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Estimating densities of birds at sea and the proportion in flight from counts made on transects of indefinite width

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Abstract

Acknowledgements

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Counts of seabirds at sea are sometimes made without defining an outer transect width or measuring the distance to each sighting. These counts can be converted into indices of abundance by expressing them as birds per unit time or per distance travelled. If the relative motion of flying birds is taken into account, then the comparability of such indices can be improved. In addition, the relative density of birds in flight and on the water can be estimated. We present methods for doing this, based on knowledge of flight speeds and range of detectability. We examine the sensitivity of our estimates to variation in input values and show that, provided that species are ranked in the correct order according to their detectability, then our corrected indices must be an improvement over uncorrected values in making interspecific comparisons.

Introduction

Surveys of seabirds at sea have been carried out over large areas during the past 15 years (King 1974, Brown *et al.* 1975, Powers 1982, Tasker *et al.* 1984). The intention of these surveys has been to identify the distribution and relative abundance of seabirds, partly to assess the possible impact of off-shore oil developments. Early surveys, including the Canadian Wildlife Service (CWS) sponsored PIROP (*Programme intégré des recherches sur les Oiseaux Pélagiques*), were based on observations of 10 min duration made over a variety of arcs of observation and without any fixed transect width. This type of survey has the advantage that it does not depend on the observer's being able to estimate transect width or handle a range finder. Consequently inexperienced observers can make a contribution, an important factor in taking advantage of every opportunity to collect observations over extensive areas.

Results from surveys not using a fixed transect width have normally been expressed either as birds per unit time or as birds per linear kilometre. Both methods are used as indices of bird densities, but both have attendant drawbacks. When observations are expressed as birds per unit time there is a high variance caused by the speed of the ship. However, the correction to birds per linear kilometre takes no account of the fact that at slow speeds most flying birds counted enter the observer's field of observation by virtue of their own motion rather than that of the ship.

These problems have been considered by most writers who have dealt with seabird observations at sea (see references in Tasker *et al.* 1984). In all cases the possibility of producing a better index of abundance by introducing factors other than time and ship's speed have been rejected because additional variables (range of detection, flight speed) could not be measured with sufficient precision to make the effort worthwhile. Intensive surveys of seabirds carried out over the past 10 years have generally involved use of a fixed transect width or estimation of the distance at which birds were observed (Ainley and Boekelheide 1983, Tasker *et al.* 1984, Weins *et al.* 1978, Briggs *et al.* 1985). In all cases they have been dependent on a corps of trained observers.

Here, we attempt to provide a better index of abundance, one which has a lower variability and which allows quantitative comparisons to be made between observations at different ship speeds and between the abundance of different species. We believe that information currently available on range of detection and flight speed, though crude, still allows us to make a big improvement on indices used previously. To test the robustness of our index when imprecise input parameters are used, we have examined the effect of errors in input parameters on the resulting indices for several simulated cases. We have also compared the performance

of our index to that of the birds-per-linear-kilometre index (hereafter, linear index).

In practice the problem presented by transect censuses of seabirds at sea differs from other line transect estimates of birds only in that a large proportion of the birds encountered are in flight. This makes it important to use a density index that incorporates the movement of flying birds into the transect area during the course of the transect. Although a considerable literature is available on line and belt transects for terrestrial birds (see Anderson *et al.* 1976, Järvinen and Väisänen 1975, Sen *et al.* 1974, Burnham *et al.* 1980, and references in Ralph and Scott 1981) these methods do not take into account bird movements unrelated to the observer.

Developing an index of density

The PIROP database has been accumulated over the past 15 years (Brown *et al.* 1975; Brown, 1986). Observations were made by a large number of observers, some of whom had only limited training, and procedures for recording were therefore deliberately kept simple. All birds seen in a 10-min period were counted, irrespective of their distance from the observer. Sometimes the activity of the bird (i.e., flying, on the water) was also recorded. A variety of other information on weather and sea conditions, height of observer, and so on, was also recorded for each watch, as was the vessel's speed. Full details are given in Brown *et al.* (1975).

Maps prepared from this database illustrate the density of birds in terms of the average numbers recorded per kilometre in a given month and grid square. These give a good picture of presence and absence and a good indication of relative abundances. Being compiled from a large number of records (c. 300 000), the resulting figures, at least for the common species, are probably based on large enough samples to make the effect of random variation in the proportion of birds seen and the amount of sea scanned (e.g., due to weather, light conditions, etc.) relatively unimportant. However, expressing the relative abundance of birds in terms of birds per kilometre results in a systematic correlation with ship's speed. As ship's speed is neither constant nor random in relation to area (e.g., in the PIROP data average ship's speeds are generally higher at higher latitudes because of a correlation with the type of vessel used and time of year), this causes bias in comparisons of different geographical areas. In addition, comparisons of relative abundance among species of differing size and colour are affected by differences in the range at which birds can be detected. Those species that are easy to detect appear commoner relative to cryptic species than they really are.

1. Basis of density index

The index is based on estimating (1) the area over which a given species could have been detected during a watch period; and (2) the number of flying birds that can be expected to enter the observer's field of vision during a watch. Our formulae are devised to apply to the 10-min watches used by the CWS's PIROP database (Brown *et al.* 1975), but could be easily modified for data based on different watch periods. We use the following terms:

- Area scanned (A) = total area over which a given species could have been detected during the course of a watch (km^2);
- Density of birds (D) = actual number of birds per unit area at a given instant (birds km^{-2});

- Detection radius (r) = distance at which a particular species can be detected (km);
- Arc of observation = the angle subtended by the observer's field of vision.

Not all birds within the observer's potential range of detection will actually be recorded and the proportion seen changes as a function of distance. This function is termed the "detection function" (Burnham *et al.* 1980) and a variety of techniques have been used to estimate it and use it to correct raw counts. The shape of the function probably varies among species (Weins *et al.* 1978), but as the shape is unknown for the majority of species under consideration we have not attempted to incorporate it. Instead we have based our model on the assumption that all birds are seen within a given radius (Type II estimator of Weins *et al.* 1978), using the arithmetic mean of the detection distances (Gates 1968, 1969).

2. Correction for birds sitting on the sea

Birds that are sitting on the sea are normally either at rest or moving slowly relative to the speed of the ship. Consequently, they can be treated as stationary objects, and the number seen per unit time will be a function of the area scanned (A_s) and the density of the birds (D_s , subscript s refers throughout to birds on the sea surface). Hence

$$N_s = A_s D_s \quad (1)$$

where N_s is the number of birds of a given species seen during a watch.

The area scanned is determined by the range at which a bird is detected (r_s), the speed of the ship ($S \text{ km h}^{-1}$) and the arc of observation over which the observer scans.

Initially, we deal with the case in which the observer scans an entire 360° arc. In that case, the area scanned is a long rectangular strip with a semicircle at each end.

$$A_s = \pi r_s^2 + 2r_s tS \quad (2)$$

where t is the length of the watch in hours. Because PIROP watches are standardized at 10 min (2) can be simplified to

$$A_s = \pi r_s^2 + r_s S/3 \quad (3)$$

Rearranging formula (1) and substituting for A_s yields

$$D_s = N_s / (\pi r_s^2 + r_s S/3) \quad (4)$$

Table 1

Formulae for calculating bird density for a) birds on the sea, and b) flying birds when ship's speed is much less than bird's speed

Arc scanned	Density of birds on sea	Density of flying birds
360°	$N_s/(\pi r_s^2 + r_s S/3)$	$N_f/(\pi r_f^2 + r_f V/3)$
180° forward symmetric about boat's heading	$N_s/(\pi r_s^2/2 + r_s S/3)$	$N_f/[\pi r_f^2/2 + r_f V(1 + 2/\pi)/6]$
180° to one side of boat	$N_s/(\pi r_s^2/2 + r_s S/6)$	$N_f/[\pi r_f^2/2 + r_f V(1 + 2/\pi)/6]$
270° forward symmetric about boat's heading	$N_s/(3\pi r_s^2/4 + r_s S/3)$	$N_f/g_s(r_f, V, S)^*$

*See Appendix 1, Case III.

In some PIROP watches the observer watches only a fraction of the entire 360° arc. The areas scanned are shown in Table 1 for 3 cases: i) scanning a 270° arc symmetrical about the boat's heading, ii) scanning a 180° arc symmetrical about the boat's heading, and iii) scanning a 180° arc on one side of the boat. Watches which are coded as 315° or 360° intermittently are treated as covering the entire 360° arc.

3. Correction for flying birds

The effective area covered by a transect must take into account the bird's speed and direction relative to the ship. (Subscript f refers throughout to flying birds.) When birds are flying in at a speed V in a direction θ relative to the boat, then Gaston and Smith (1984) have shown that the speed of the birds relative to the boat is

$$V_o(\theta) = V \sqrt{\cos^2(\theta - S/V)^2 + (\sin \theta)^2} \quad (5)$$

and the birds appear to be approaching from a direction $\alpha(\theta)$ where

$$\tan \alpha(\theta) = \frac{\sin \theta}{\cos \theta - S/V} \quad (6)$$

For an observer scanning 360°, the area covered is a long rectangular strip, at an angle $\alpha(\theta)$ to the boat's heading, with a semicircle at each end. This strip has width $2r_f$ and length $V_o(\theta)/6$ (for a standard PIROP watch of 10 min). Thus, the area of the strip seen for birds on heading θ is

$$A(\theta) = \pi r_f^2 + 2r_f V_o(\theta)/6 \quad (7)$$

Let $D_f(\theta)$ denote the density of birds flying in direction θ . Assuming birds are equally likely to be travelling in any direction, then $D_f(\theta) = D_f/2\pi$ where D_f is the overall density of flying birds. The density of birds recorded that are flying in direction θ is given by the product $D_f(\theta) A(\theta)$ and the total number of birds seen is calculated by integrating over θ .

$$N_f = \int_{-\pi}^{\pi} \frac{D_f}{2\pi} [\pi r_f^2 + r_f V_o(\theta)/3] d\theta \quad (8)$$

This equation is difficult to manipulate algebraically but it can be solved through numerical integration. However, if the ship's speed is much smaller than that of the birds, then $V_o(\theta)$ will be close to V . Substituting V for $V_o(\theta)$ in (8) gives

$$N_f = D_f(\pi r_f^2 + r_f V/3) \quad (9)$$

The impact of substituting V for $V_o(\theta)$ was evaluated through a numerical integration of (8). The integral was evaluated using the trapezoid rule with 1000 division points. It was found that if the boat's speed was one-fifth the bird's speed or less, then the error caused by the substitution was less than 1%, whereas if the boat's speed was one-half of the bird's speed the error climbed to 6%.

Rearranging equation (8) gives the formula for the density of flying birds

$$D_f = \frac{N_f}{\int_{-\pi}^{\pi} [\pi r_f^2 + r_f V_o(\theta)/3] / 2\pi d\theta} \quad (10)$$

In the special case where S is much smaller than V , the density of flying birds is

$$D_f = \frac{N_f}{\pi r_f^2 + r_f V/3} \quad (11)$$

The derivation of the formulae for the three cases in which the observer watches only a portion of the 360° arc are given in Appendix 1. The formulae for the case in which S is much less than V are given in Table 1.

The formulae (10), (11) and those in Table 1 apply only where birds are equally likely to be flying in any direction. If the birds are flying with uniform headings and the ship is in motion, then the number seen will be affected by the angle between the ship's heading and the bird's heading. This information was not recorded in most records in the PIROP files. We have therefore assumed that errors introduced by this effect will be randomized with respect to different areas and species.

In practice, whether birds were flying or on the water was not always recorded. Consequently, we must use the proportions of these two categories derived from the subset of observations (usually $\geq 50\%$) where this information is present. If p is the proportion of birds that are recorded as flying then $N_f = N_p$ and $N_s = N(1 - p)$.

Further modification of this formula is necessary for the case of birds that maintain a zigzag course. The rate at which these birds enter the observer's field is proportional to their ground speed averaged over a number of zigzags and we have used a species-specific constant (K) to estimate average ground speed (V') where

$$V' = V/K$$

with K varying from 1.0 for the most direct fliers (alcids) to 1.5 for the least direct (procellarids) (cf. Croxall *et al.* 1984).

Where this modification is included V' is substituted for V throughout.

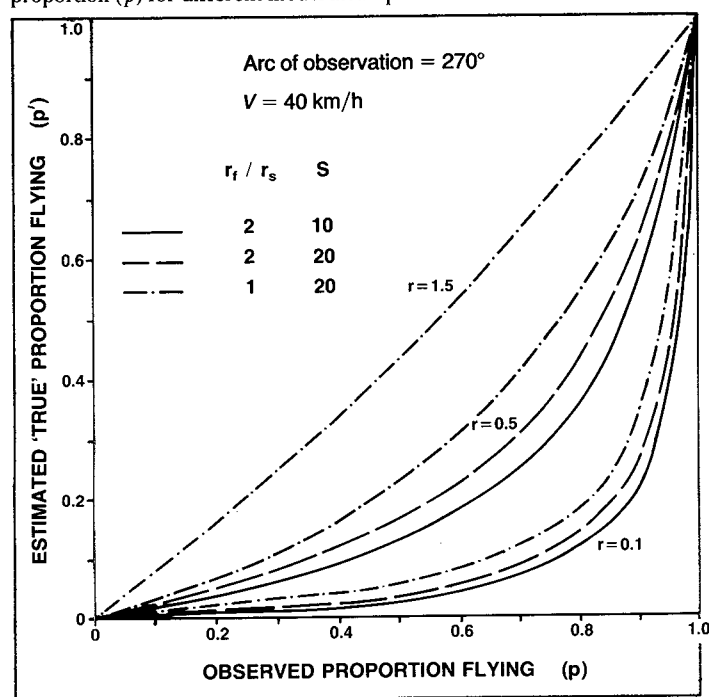
4. Proportions of birds in flight and on the water

The true proportion of birds in flight (p') can be estimated from

$$p' = D_f/(D_f + D_s) \quad (12)$$

By substituting for D_s and D_f from formulae (4) and (11) we can estimate p' from p , r_f , r_s , V and S . When S is less than half V , p' can be simplified using the procedures

Figure 1
Relationship of true proportion of birds in flight (p') to observed proportion (p) for different model assumptions



described above. Explicit formulae for p' are given in Appendix 2.

Estimates of p' for different values of p show that the difference between the two is greatest where p is about 0.5, and least in the extreme cases where p approaches 0 or 1 (Fig. 1). Using hypothetical values for r_s , r_f , and V there seems to be relatively little difference in estimates of p' for different values of r_f relative to r_s . The difference between the two decreases with increasing ship's speed and decreasing flight speed, but remains substantial for $V = 40$, $S = 20$ and $V = 20$, $S = 10$ (Fig. 1).

Results

1. Comparison of observed and calculated proportions of birds in flight

The proportions of birds in flight (p) were calculated for 19 taxa from the PIROP data sets for each of the 7 months September through March (Table 2). (Birds in behaviour categories 10, 40–43, 60 and 65 were counted as “flying” [F], and those in categories 20–30 inclusive as “swimming” [S] [Brown *et al.* 1975]; thus $p = F/[F + S]$.)

These values of p were then used to estimate true proportions of birds in flight in each month, from equations 10 and 12. The mean ship's speed in each month was also calculated from the PIROP data. Values of bird flight speed (V), radius of detection (r_s), and the ratio r_f/r_s were obtained from the literature (Table 3). Zigzag indices (K) were assigned on the basis of casual observations. To increase comparability we have taken all estimates of r_s from a single source (Dixon 1977).

Calculated values of p are given in Table 4; comparison with Table 2 shows the extent to which the number of flying birds can be overestimated if this correction is not made. For “species-months” where $\geq 95\%$ of observations are of birds in flight the effect is fairly small, with estimates of the true proportions in flight exceeding 80%. However, where the proportion seen in flight is less than 80% the effect is striking, with estimates of true values mainly less than 70% of observed proportions. The correction therefore has important implications in the use of counts made at sea to derive the proportions of time spent in flight by certain species; this would be the case where the data are to be used in estimates of daily energy expenditure.

2. The effect of inaccuracy in the estimation of input parameters on the estimate of bird density

To test the effect of variation in input parameters we considered two models: (1) a “puffin” type species, with low contrast when seen against the sea, and flying fast and direct and (2) a “fulmar” type species, with good contrast when viewed against the sea, and flying at a slower speed with much zigzagging. The values adopted for the variables are taken from Table 3. In each case we assumed a density of 100 birds km^{-2} and, using formulae (4) and (7), calculated how many birds would be seen by an observer scanning 360° , and what proportion of those counted would be flying. We then kept the number of birds seen constant and recalculated the estimated density changing each input value in turn by $\pm 50\%$ (Table 5).

The estimated density (D) for both models was most sensitive to changes in r_s and least sensitive to changes in V' .

The true value of V' probably falls well inside the extreme values tested for both model species and the level of accuracy for this variable therefore appears sufficient for the demands of the model. The proportion of birds flying, being derived directly from the observations to be transformed, is also probably known with sufficient accuracy. Unfortunately, the variable to which the model is most sensitive, r_s , is the one most difficult to measure, and for which available measurements are therefore least precise.

3. Comparison with estimates of birds per kilometre

Because of the large effect of the poorly known variable r_s on estimated densities it seems inappropriate at present to use formulae (4) and (7) as estimates of actual density. However, they can be used to indicate relative density, and have several advantages over the previously used index, birds km^{-1} (N/S).

First, the new index (hereafter referred to as the "area index," as opposed to the "linear index"), is much less affected by the speed of the vessel. For estimates of D where all input variables are correct the area index is, of course, unaffected by ship's speed. The ratio of the area index at 4 km h^{-1} to that at 20 km h^{-1} for a 50% error in input variables is shown in Table 6. For the initial assumptions that we

Table 2
Observed (uncorrected) proportions of birds in flight

Species	Jan	Feb	Mar	Sep	Oct	Nov	Dec
Northern Fulmar (<i>Fulmarus glacialis</i>)	.80	.83	.43	.37	.69	.79	.98
Greater Shearwater (<i>Puffinus gravis</i>)				.79	.60	.98	1.0
Sooty Shearwater (<i>Puffinus griseus</i>)				.96	.57		
Petrels (<i>Oceanites oceanicus</i> and <i>Oceanodroma leucorhoa</i>)				.97	.72		
Northern Gannet (<i>Sula bassanus</i>)				.92	.79	.66	.97
Phalaropes (<i>Phalaropus</i> spp.)				.37	.82	.51	
Jaegers (<i>Stercorarius</i> spp.)				.75	.70	.95	
Skuas (<i>Catharacta</i> spp.)				.87	1.0		
Black-legged Kittiwake (<i>Rissa tridactyla</i>)	.37	.59	.67	.44	.55	.78	.55
Ivory Gull (<i>Pagophila eburnea</i>)	.11	.92		.81		1.0	.90
Herring Gull (<i>Larus argentatus</i>)	.88	.85	.93	.23	.70	.80	.94
Iceland Gull (<i>Larus glaucoides</i>)	.50	.88	.82	.75	.29	.51	
Great Black-backed Gull (<i>Larus marinus</i>)	.65	.55	.58	.39	.78	.82	.99
Glaucous Gull (<i>Larus hyperboreus</i>)	.89	.68	.06	.46	.50	.58	.93
Dovekie (<i>Alle alle</i>)	.93	.92	.85	.18	.71	.75	.62
All murrees (<i>Uria</i> spp.)	.66	.56	.76	.56	.53	.70	.83
Black Guillemot (<i>Cepphus grylle</i>)		.37	.06	.80	.91		
Atlantic Puffin (<i>Fratercula arctica</i>)	.50			.68	.40	.20	
Mean ship's speed, km/h	19.5	21.6	16.7	18.9	19.3	18.5	23.2
Mean arc of observation*	.64	.66	.73	.73	.73	.61	.62

*1.0 = 360°.

have adopted, these ratios are all much closer to unity than the corresponding ratios for the linear index (Table 6). This remains true except for very small values of r , where the two indices converge.

Secondly, the area index reduces the bias against less visible species. Using our initial assumptions, the linear index yields a figure for "fulmars" that is 2.9 times that for "puffins" at a ship's speed of 20 km h⁻¹ and this discrepancy is larger at lower speeds. In contrast, a 50% error in the most important variable (r) for "fulmars" yields an area index only 2.1 times that for "puffins" at 20 km⁻¹. Similar errors in the same direction for both species yield negligible differences in the relative value of their area indices. Consequently, the accuracy with which area indices estimate the relative abundance of different species reflects the relative accuracy with which the input variables are measured among species. In the case of r , relative values can probably be assigned with greater confidence than actual values. For instance, we might consider that r_s for murres falls somewhere between 0.2 and 0.5 km and for fulmars between 0.4 and 0.8 km. However, if we assume a value of 0.5 km for murres we shall certainly require a value of 0.6 km or greater for the paler-coloured fulmar which is more readily detectable on the sea and in flight.

Table 3

Input parameters used in estimating true proportions of birds in flight (p'). Sources are numbered in parentheses

Species	Speed, km h ⁻¹	r_s , km	r_t/r_s	Zigzag, K
Northern Fulmar	43 ± 4(1)	0.35 ± 0.19(2)	1.3(6)	1.5
Greater Shearwater	40	0.3	1.3	1.3
Sooty Shearwater	40	0.25	1.1(6)	1.3
Petrel spp.	35	0.15	1.3	1.5
Northern Gannet	72 ± 7(3)	0.36 ± 0.14(2)	1.3	1.3
Phalarope spp.	35	0.15	1.3	1.0
Jaeger spp.	40	0.27 ± 0.18(2)	1.3	1.3
Skua	40	0.40 ± 0.11(2)	1.3	1.3
Black-legged Kittiwake	34 ± 6(4)	0.22 ± 0.08(2)	1.9(6)	1.3
Ivory Gull	35	0.4	1.3	1.3
Herring Gull	39 ± 4(4)	0.5	1.0(6)	1.3
Iceland Gull	39	0.5	1.0	1.3
Great Black-backed Gull	40	0.54 ± 0.11(2)	1.0	1.3
Glaucous Gull	40	0.6	1.0(6)	1.3
Dovekie	45	0.15	1.8	1.0
All murres	58(5)	0.22 ± 0.09(2)	1.3(6)	1.0
Black Guillemot	50(5)	0.2	1.2	1.0
Atlantic Puffin	50	0.21 ± 0.08(2)	1.8(6)*	1.0

SOURCES: (1) Pennycuik (1960); (2) Dixon (1977); (3) Nelson (1978); (4) Schnell and Hellack (1979); (5) Bradstreet (1982); (6) Wiens *et al.* (1978).

*Using figures for Horned Puffin (*Fratercula corniculata*).

Provided that the values chosen for r_s for different species can be correctly ranked, the accuracy of inter-specific comparisons made on the basis of the area index will always be greater than similar comparisons based on the linear index.

Table 5

Changes in estimates of density (D) for a 50% change in input parameters. Ship's speed 10 km h⁻¹

Input parameter	"Puffin" model*		"Fulmar" model†	
	+50%	-50%	+50%	-50%
Radius of visibility on sea, r_s	-36	+109	-37	+114
Ratio $r_t/r_s(x_i)$	-5	+15	-9	+27
Flight speed, V	-6	+7	-5	+10
Proportion in flight, p'	-36	+36	-25	+25

* $r_s = 0.21$ km, $r_t = 0.315$ km, $V = 50$ km h⁻¹, $K = 1.0$.

† $r_s = 0.35$ km, $r_t = 0.45$ km, $V = 43$ km h⁻¹, $K = 1.5$.

Table 6

Relationship between estimated density at 4 km h⁻¹ and at 20 km h⁻¹ (D_4/D_{20}) for 50% change in input parameters

Input parameter	"Puffin" model*		"Fulmar" model†	
	+50%	-50%	+50%	-50%
Radius of visibility on sea, r_s	0.90	1.14	0.89	1.18
Ratio $r_t/r_s(x_i)$	1.03	0.92	1.05	0.90
Flight speed, V	1.02	0.97	1.02	0.99
Proportion in flight, p'	0.86	1.06	0.84	1.10
N/S (linear index)	1.50		1.82	

*†Input parameters as for Table 4.

Table 4

Estimated true proportion of birds in flight for selected months

Species	Jan	Feb	Mar	Sep	Oct	Nov	Dec	\bar{x}
Northern Fulmar	0.66	0.71	0.25	0.26	0.57	0.65	0.97	0.58
Greater Shearwater				0.64	0.41	0.96	1.00	0.75
Sooty Shearwater				0.93	0.42			0.67
Petrel spp.				0.95	0.59			0.77
Northern Gannet				0.77	0.52	0.36	0.90	0.64
Phalarope spp.				0.20	0.65	0.19		0.35
Jaeger spp.				0.58	0.52	0.90		0.67
Skua				0.76	1.00			0.88
Black-legged Kittiwake	0.17	0.33	0.41	0.21	0.29	0.55	0.29	0.32
Ivory Gull	0.06	0.85		0.69		1.00	0.82	0.68
Herring Gull	0.83	0.79	0.90	0.16	0.60	0.72	0.91	0.70
Iceland Gull	0.39	0.83	0.75	0.66	0.21	0.40		0.54
Great Black-backed Gull	0.54	0.44	0.47	0.29	0.69	0.74	0.98	0.59
Glaucous Gull	0.84	0.58	0.04	0.35	0.39	0.47	0.90	0.51
Dovekie	0.76	0.73	0.57	0.05	0.37	0.42	0.28	0.45
All murres	0.35	0.26	0.46	0.26	0.24	0.39	0.57	0.36
Black Guillemot		0.16	0.02	0.57	0.77			0.38
Atlantic Puffin	0.18			0.32	0.13	0.05		0.17

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Appendices

Appendix I

Calculation of density of flying birds when the observer watches less than 360° of arc

If birds are flying at a speed V in a direction θ relative to the boat, then their apparent speed and direction relative to the boat are $V_o(\theta)$ and $\alpha(\theta)$ as defined in equations (5) and (6). When the observer watches less than 360° of arc, the area covered, $A(\theta)$, is a complex shape given by sweeping the observation field along the angle $\alpha(\theta)$ for a distance $V_o(\theta)/6$ (for a standard PIROP watch of 10 min). We assume that birds are equally likely to be travelling in any direction.

Case I. Observing 180° forward centered on direction of boat's travel

In this situation the area covered for birds travelling in apparent direction $\alpha(\theta)$ is shown as the shaded area in Fig. A1. It can be seen that the area is equivalent to a rectangle of length $V_o(\theta)/6$ and width $w(\theta) = r_f(1 + |\cos \alpha|)$ plus a semicircle of radius r_f . Giving an area

$$A(\theta) = \pi r_f^2/2 + r_f(1 + |\cos \alpha|) V_o(\theta)/6 \quad (\text{A1})$$

Multiplying this area by the bird density and integrating over θ gives the formula for the number of flying birds seen

$$N_f = \int_{-\pi}^{\pi} \frac{D_f}{2\pi} A(\theta) d\theta$$

which can be simplified to

$$N_f = D_f \left[\pi r_f^2/2 + \frac{r_f}{12\pi} \int_{-\pi}^{\pi} V_o(\theta) d\theta + r_f \frac{\sqrt{V^2 - S^2}}{3\pi} \right] \quad (\text{A2})$$

$$= D_f g_1(f, V, S) \quad (\text{A3})$$

If S is much smaller than V , then $V_o(\theta)$ is close to V and $\sqrt{V^2 - S^2}$ close to V so equation (A2) can be simplified to

$$N_f = D_f [\pi r_f^2/2 + r_f V(1 + 2/\pi)/6] \quad (\text{A4})$$

Rearranging equation (A3) gives the formula for density of flying birds

$$D_f = \frac{N_f}{g_1(r_f, V, S)} \quad (\text{A5})$$

Case II. Observing 180° to one side of boat

This situation is similar to Case I above. The area covered for birds travelling in apparent direction θ is equivalent to a rectangle of length $V_o(\theta)/6$ and width $w(\theta) = r_f(1 + |\sin \alpha|)$ plus a semicircle of radius r_f (see Fig. A2). Giving an area

$$A(\theta) = \pi r_f^2/2 + r_f(1 + |\sin \alpha|) V_o(\theta)/6 \quad (\text{A6})$$

Multiplying by bird density, integrating over θ and simplifying gives the formula for number of flying birds seen

$$N_f = D_f \left[\pi r_f^2/2 + \frac{r_f}{12\pi} \int_{-\pi}^{\pi} V_o(\theta) d\theta + \frac{r_f V}{3\pi} \right] \quad (\text{A7})$$

$$= D_f g_2(r_f, V, S) \quad (\text{A8})$$

Figure A1

Effective area covered when watching 180° centered on the boat's heading

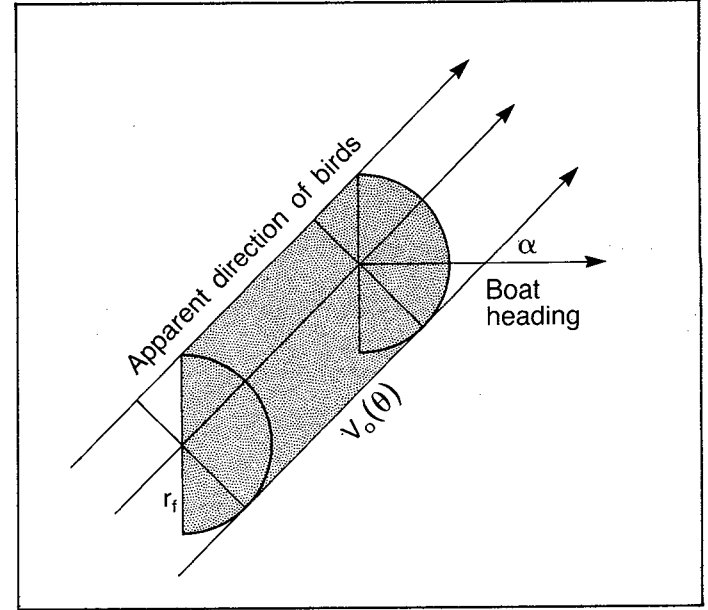
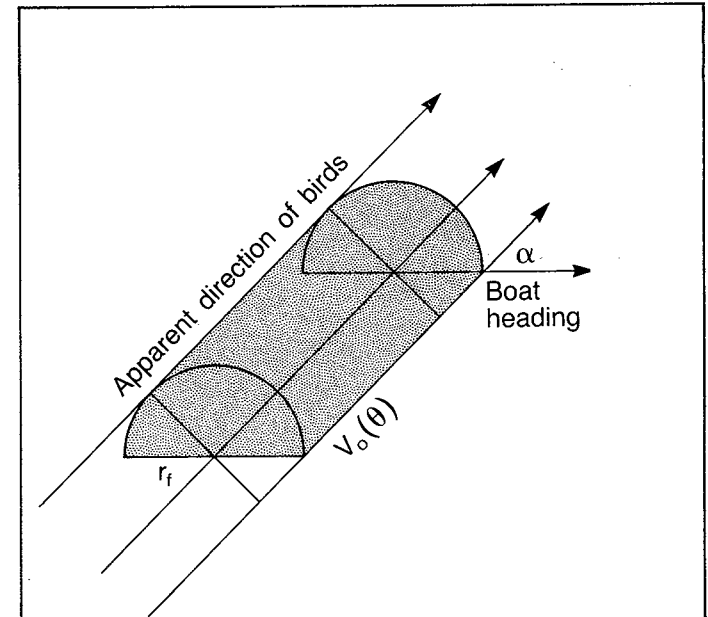


Figure A2

Effective area covered when watching 180° to one side of the boat



If V is much larger than S , then (A7) can be simplified by substituting V for $V_0(\theta)$ to yield

$$N_f = D_f[\pi r_f^2/2 + r_f V(1 + 2/\pi)/6] \quad (\text{A9})$$

Rearranging equation (A8) gives the formula for density of flying birds

$$D_f = \frac{N_f}{g_2(r_f, V, S)} \quad (\text{A10})$$

Case III. Observing 270° forward centered on boat's heading

In this situation, the area covered for birds flying in apparent direction $\alpha(\theta)$ is shown as the shaded area in Figure A3. It can be seen that, for the angle presented in this figure, the area covered is equivalent to i) a rectangle of length $V_0(\theta)/6$ and width $r_f[1 + \cos(\alpha - \pi/4)]$, ii) three-quarters of a circle of radius r_f , and iii) a small triangle contained in the quarter circle not seen at the end of the watch. This small triangle represents an area which passes through the area watched but which is out of the viewing area at the time the watch concludes. This triangle is only present for some values of α . The formulae for the area swept out varies with α

$$-\pi < \alpha < -3\pi/4$$

$$A(\theta) = 3\pi r_f^2/4 + r_f V_0(\theta)/3$$

$$-3\pi/4 < \alpha < -\pi/2$$

$$A(\theta) = 3\pi r_f^2/4 + r_f(1 + \sin(7\pi/4 - \alpha)) V_0(\theta)/6 + r_f^2 \tan(\alpha - 5\pi/4)/2$$

$$-\pi/2 < \alpha < -\pi/4$$

$$A(\theta) = 3\pi r_f^2/4 + r_f(1 + \cos(7\pi/4 - \alpha)) V_0(\theta)/6 + r_f^2 \tan(7\pi/4 - \alpha)/2$$

$$-\pi/4 < \alpha < \pi/4$$

$$A(\theta) = 3\pi r_f^2/4 + r_f V_0(\theta)/3$$

$$\pi/4 < \alpha < \pi/2$$

$$A(\theta) = 3\pi r_f^2/4 + r_f(1 + \cos(\alpha - \pi/4)) V_0(\theta)/6 + r_f^2 \tan(\alpha - \pi/4)/2$$

$$\pi/2 < \alpha < 3\pi/4$$

$$A(\theta) = 3\pi r_f^2/4 + r_f(1 + \sin(\alpha - \pi/4)) V_0(\theta)/6 + r_f^2 \tan(3\pi/4 - \alpha)/2$$

$$3\pi/4 < \alpha < \pi$$

$$A(\theta) = 3\pi r_f^2/4 + r_f V_0(\theta)/3$$

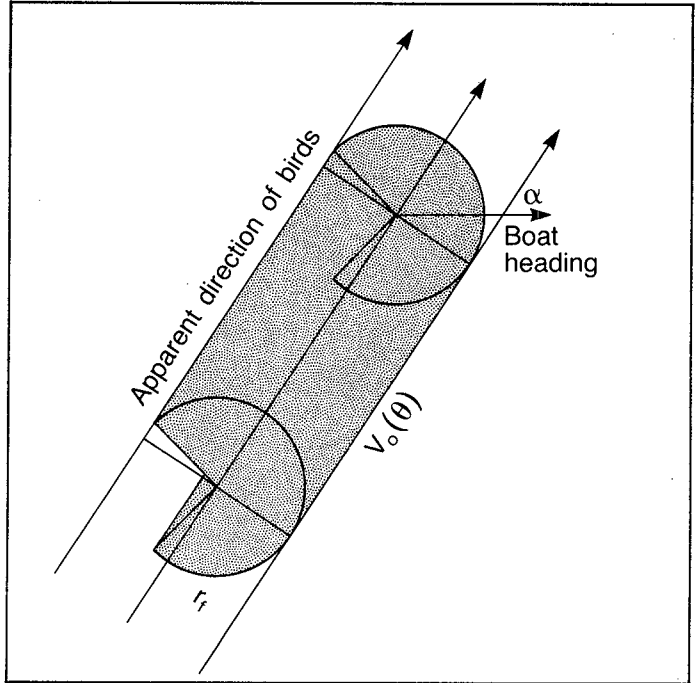
Multiplying by bird density and integrating over θ gives the formula for number of flying birds counted

$$\begin{aligned} N_f &= \frac{D_f}{2\pi} \int_{-\pi}^{\pi} A(\theta) d\theta \\ &= D_f g_3(r_f, V, S) \end{aligned} \quad (\text{A11})$$

This equation is difficult to simplify but specific cases can be calculated through numerical integration.

Figure A3

Effective area covered when watching 270° centered on the boat heading



Appendix 2

Formulae to calculate true proportions of birds in flight for observations over various arcs, assuming ship speed is much lower than bird speed

(1) for 360°

$$p' = 1 / \left(1 + \frac{(1-p)(\pi r_f^2 + r_f V/3)}{p(\pi r_s^2 + r_s S/3)} \right) \quad (\text{A12})$$

(2) for 180° ahead

$$p' = 1 / \left(1 + \frac{(1-p)[\pi r_f^2/2 + r_f v(1 + 2/\pi)/6]}{p(\pi r_s^2/2 + r_s S/3)} \right) \quad (\text{A13})$$

(3) for 180° abeam

$$p' = 1 / \left(1 + \frac{(1-p)[\pi r_s^2/2 + r_f V(1 + 2/\pi)/6]}{p(\pi r_s^2/2 + r_s S/6)} \right) \quad (\text{A14})$$

(4) for 270° ahead

$$p' = 1 / \left(1 + \frac{(1-p)g_3(r_f, V, S)}{p(3\pi r_s^2/4 + r_s S/3)} \right) \quad (\text{A15})$$

for a definition of $g_3(r_f, V, S)$ see Appendix 1.

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