bird movement by multiplying the apparent density by the inverse of K (i.e. K^{-1}) to obtain an estimate of absolute density.

To apply this method, we consider first the simplest case, in which birds are stationary (e.g. sitting on the water or milling over a stationary food source). In this case, the relative movement of the birds to that of the ship is equal to the ship's absolute movement and, thus, $K = K^{-1} = 1$. However, if birds are in directional flight, we first determine relative bird movement, vector \vec{C} , using the law of cosines:

$$C = (A^2 + B^2 - 2AB \cos \theta)^{0.5}, \tag{1}$$

where A equals the distance traveled by the ship in one unit of time (length of ship vector, \vec{A}), B is the distance traveled by the bird in one unit of time (length of the bird vector, \vec{B}), and angle θ is the difference between the ship course and the bird's flight direction. The correction factor (K^{-1}) is then calculated from the relationship: A/C .

The combined effect of bird flight speed and direction on estimation of absolute densities is presented in Figure 2. Because the flight speed of seabirds can range from 25 to 75 km/h (Schnell and Hellack 1979, Pennycuick 1982, 1987, Jouventin and Weimerskirch 1990), and ship speed generally from 10 to 30 km/h, we calculated values of K^{-1} for ratios of bird flight speed to ship speed (B/A) ranging from 1.0 to 6.0. Flight speed can have a large effect on density estimation. For example, when θ is 60° , apparent density can be 0.0 to 5.5 times greater than absolute density, as the ratio of bird to ship speed varies from 1.0 to 6.0. Thus, the magnitude of the effect of flight speed is greater than that predicted by Wiens et al. (unpubl. report). Direction of bird flight, relative to the ship, also can have a large effect on absolute density estimation. For example, a bird flying twice as fast as the ship can have an apparent density from 0.0 to 3.0 times greater than its absolute density, depending on the angle, which varies from 0° to 180° . In the special case when flight speed and ship speed are equal and the angle θ approaches 0° , K^{-1} approaches infinity (i.e. the relationship breaks down). In this case, the angle θ should be set at 10° . Finally, the effect of flight direction depends on flight speed. In particular, at low relative flight speeds, the effect of flight direction is greatest. Note that when bird flight speed is equal to, or less than, that of the ship and the difference between the bird's flight direction and the ship's course is less than 75° , apparent density underestimates absolute density.

Flight speeds of seabirds have been estimated with the aid of a portable radar unit (Schnell and Hellack 1979) and an "ornithodolite" (Pennycuick 1982, 1987), as well as by satellite tracking (Jouventin and Weimerskirch 1990). A radar unit might be difficult to use from a moving ship on most procellariiforms; if birds are not flying directly towards or away from the observer or if they vary in altitude, a correction for angle would be needed, and speeds of birds flying perpendicular to the radar beam cannot be determined. The ornithodolite is difficult to use aboard

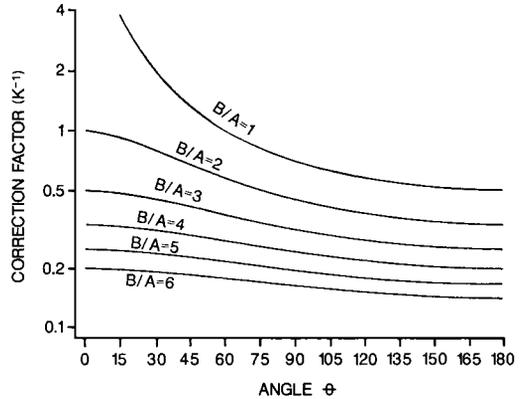


Fig. 2. Correction factor (K^{-1}) in relation to bird flight speed and direction. Angle θ equals difference between bird course and ship course. B/A equals bird flight speed divided by ship speed. Note logarithmic scale for correction factor.

ship because of instability of the observation platform (C. J. Pennycuick, pers. comm.). As an alternative method, we have found that flight speeds of seabirds can be obtained relatively easily by timing them as they fly through a 90° quadrant from a point (a), perpendicular to the ship's beam, to a point (b), directly off its bow, or from b to a , depending on the bird's flight direction (Fig. 3). If birds are being timed as they fly from a to b , then it is necessary that they be flying faster than the ship. Note that C represents a linear approximation of a trajectory that often is not linear, because birds (e.g. procellariiforms) may swerve from side to side or even reverse direction momentarily as they pass between the two points.

The distances of the two points from the ship (lengths of A and B , Fig. 3) can be quickly and accurately measured with a rangefinder and the method described in Heinemann (1981). The distance traveled by a bird (C) flying from a to b can then be estimated from the relationship:

$$C^2 = A^2 + (B')^2, \tag{2}$$

where length B' is equal to length B plus the distance traveled by the ship in the time (t) that a bird requires to pass between the points a and b . Then, the speed of the bird is C/t . If the bird is traveling from b to a , then the method of calculating C is the same, except that B' is equal to the length of B minus the distance traveled by the ship in the time t that the bird requires to pass from b to a .

Usually, it is not possible for one to determine the flight speed of birds observed at sea while simultaneously conducting seabird transects because of time constraints imposed by either activity. Because of this, and because variation in the flight speed of individual seabirds of a given species enroute from one location to another does not appear to be great (see references

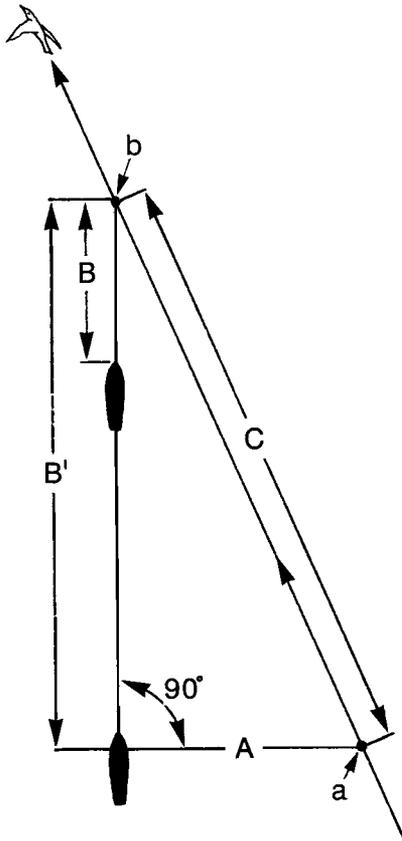


Fig. 3. Example of trigonometric relationship used for estimating bird flight speed. A is distance from bird to ship when bird passes through point a ; B is distance from bird to ship when bird passes through point b ; and B' is distance traveled by ship during time interval t (=time required for bird to pass from a to b), plus length of B . C is distance traveled by bird in time interval t .

above), it is desirable to obtain average flight speeds for each species and to use these values for calculating absolute densities in subsequent observations. Average flight speeds should be known for a range of different wind speeds, and for wind directions relative to the flight direction of the bird. This is particularly important when estimating absolute densities of procellariiforms; flight speeds of these species vary considerably with wind speed (Pennycuick 1982; Spear and Ainley, pers. observ.).

Random error resulting from imprecise measurement of bird flight direction relative to that of the ship can be reduced (with minimal practice) to a maximum of $\pm 15^\circ$, as indicated by variation in values estimated by different (experienced) observers for flight direction of the same bird (Spear and Ainley, pers.

observ.). This type of error is greatest when the difference between bird flight direction and ship course is greatest (i.e. when the effect of flight direction on correction of apparent density estimates is least; Fig. 2). Conversely, when the effect of flight direction on correction of density estimates is greatest, the angle of bird flight relative to ship course is least, as is variation in estimates of the angle by different observers.

Precision in measurement of bird flight direction sometimes is reduced when bird densities are high, because more time is needed to observe, identify and record birds. We believe it unnecessary or inappropriate to record flight direction where concentrations of seabirds are flying in random directions while they search for food over areas that can be several meters to many kilometers wide. In these cases, we record behavior as "milling," where K^{-1} is 1, as noted above. In situations where patterns in flight direction are apparent and bird densities are too high to allow determination of flight direction for each bird, we suggest that an average flight direction be estimated for groups of birds passing in the same general direction. The number of birds arbitrarily grouped and the time interval between estimates of average flight direction should be no larger, or longer, respectively, than will allow adequate time for observation, identification, and recording. Although measurements of flight direction will be less precise, estimates of absolute density should be more accurate than would be expected if flight direction was ignored. Finally, birds often change their flight direction as a result of the presence of a ship in their flight path (i.e. they fly around it). To reduce error resulting from this factor, we suggest that whenever possible observers should record flight direction of an approaching bird when it is greater than 300 m from the ship, or after it has passed the ship. An exception includes hydrobatids, whose flight direction is seldom affected by the presence of a ship until they are less than 100 m away (Spear and Ainley, pers. observ.).

In conclusion, between-study standardization of methods to correct for the bias in apparent density estimates caused by the effect of seabird movement is possible, and important. Correcting for this bias also is important for within-study comparisons, because of the effect on apparent densities caused by a change in ship course and/or speed when bird flight speed and direction remain constant. The converse also is true. If bird flight direction changes, or if different species fly at different speeds and/or directions, bias in apparent densities will result. This is particularly obvious among procellariiforms, where the flight speed of most species is considerably greater than that of hydrobatids. The integrity of between- or within-study comparisons depends on accurate determination of ship speed and course (see Gould and Forsell 1989), wind speed and direction, bird flight

direction, and average flight speed of different species at varying wind speeds and varying wind directions relative to that of the bird.

The methods we have suggested cannot be applied to birds that are attracted to a ship. Estimating absolute densities of these birds poses a problem that remains unresolved, primarily because little is known about the distance from which a given species of bird will respond to a ship. Progress along these lines has been made by Haney et al. (in press), who estimated response distances of some species of seabirds being attracted to ephemeral food sources. More studies of this sort are needed.

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Cost of Short Flights in the Willow Tit Measured with Doubly-labeled Water

ALLAN CARLSON AND JUAN MORENO¹

Department of Wildlife Ecology, Swedish Agricultural University,

P.O. Box 7002, S-75007 Uppsala, Sweden; and

Department of Zoology, Uppsala University, P.O. Box 561, S-75122 Uppsala, Sweden

Accurate measurement of the daily energy expenditures (DEE) of free-living birds depends on the use of realistic values for energy expended in high-cost activities like flight (Mugaas and King 1981, Weathers et al. 1984). Aerodynamic theory (Pennycuick 1968, 1975, Tucker 1970, Greenewalt 1975, Rayner 1979),

material balance (Kespaik 1968 as cited in Hails 1979), and wind-tunnel studies (Teal 1969, Torre-Bueno and LaRochelle 1978) have been employed for determining avian flight costs. Allometric equations based solely on body mass (Berger and Hart 1974, Kendeigh et al. 1977, Hails 1979) and standard multiples of basal metabolism (King 1974) are routinely used to estimate flight costs in studies of energy budgets (Goldstein 1988). The validity of aerodynamic models and wind-tunnel studies for predicting the energetic costs of free flight has been questioned on the basis of studies

¹ Present address: Museo Nacional de Ciencias Naturales-C.S.I.C., J. Gutierrez Abascal 2, 28006 Madrid, Spain.