SHORT COMMUNICATION

OPTIMISATION OF THE FLIGHT SPEED OF THE LITTLE, COMMON AND SANDWICH TERN

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Studies of the mechanical performance of birds during flight are rarely accomplished with wild birds because accurate tracking of flight paths is necessary. In this study, we present data from three species of tern as they flew along a straight flight path on the north Norfolk coast, UK. Measurement of wind speed and the time taken to fly a set distance allowed direct calculation of the airspeed. The airspeeds were compared with the maximum range speed, V_{mr}, and the minimum power speed, V_{mp}, values predicted from aerodynamic models generated with data from, for example, observations made in wind tunnels (Tucker, 1969) and from both radar and double theodolite tracking systems (Tucker and Schmidt-Koenig, 1971).

Data for the little tern, *Sterna albifrons*, the common tern, *Sterna hirundo*, and the sandwich tern, *Sterna sandvicensis*, were recorded over a period of 7 days at the end of July 1991. Observations were made at two sites at Blakeney Point, and at Scolt Head Island. The shoreline at these locations was very straight and offered clear views in both directions. Terns flew a straight course along the coast, and a 40 m segment of their flight was measured as they flew in front of a set of marker posts, aimed like gunsights, on the beach. Recordings were made at each end of the 40 m course for both the time that the terns passed (on synchronised stopclocks) and for the number of wingbeats counted during the course. Because of the nature of this technique, terns measured flying on a slightly oblique path will bias the calculated airspeeds to be too low; it is estimated that this will introduce an error of not more than 2%. The calculated airspeeds were most sensitive to timing errors, and it is estimated that these can produce deviations of up to 3%; any bias due to anticipation of the terns' arrival may have been duplicated at both ends of the course, and thus may have been removed when the two absolute times were subtracted. The wind speed was measured with an anemometer at a height of 1.5 m, and the wind direction was measured with a magnetic compass and a piece of freely blowing cotton. The wind speed profile was measured up to a height of 4.5 m for two wind speeds, $6.2 \, \text{m s}^{-1}$ and $9.4 \, \text{m s}^{-1}$ (at 1.5 m); it was estimated that there was greater than 95% confidence for the wind speed measurements for all

Table 1. *Analysis of variance showed the mean airspeeds (m s^{-1}) for the little and sandwich terns to be significantly different for flying into the wind, flying in a crosswind and flying downwind*

Species	Airspeed			F	P
	Upwind	Crosswind	Downwind		
Little tern	12.2±2.2 (73)	9.5±2.9 (65)	6.5±2.9 (32)	37.20	<0.001
Common tern	12.2±2.9 (5)	8.2±3.4 (14)	8.9±3.1 (7)	2.75	0.085
Sandwich tern	14.3±2.1 (60)	12.1±2.3 (56)	9.2±2.3 (6)	23.20	<0.001

Values for airspeed are mean±s.D. (*N*).

the birds flying above 2.5 m from the sea. All except one of the observed flights were above this height, and so the terns were not significantly affected by the boundary layers of air lower down. The wind conditions were relatively constant and varied between readings every half hour by a mean of 0.54 m s^{-1} (s.D.=0.62, *N*=24) and 4.4° (s.D.=9.82, *N*=24).

The airspeeds were calculated by subtracting the vector for wind speed from that for ground speed (Pennycuick, 1975). A measure of how much the wind affects the airspeed is the wind effect which is calculated by subtracting the magnitude of the airspeed from that for ground speed (Pennycuick, 1978). For the rest of the discussion, speeds are quoted as scalar quantities. Positive values of wind effect represent flying with the wind, negative values of wind effect represent flying into the wind.

If crosswinds are defined as wind directions greater than 45° from the flight direction (Schnell and Hellack, 1979), then the airspeeds of the little and sandwich terns were significantly different for flying upwind, flying in a crosswind and flying downwind; with the airspeeds being fastest flying into the wind and slowest flying downwind (Table 1). The common terns flew with a faster mean airspeed into the wind than flying downwind, but this difference is not significant at the 95 % confidence level. Schnell and Hellack (1979) have also reported that gulls, terns and skimmers fly faster into the wind than downwind, using this 45° cut-off for wind direction. This strategy of working harder when flying upwind, and drifting more when flying downwind, can increase a bird's flight range in windy conditions (Pennycuick, 1969).

The power requirement during horizontal flight can be predicted using aerodynamic theories and shows a U-shaped curve with speed, (Greenewalt, 1975; Pennycuick, 1969, 1975, 1989; Rayner, 1979; Tucker, 1973; body mass and wingspan data from Cramp, 1988, Table 2). The minimum power speed is V_{mp}; this airspeed is constant at all wind strengths. The maximum range speed, V_{mr}, is

Table 2. *Data used for the calculation of the power curves*

	Little tern	Common tern	Sandwich tern
Body mass* (kg)	0.057	0.126	0.229
Wing span* (m)	0.52	0.88	1.00
Disc area† (m²)	0.212	0.608	0.786
Flat plate area† (m²)	0.000483	0.000189	0.00116
Profile power ratio, X_1†	1.2	1.2	1.2
Metabolic power ratio, X_2†	0.612	0.636	0.444
Gravity (m s⁻²)	9.81		
Air density (kg m⁻³)	1.23		
Induced power constant, k	1.1		
Metabolic power constant, R	1.2		

* Taken from Cramp (1988).
† Generated by program 1 from Pennycuick (1989).

the airspeed at which a bird can travel the maximum distance over the ground per unit of energy consumed in flight. V_{mr} is calculated by taking the tangent to the power–speed curve from the corresponding wind effect value on the abcissa (Pennycuick, 1978); it shows an inverse relation with wind effect.

Most models of foraging behaviour concentrate on the maximisation of energy intake per unit time. Energy consumed during flight is considerable, and the foraging strategy for birds must be a balance between minimising the energy output during flight and the energy intake from feeding (Rayner, 1982). Flying at V_{mr} would maximise the amount of sea the little terns searched per unit of energy consumed in flying; this would seem a reasonable foraging strategy for the little tern, as most were observed to be fishing. The majority of common terns were starting their migration to Africa (Langham, 1971), and flying at V_{mr} would maximise their migration range. Most of the sandwich terns observed were returning to their colony from their fishing grounds. Flying at V_{mr} would enable the terns to return to their colony using the minimum energy expenditure for flying. The observed airspeeds for all three species of tern show changes with wind effect that are similar to the changes for V_{mr} (Fig. 1, values calculated by program 1 in Pennycuick, 1989, using data from Table 2). It should be noted that airspeeds a bit faster than V_{mr} are predicted for birds maximizing the rate of food delivery to young at nesting sites (Norberg, 1981) or maximizing the overall speed of migration (Alerstam, 1991). Although the little and sandwich terns breed extensively in the area, the breeding season was over and no food was being carried back to the nests. The common terns, which had started migrating, were flying at a speed slightly lower than V_{mr}.

The following discussion is based on linear regressions of airspeed with wind effect. However, if the terns are flying at V_{mr}, one would expect the data to show a curved trend, so fitting a linear regression line may not be the best way to describe their airspeeds.
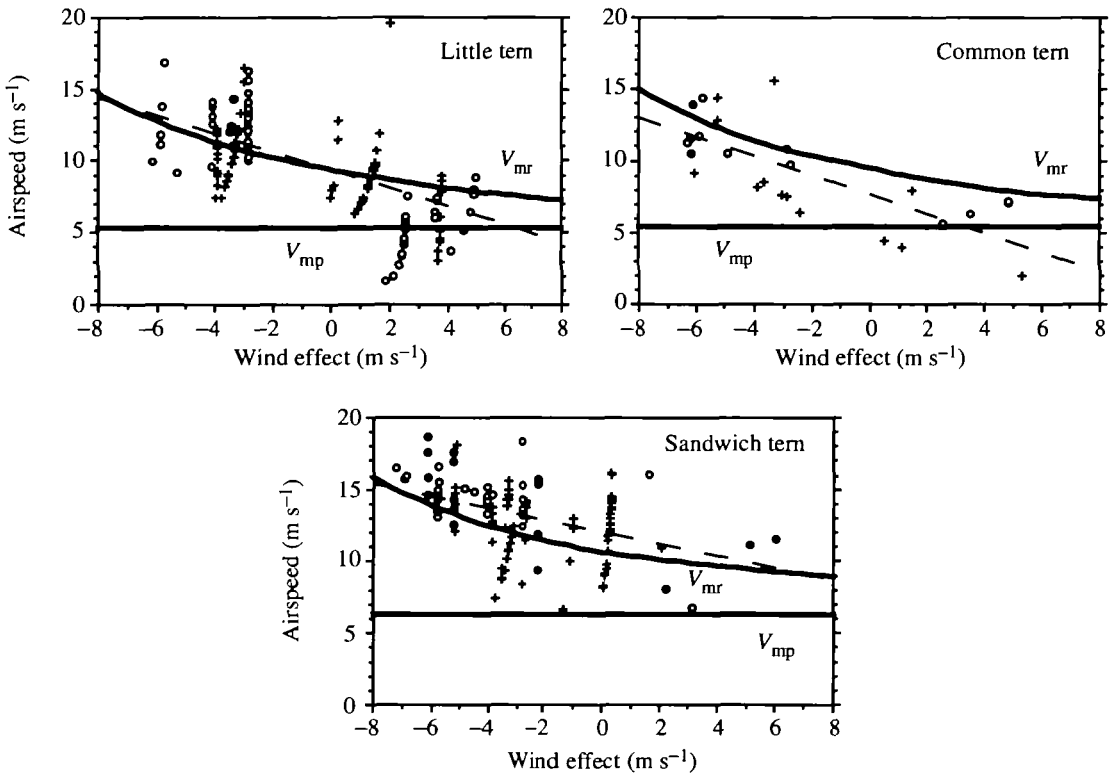
Fig. 1. The airspeed for each species of tern showed significant regression with wind effect. (●) terns flying 12° from the wind, (○) terns flying 28° from the wind, (+) terns flying with all intermediate crosswind directions. The dashed lines represent regression lines calculated for all wind directions. Little tern: $y=9.0-0.69x$; $N=133$, $s=2.54$, $r^2=0.44$, $P<0.001$. Common tern: $y=7.7-0.67x$; $N=25$, $s=2.34$, $r^2=0.56$, $P<0.001$. Sandwich tern: $y=12.1-0.42x$; $N=119$, $s=2.25$, $r^2=0.19$, $P<0.001$, where y is airspeed and x is wind effect. The curve for V_{mr} represents the airspeeds at which the terns' maximum range can be obtained. It occurs where the terns have a maximum ratio of ground speed to power consumed. The line for V_{mp} represents the airspeed at which the terns consume least energy per unit time.

The airspeeds of petrels and albatrosses (Pennycuick, 1982), of auks (Pennycuick, 1987) and of the Arctic tern (Gudmundsson et al. 1992) have been shown to regress with wind effect, with negative slope coefficients; it seems that in these studies the regressions were calculated for birds flying in all wind directions. Our data show that all three species of tern have significant regressions with wind effect when all the wind directions are considered (Fig. 1). These regressions are all significantly different from zero, and so there is no evidence to suggest that the terns are flying at V_{mp}.

When only the data for terns flying within 28° from the wind direction are considered, each species still shows a significant regression with wind effect, and these regression lines are not significantly different from those considering all the

Table 3. *Mean wingbeat frequencies (s⁻¹) for the three species of tern*

Species	N	Mean	S.D.
Little tern	119	4.4	1.3
Common tern	21	3.7	0.7
Sandwich tern	111	3.1	0.6

wind directions (at the 95 % confidence level). There were sufficient data for the sandwich terns to show significant regression between airspeed and wind effect for those birds flying only 12° from the wind direction; again this line is not significantly different from the lines for 28° and for all wind directions for the sandwich tern. It would appear that the wind direction does not significantly affect the way the terns' airspeed regresses with wind effect.

Scaling theories for flight power and speed assume isometric scaling of the body dimensions (Lighthill, 1974; Pennycuick, 1969, 1975). The mean wingspans of the three species of tern do not show interspecific isometric scaling (data from Cramp, 1988), and thus it was not surprising to find no correlation between airspeed and body mass. The terns' wingbeat frequency showed little intraspecific variation (Table 3): the distribution for each species was not significantly different from normal. Our data showed the regression of wingbeat frequency with airspeed to be not significantly different from zero for all three species of tern. For the little terns there was approximately an eightfold range in airspeed and a twofold range in wingbeat frequency; 119 frequencies were recorded. To find no significant correlation with this data (and for the other two species) is quite notable. Tsvyelyikh (1986) has reported that the sandwich tern shows a positive regression between wingbeat frequency and flight speed ($N=29$): this is contrary to our findings. Scaling of stroke period, T (s) (1/wingbeat frequency), has been shown to vary between $M_b^{0.19}$ for shorebirds to $M_b^{0.36}$ for passeriforms (Rayner, 1979), where body mass, M_b, is measured in kilograms. The three species of tern show scaling of stroke period as:

$$T = 0.45M_b^{0.24}.$$

The 95 % confidence intervals for T are $(0.43-0.47)M_b^{(0.17-0.31)}$, with $N=3$, d.f.$=1$. Body mass data are from Cramp (1988). The regression is significant at $P<0.05$, $r^2=0.99$.

Terns observed fishing always turned into the wind prior to hovering and diving, and rose out of the water facing into the wind. Most aerodynamic control is obtained when the terns face into the wind, and this control is needed when the terns are manoeuvring to fish.

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