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Wind-dependent foraging flight in the Osprey *Pandion haliaetus*

Vindberoende flygteknik hos födosökande fiskgjusar Pandion haliaetus

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Abstract

We studied the foraging technique of Ospreys *Pandion haliaetus* during different wind speed conditions at Lake Hammarsjön, Sweden in autumn 2003. Different fishing techniques were used with a shift in relation to wind speed: (1) without hovering, (2) hovering with pure flapping flight, (3) hovering with flapping flight and gliding into the wind, and (4) hovering with pure gliding. The results supported our predictions that hovering is constrained at low wind speeds and gliding restricted to wind speeds exceeding 7 m/s. Mixing flapping and gliding flight when hovering may be done as a trade-off between increased fishing efficiency associated with flapping flight and energy-saving combined with gain in total hovering time associated with gliding intervals. The relationship between hovering time and wind speed differed significantly between males and females. At wind speeds up to about 3.0 m/s, the hovering time increased more steeply with increasing wind speed for males than for females. In contrast, hovering time was shorter for males than for females at high wind speeds. The juveniles showed a lower mean, smaller scatter, and less increase in hovering time along the wind speed gradient.

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Introduction

The fishing technique and success of foraging Ospreys *Pandion haliaetus* have been studied during different weather conditions (Grubb 1977a, Grubb 1977b, Stinson et al. 1987, Machmer & Ydenberg 1990). These studies indicate that wind speed affects the foraging technique and success, but the gradual change in foraging technique over a wide range of wind speeds, which is the objective of this study, has not been analyzed. Studies on the wind-dependence of the Osprey's foraging may be important for evaluating the overall foraging performance of the species and for understanding how foraging constraints relate to ecological and evolutionary aspects such as migration performance, survival and reproduction.

Ospreys regularly hunt by hovering, keeping a stationary position in the air while flying into the wind, before diving into the water to catch a fish. We use the term hovering in a wide sense, not only reflecting stationary flight in still air but also stationary (relative to ground) flapping or mixed flapping/gliding flight into the wind (sometimes called wind hovering). Dives of Ospreys that have been preceded by such hovering bouts, typically lasting 2–10 s, have a clearly higher success rate than dives initiated directly from search and gliding flight (Grubb 1977a). However, Ospreys are relatively heavy birds (1.4–2.0 kg; with females having a significantly larger body mass than males) for which hovering in still air or at low wind speeds requires extremely high flight power. In fact, Ospreys are much too large to be capable of sustained hovering in still air or at the lowest wind speeds (Rayner 1979). Hence, even if they can perform very short hovering bouts under these conditions, we expect the high flight costs to seriously constrain the Ospreys' hovering performance under weak winds. Therefore we also expect the Ospreys to increase hovering length into winds of increasing speed, up to a wind speed that matches the Ospreys' flapping flight speed with minimum power. We also expect that they may use gliding flight during their stationary flight phases in wind speeds exceeding their minimum possible gliding speed, and that hovering behaviour may differ between females and males because of the significant size dimorphism, and between adults and juveniles because of the importance of experience in mastering hovering flight and fishing under different wind speeds (cf. Edwards 1989, Bustamante 1995).

We present our specific predictions about possible constraints and adaptations in the Ospreys' foraging flight and hovering in view of general flight mechanical considerations. Then we proceed to investigate and test these predictions by analysing foraging techniques and hovering times in relation to wind speed for breeding and migrating Ospreys observed at a lake in southern Sweden.

In addition to hunting on its wings by search and hovering flights, Ospreys may also fish from a perch using an energy-saving "sit-and-wait" strategy and diving directly from the perch. However, this was not recorded at our study site, where there are mainly meadows or reed beds along the shores of the lake and no suitable trees with branches reaching out over the open water. Hence, our analysis involves only flight behaviour and its relationship to wind speed.

Predictions

The power requirements for a bird in horizontal flapping flight is related to flight speed (airspeed) according to a U-shaped curve, with high power at zero, slow, and very fast flight speeds (e.g. Pennycuick 1969, 1975, Tucker 1973, Greenewalt 1975, Tobalske et al. 2003). Thus, the minimum power occurs at an intermediate flight speed, V_{mp}. Flying stationary (hovering) into winds of different speeds is equivalent to flying horizontally forwards in still air at the corresponding airspeeds. Consequently, the power for hovering into the wind will decrease with increasing wind speed from a very high level at zero wind to a minimum at wind speed = V_{mp}, according to the power curve for flapping flight.

In stable gliding flight the rate of loss of potential energy (which is directly proportional to the vertical sinking speed) is related to forward gliding speed according to a similar U-shaped curve (the glide polar) with an intermediate gliding speed of minimum sink, V_{ms}. However, gliding flight is not possible at low speeds, below the minimum gliding speed (stalling speed), V_{min} (e.g. Pennycuick 1975, Tucker 1987). A bird may of course maintain its horizontal position by pure gliding into the wind, with its gliding speed equal to the wind speed provided wind speed exceeds V_{min}. However, it will not maintain its vertical position but loose height according to the sinking speed given by the glide polar.

Table 1. Biometric measurements of breeding male and female Ospreys captured at their nests in south-central Sweden (approx. 60°N, 15°E) 1988–2001. Wing area measurements include the area of the body between the wings, as described by Pennycuick (1989).
Biometriska mått för könsbestämda adulta fiskgjusar fångade vid boet i centrala Sydsverige (ca 60°N, 15°E) 1988–2001. Vingytemått inkluderar kroppsytan mellan vingarna, vilket beskrivs av Pennycuick (1989).

	Males			Females		
Measurements	Mean	SD	N	Mean	SD	N
Body mass (kg)	1.44	0.10	23	1.81	0.13	14
Wing span (m)	1.56	0.04	9	1.66	0.03	6
Wing area (m^2)	0.300	0.014	9	0.353	0.011	6
Aspect ratio	8.1	0.3	9	7.8	0.2	6

Among Ospreys, females are considerably larger than males, and we will use the mean body masses recorded for females and males that have been captured during the breeding season in south-central Sweden (Table 1). These mean values give a body mass ratio of 1.26 between females and males. Assuming that the sexes are isometrically scaled (of the same geometric shape with respect to wing span and wing area) the flight power is expected to be proportional to $m^{7/6}$, where m is body mass (Pennycuick 1975). Hence, the power for hovering into low wind speeds, which is already very high, is expected to be $(1.26)^{7/6} = 1.31$ times higher for females than for males. Even if females have more muscle mass than males we thus predict that they will be more restricted in their hovering at the lowest wind speeds. The mean aspect ratio differed slightly between the sexes (Table 1), indicating a possible departure from isometric scaling. However, this difference was not statistically significant (t-test; $p = 0.075$). Furthermore, scaling of wing span, as well as of wing area according to the body mass difference between the sexes, shows that the expectations from isometry fall within the 95% confidence intervals for the means of the wing measurements (Table 1). Hence, according to the measurements in Table 1, there appears to be no important deviations from isometric scaling between the Osprey sexes.

Characteristic flight speeds, like V_{mp} in flapping flight, V_{min} and V_{ms} in gliding flight, are all expected to scale with $m^{1/6}$ (Pennycuick 1975). This means that females are predicted to be tuned to slightly faster flight speeds and thus also to hovering into faster wind speeds than the males by a factor of $(1.26)^{1/6} = 1.04$.

Quantitative predictions about characteristic speeds in flapping and gliding flight must be considered as very rough and provisional estimates, because of significant uncertainties about the aerodynamics and physiology of bird flight. A power curve and glide polar for the Osprey were calculated mainly according to Pennycuick (1975, 1989) with a few modified assumptions as described by Alerstam (2000). Using this procedure for a typical female of body mass 1.81 kg, wing area 0.35 m^2 and wing span 1.66 m (Table 1) gives estimated $V_{mp} = 10.3$ m/s in flapping flight, and $V_{min} = 7.2$ m/s and $V_{ms} = 8.7$ m/s in gliding flight.

Juvenile Ospreys, during their first autumn migration, are still in their learning process of foraging and flight technique. According to Prevost (1982) they have not got fully developed foraging skills until they are about 6 months old. This probably means that they are affected by the wind in a different way than adults.

This leads to the following main predictions about hovering of Ospreys:

(1) Hovering into the wind becomes increasingly restricted with decreasing wind speed, and more so among females compared to males.

(2) Gliding flight will not be possible during stationary flights into wind speeds below about 7 m/s.

(3) Hovering into the wind (both by flapping and mixed flapping/gliding flight) is used most freely at wind speeds about 9–11 m/s when power requirements are minimal.

(4) Hovering will be more well adapted and efficient in its relationship with wind speed among adults compared to juveniles.

Methods

The fieldwork was conducted at Håslövs ängar, Lake Hammarsjön, Scania, southern Sweden (55°95' N, 14°20' E), from 1 August to 30 September 2003. Two different observation spots were used: a 6 m high watchtower, and a 3.5 m high platform, both of which provide a good view over most of the 16.8 km^2 lake area. From the platform it is also possible to look straight at an Osprey nest, situated at a small island in the lake. The distance between the observer and the Ospreys fishing along the shorelines of the lake varied between approximately 150 and 3200 m. No bird was sexed at distances more than approximately 800 m (most birds arrived at the northeast end of the lake, which is close to the observation points). A total of 50 days, covering 277 observation hours, were spent at the lake. The observation hours covered the light part of the day from 0600 to 1900 hours local normal time (= GMT + 1h). Observations predominantly started at either 0600 or 1100 hours and continued to 1400 or 1900 hours respectively, decreasing in length with season because of gradually shorter days. Observation days were chosen with respect to weather conditions, to cover as wide range of wind speeds as possible, and also to cover the most favourable migration days. No observations were made during days/hours with bad weather conditions, such as haze and continuous rainfall. On days with no migration activity and no stopover birds at the lake, the observations were interrupted.

Notes were taken for every migrating Osprey observed at Lake Hammarsjön. Fishing trips made by the breeding pair at the lake were also included in the observations. As far as possible, all Ospreys were aged and sexed, and distinguished individually on the basis of patterns of underwing coverts, breastband extent, size, shape and moulting pattern (M. Hake and R. Strandberg, unpubl. data). Juvenile birds were identified by their fresh plumage, pale scaling to upperparts and white trailing edge to wings and tail (Forsman 1999). Because of the open habitat of the lake surroundings, it was easy to keep track of Ospreys perching, and resuming foraging at the lake. Stopover birds were also separated by favoured perch/roost branch at lakeside (which was individually specific to a great extent).

Four different flight-fishing techniques were distinguished: (1) Without hovering. The Ospreys did not stop to hover at all during their continuous flapping search flights but changed directly from search flight to diving when trying to catch a prey. (2) Hovering by pure flapping flight. The Ospreys stopped to hover into the wind for a shorter or longer period, maintaining its hunting position constant both horizontally and vertically by active flight, before diving or resuming search flight. (3) Hovering by flapping flight and gliding. The Ospreys stopped in hunting position by flapping flight interrupted by short moments of gliding into the wind before diving or resuming search flight. Normally, hovering was the dominating element during these fishing trips. (4) Hovering by pure gliding into wind. The Ospreys stopped in hunting position by pure gliding flight, maintaining its horizontal position by gliding into the wind while slowly loosing height until diving or resuming search flight.

A fishing trip was clocked from the appearance at the lake of an Osprey with obvious foraging behaviour (scanning water surface, hovering, diving etc.) until the bird caught a fish, perched at the lakeside, or disappeared out of view (left the lake). The foraging altitude was estimated at the nearest 5 m. For clocking of hovering bouts, a TC56A 1/1000 second digital stopwatch was used. Interrupted hovering attempts (< 0.5 s) were excluded.

The wind speed was measured immediately after the fishing trips made by the Ospreys, and also when wind changes were noticed throughout the observation periods. A telescope (Kowa TSN 821M, 32x82), and a binocular (SWIFT 10x42) were used for observing the Ospreys. Wind speed measurements were made with a SILVA windwatch (speed range: 0.6 m/s to 40 m/s, accuracy: ± 4%). Wind speeds were measured at heights of 5 or 7 m above the water surface from the two observation sites at the watchtower or platform situated on the flat meadows at the shore of the lake. However, the Ospreys were typically hovering at slightly higher altitudes, ranging between 8 and 50 m with a mean height close to 20 m according to subjective estimates. Actually, 212 of the 278 fishing trips including hovering bouts were made at estimated altitudes between 15 and 25 m.

To estimate a wind correction factor for this difference in height, we measured wind speed at three heights between 0.5 and 5 m on two occasions (two series of measurements on each occasion) with strong (wind speed 12–14 m/s at 5 m) and moderate winds (6 m/s), respectively. From these data, roughness z_0 was calculated and it ranged between $z_0 = 0.01$ m and $z_0 = 0.03$ m for the four measurement series, with a mean at $z_0 = 0.02$ m (Sutton 1953, Glaumann and Westerberg 1988). Such a roughness is typical for wind profiles over a flat and very open landscape, as found at the study site. By using the mean roughness value to calculate the ratio of expected wind speed at 20 m (mean height of Ospreys) to the measured wind speed at 6 m, we get a value of 1.21. We have multiplied the original wind measurements with a factor of 1.2 to reflect more accurately the wind speed actually experienced by the Ospreys.

The hovering behaviour of sex and age categories were compared statistically using SPSS for Windows 14.0. The hovering time/wind speed relationship was tested using linear and quadratic regression. By analysing hovering time as the dependent variable in a GLM mixed model with wind speed as independent variable in combination with sex-age as independent category variable and individual as random factor, we investigated whether there were any significant interaction effects of wind and sex-age category (independently of possible differences between individuals). Such interaction effects would reveal if the relationships between hovering time and wind speed were significantly different between the categories.

General linear models (GLM) were used for identifying differences in hovering versus wind relationships between seven specific individuals (four adult males and three adult females) for which more than 50 hovers were recorded for each individual (all of these individuals were identified with a high degree of confidence). The four males were: M1 (male no 1), the local breeding male, who made 53 fishing trips in 17 different days during 1–25 August; M5, probably from a nesting site at a nearby lake situated to the north of Lake Hammarsjön, who made 8 trips in 4 different days during 7–24 August; M12, who made 3 trips during a shorter stopover in the afternoon 20 August; M21, who made 2 trips during stopover 27–28 August. The three females were: F1 (female no 1), the local breeding female, who made 15 fishing trips in 8 days during 1–14 August; F3, who made 12 trips in 5 days during 1–7 August; F6, who made 51 trips in 20 days during 11 August–22 September.

We estimated fishing success in a very coarse and provisional way by the number of fishing trips leading to capture of fish (successful trip) or not (unsuccessful trip).

Results

Foraging technique

A total of 161 Ospreys, including local breeders, were seen at Lake Hammarsjön during the study period. Fishing trips were made by 109 of these birds, and a total of 300 trips were observed. During 278 of these trips as many hovering bouts as possibly were clocked, and for 262 trips the foraging success was recorded. 27 of the Ospreys made more than one fishing trip, and 12 of them stayed for more than one day at the lake. Altogether 3480 minutes (58 hours) of foraging were recorded, with 3040 minutes referring to adults (males: 1500 minutes; females: 1294 minutes; uncategorized adults: 246 minutes), 324 minutes to juveniles, and 116 minutes to uncategorized Ospreys. The foraging altitude ranged from approximately 8 to

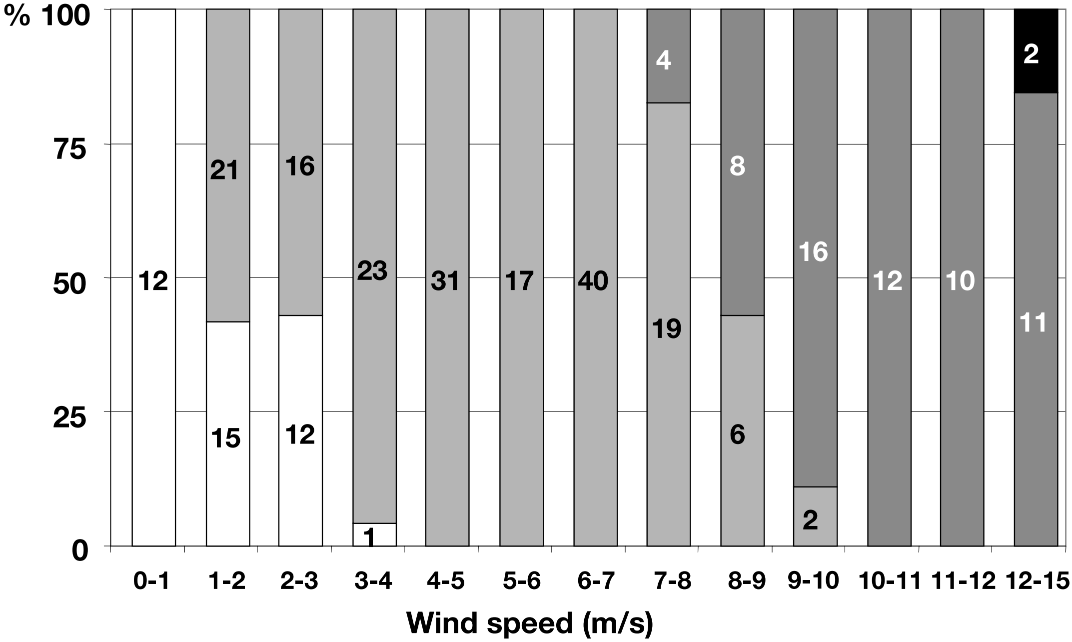

Figure 1. Fishing techniques used by Ospreys at different wind speeds. Open bar = without hovering, light grey bar = hovering by pure flapping flight, dark grey bar = hovering by flapping flight and gliding into the wind, closed bar = hovering by pure gliding. Figures in the bars show the number of fishing trips (total number of trips = 278). Note that flapping flight was used between hovering bouts in all categories of fishing techniques where hovering occurred.
Fiskgjusarnas fisketeknik vid olika vindhastigheter. Öppen stapel = ryttlar inte alls, ljusgrå stapel = ryttlar enbart med aktiv flykt, mörkgrå stapel = ryttlar med aktiv flykt och glidmoment, fylld stapel = ryttlar enbart genom att glida mot vinden. Siffrorna i staplarna anger antal fisketurer (totalt antal turer = 278). Notera att aktiv flykt förekommer i samtliga fisketeknikskategorier, det vill säga även när fågeln förflyttar sig mellan ryttlingssekvenserna.

50 m ($n_{(trips)}$ = 278, mean = 18.9 m, standard deviation (SD) = 5.5 m).

The four different fishing techniques were used under different wind speeds as shown in Figure 1. A shift in technique occurred with a clear relation to wind speed. Fishing without hovering was the only technique used under calm conditions (wind speed ≤ 1 m/s). Hovering with pure flapping flight was used during 175 fishing trips at wind speeds ranging from 1 to 10 m/s, and it was the dominant technique at wind speeds of 3–8 m/s. At wind speeds exceeding 8 m/s it was replaced by the hovering including flapping and gliding technique.

Hovering by flapping flight and gliding occurred during 61 fishing trips made by the Ospreys, and during these trips, 13% of the hovers included obvious glides. On a few occasions, hovering by pure gliding into wind also occurred. At the strongest wind speeds, approaching 14.5 m/s, Ospreys were recorded during two fishing trips to hunt by hovering by pure gliding into the wind without any elements of flapping flight at all. At even higher wind speeds (14.5–20.5 m/s), occurring during five observation days spread out through the study period, Ospreys did not forage at all.

Hovering

A total of 2065 hovers were clocked for 62 Ospreys identified to sex and age (overall mean hovering time = 4.2 s, SD = 3.1 s), with maximum hovering time of 40.6 s for males (mean = 4.4 s, SD = 3.3 s, n = 981), 28.3 s for females (mean = 4.0 s, SD = 3.1 s, n = 926), and 10.1 s for juveniles (mean = 3.1 s, SD = 1.7 s, n = 158). As seen in Figure 2, the ranges of hovering times were equally distributed for males and females, while juveniles showed a smaller scatter. The majority of hovers lasted 2–5 s, with only 97 hovers exceeding 10 s. Gliding occurred in hovers lasting longer than 3.6 s, with mean time 11.1 s (SD 5.8 s, n = 91) for hovers including gliding.

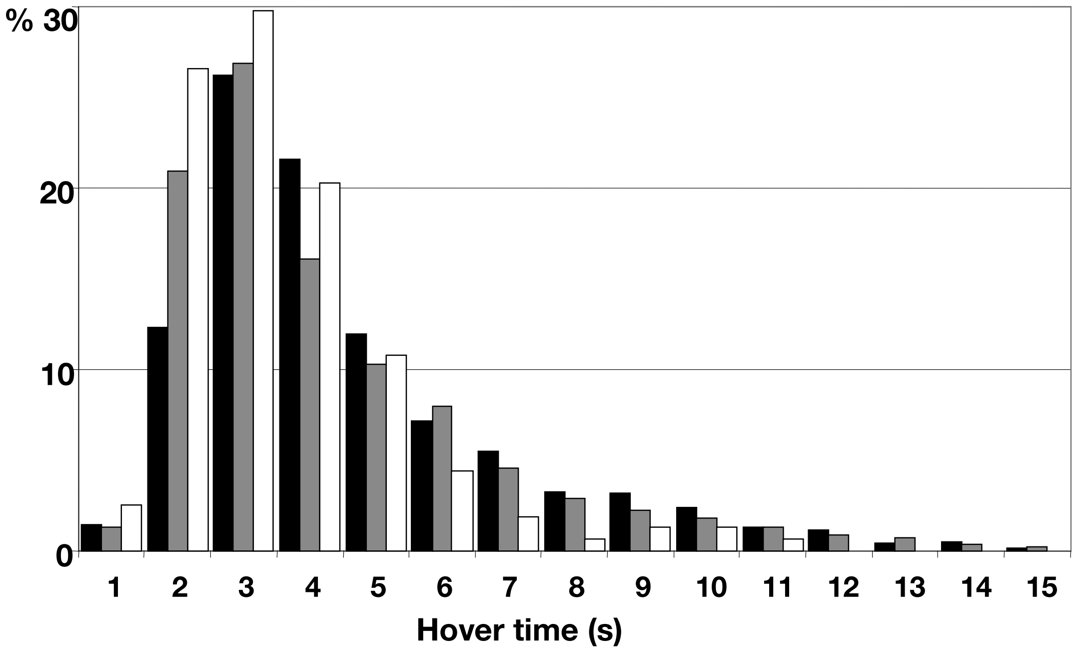

Figure 2. Distribution of observed hovering times of male, female and juvenile Ospreys. Males = closed bars, females = grey bars, and juveniles = open bars. The figure is based on 981 hovers for males, 926 hovers for females and 158 hovers for juveniles. Hovers exceeding 15 s (n = 29) are not presented in the figure.
Fördelning av observerade ryttlingstider för hanar, honor och unga fiskgjusar. Hanar = fyllda staplar, honor = grå staplar, och ungfåglar = öppna staplar. Figuren baseras på 981 ryttlingar utförda av hanar, 926 av honor och 158 av ungfåglar. Ryttlingar överstigande 15 sekunder (n = 29) presenteras inte i figuren.

Hovering times for adult males, adult females and juveniles in relation to wind speed are presented in Figure 3. In weak winds, the hovering time increased more steeply with increasing wind speed for males than for females, and mean hovering time was slightly longer for males compared to females (at wind speeds < 3.0 m/s; mean hovering time for males = 2.04 s, SD = 0.82 s, n = 136 and for females = 1.81 s, SD = 0.75 s, n = 111; t-test; p = 0.022). The maximum hovering time for males occurred at a wind speed of 10.5 m/s, while for females, the hovering time seemed to increase throughout the measured wind speed scale. As a consequence, females performed significantly longer hovers than males at wind speeds from approximately 10 to 12 m/s (mean hovering time for males = 5.77 s, SD = 0.26 s, n = 177, and for females = 6.65 s, SD = 0.30 s, n = 160; t-test; p = 0.026). The hovers clocked for juveniles were short and erratic, and the hovering time did not increase much along the wind speed gradient.

In the regressions of hovering time on wind speed, the quadratic term was included if statistically significant, which was the case for males but not for females and juveniles (Figure 3, Table 2).

Wind speed accounted for a substantial proportion of the variance in hovering time for males and females, but only for a very small proportion in juveniles according to the r^2-values in Table 2.

As seen from Table 3, there were significant interactions effects of wind and sex-age category between males and females, showing that males and females respond differently to wind in their hovering behaviour. No such significant relationships were found between juveniles and males or between juveniles and females (small dataset for juveniles). The GLM analysis of the seven individuals for which more than 50 hovering bouts were recorded confirmed the existence of a strong difference in hovering-wind relationship between males and females (p = 0.001). Analysis of this relationship for different individuals within each sex category, failed to reveal any significant differences among both male and female individuals ($p_{(males)} = 0.73$, $p_{(females)} = 0.12$). This suggests that the difference in hovering-wind relationship

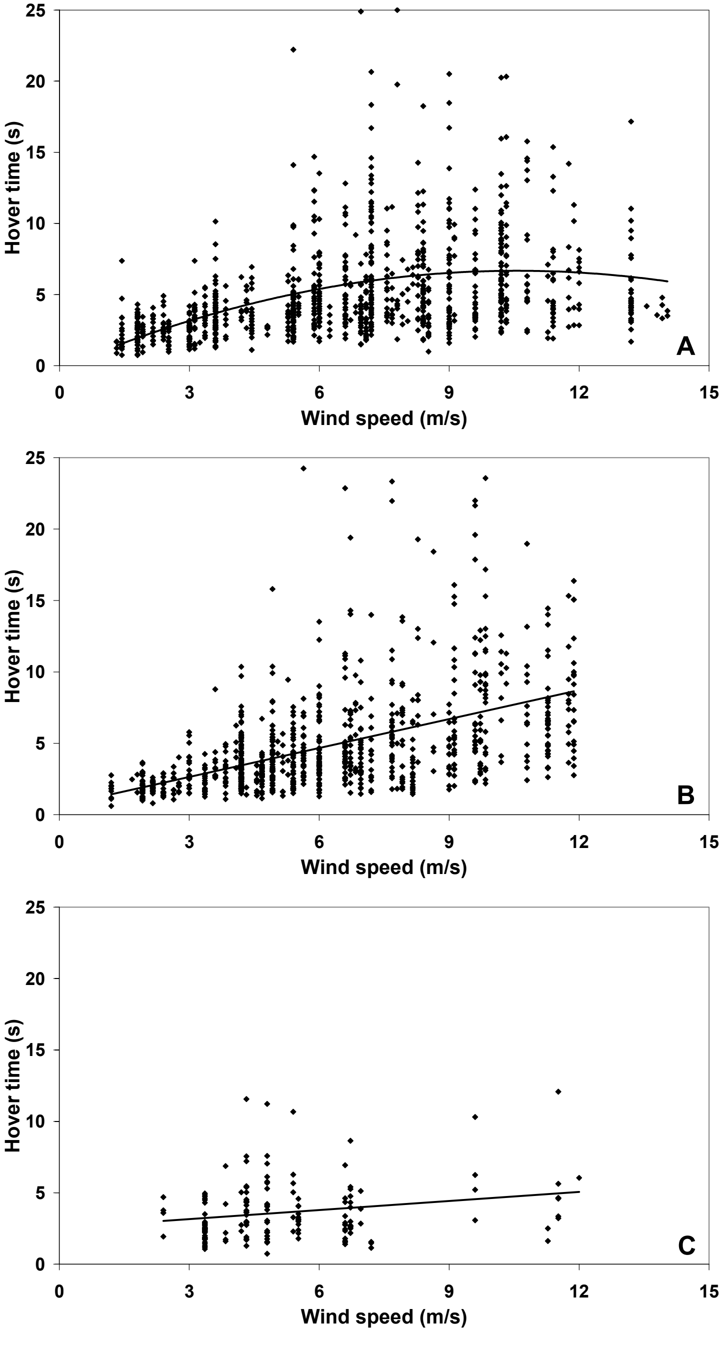

Figure 3. Hovering times for male (A), female (B) and juvenile (C) Ospreys, respectively, at different wind speeds ($n_{(males)}$ = 981, $n_{(females)}$ = 926, $n_{(juveniles)}$ = 158). There are 5 hovers by males and 2 hovers by females exceeding 25 seconds (max = 40.6 s), which are not shown in the diagrams. All of these hovers were made at wind speeds between 7.0 and 12.0 m/s.

Ryttlingstider för fiskgjusar i respektive kategorier: hanar (A), honor (B) och ungfåglar (C) vid olika vindhastigheter ($n_{(hanar)}$ = 981, $n_{(honor)}$ = 926, $n_{(ungfåglar)}$ = 158). Totalt varade 5 ryttlingar utförda av hanar och 2 ryttlingar utförda av honor mer än 25 sekunder (max. = 40.6 s). Samtliga av dessa ryttlingar utfördes vid vindhastigheter mellan 7.0 och 12.0 m/s (visas ej i diagrammet).

Table 2. Regressions of hovering time vs. wind speed for male, female and juvenile Ospreys observed at Lake Hammarsjön, Scania, southern Sweden 1 August to 30 September 2003. The data are plotted in Figure 3. p-values are given for the linear and quadratic relationships between hovering time and wind speed (y = hovering time in seconds, w = wind speed in m/s).

Regressioner för ryttlingstid mot vindhastighet för hanar, honor och juvenila fiskgjusar som observerades vid Hammarsjön, Skåne den 1 augusti till 30 september 2003. Se även fördelningsdiagrammet i figur 3. p-värden ges för linjära och kvadratiska samband mellan ryttlingstid och vindhastighet (y = ryttlingstid i sekunder, w = vindhasighet i m/s).

Categories	Equations	r^2	p(w)	p(w^2)	n(hovers)	n(ind.)
Males	$y = -0.2 + 1.30w - 0.062w^2$	0.15	0.000	0.000	981	31
Females	$y = 0.6 + 0.67w$	0.24	0.000	0.47	926	14
Juveniles	$y = 2.5 + 0.21w$	0.04	0.005	0.97	158	17

Table 3. Comparison of hovering performance in relation to wind speed between male, female, and juvenile Ospreys observed at Lake Hammarsjön, Scania, southern Sweden in autumn 2003. n = number of hovers, w = wind, cat. = category (males/females/juveniles). The data are plotted in Figure 3. p-values are given according to a GLM mixed model analysis with hovering time as the dependent variable, wind speed as independent variable in combination with sex-age as independent category variable, and individual as random factor.

Jämförelse mellan hanar, honor och juvenila fiskgjusar med avseende på ryttlingsutförande i förhållande till vindhastighet vid Hammarsjön hösten 2003. n = antal ryttlingar, w = vind, cat. = kategorier (hanar/honor/juvenila). Se även fördelningsdiagrammet i figur 3. p-värden ges enligt en GLM multivariat analys med ryttlingstid som beroende variabel, vindhastighet som oberoende variabel i kombination med kön-ålder som oberoende kategori variabel, samt individ som slumpmässig faktor.

Categories	n_1	n_2	n_3	p(w)	p(w^2)	p(cat.)	p(cat.*w)	p(cat.*w^2)
Males/Females/Juveniles	981	926	158	0.009	0.25	0.53	0.14	0.035
Males/Females	981	926		0.000	0.001	0.67	0.12	0.016
Males/Juveniles	981	158		0.07	0.29	0.27	0.17	0.28
Females/Juveniles	926	158		0.24	0.86	0.36	0.44	0.89

between males and females is indeed sex-linked and not due to individual variation in hovering behaviour.

Fishing success

The fishing success (successful or unsuccessful fishing trips) was compared between Ospreys fishing at low (0–5 m/s), moderate (5–10 m/s), and high (10–15 m/s) wind speeds. Because of low number of fishing trips for females and juveniles at high wind speeds, they were not separately tested. No significant effects of wind were found on fishing success for males (n = 112, χ^2-test = 3.55, 2 df, p = 0.17), adults (n = 222, χ^2-test = 1.80, 2 df, p = 0.41), or all Ospreys (n = 262, χ^2-test = 3.09, 2 df, p = 0.21). Furthermore, fishing success did not differ significantly between the three major fishing techniques (n_{trips} = 260, χ^2-test = 2.25, 2 df, p = 0.33). The "gliding into wind"-technique was used during two fishing trips without successful outcome.

Discussion

Limited hovering at low wind speeds

Our observations support the prediction that hovering is constrained at low wind speeds. At the lowest wind speeds, ≤ 1 m/s, Ospreys did not use the hovering technique at all. Furthermore, hovering times were distinctly shorter at low wind speeds compared to moderate and strong winds. In weak winds, the males' mean hovering time were longer and increased more steeply with increasing wind speed than for females. This is in agreement with the prediction that females, because of their larger body size (and possibly also because of a lower aspect ratio; Table 1), are more seriously limited in their hovering behaviour at low wind speeds than males.

This size-dependent constraint in foraging technique at low wind speeds may have significant ecological, behavioural and evolutionary implications. It may prevent Ospreys from foraging efficiently in the earliest morning hours and latest evening hours when winds are often weakest. This is also supported by the frequent use of the energy saving "sit-and-wait" fishing in early mornings and late evenings at lakes with suitable trees along the shoreline in a breeding area in south-central Sweden (M. Hake unpubl. data).

On migration, Ospreys most often use thermal soaring flight during a daily travelling period between approximately 0800 and 1700 hrs, when thermals develop (Kjellén et al. 1997, 2001). This would allow Ospreys to spend the morning and evening hours before and after the daily migration period to foraging. However, if windless conditions prevent efficient foraging during these periods, we must expect Ospreys to solve their foraging and fuelling needs on migration in other ways. Of course, one possibility is to deposit all energy reserves required for the migration prior to departure as indicated by one male Osprey covering the distance between south-central Sweden and West Africa in only 13 days (Kjellén et al. 2001). Another possibility would be to interrupt migration for one or more days and devoting these stopover days to foraging at suitable feeding sites. Yet another possibility would be to make brief and opportunistic deviations and fishing attempts as Ospreys encounter suitable fishing habitats en route, thus combining migration and foraging during the travelling days. Satellite tracking shows that stopover periods of several days or even a few weeks are common during autumn migration (Hake et al. 2001), while such stopover days occur less frequently on spring migration (Alerstam et al. 2006). In addition, a combination of migration and foraging en route during travelling days is regularly observed and appears to be important during both autumn and spring migration (Strandberg et al. in prep.).

Are there any alternative possible explanations, besides size-dependent flight constraints, for Ospreys' restricted hovering at the lowest wind speeds, and for the difference between the sexes at these wind speeds? One possibility is that fishing under more windy conditions, when the water surface is ruffled, is more difficult and requires longer hovering times. This possibility would be supported if fishing success is higher under weak compared to stronger winds, which is the opposite of what would be expected if hovering is seriously constrained at low wind speeds. We did not find significant differences in fishing success at different wind speeds, for any of the Osprey categories.

Gliding during hovering

As predicted, Ospreys' use of gliding was restricted to wind speeds exceeding 7 m/s, and the dominant technique was for Ospreys to hover by flapping flight, with short periods of gliding interspersed between the flapping bouts. Such gliding intervals contributed to prolong the total hovering time (including both flapping and gliding parts) up to ten seconds or even longer. However, there were also many flapping flight hovers of shorter duration under these wind speeds.

The kestrel *Falco tinnunculus* which is much smaller in size (about 0.20 kg) than the Osprey, is another raptor often using hovering for hunting. The kestrel incorporates short gliding periods in the hovering bouts in an increasing extent related to the gustiness of the wind. By using the gliding pauses the kestrel could both save energy and prolong the stationary hunting period (Videler et al. 1983).

Why did Ospreys not adopt gliding flight as a more dominant element of its fishing technique at wind speeds exceeding 7 m/s? One possible explanation is that in gliding flight, the Osprey will inevitably loose height (by at least 0.6 m/s according to gliding flight calculations; cf. Pennycuick 1989), thus gradually running out of time for adjustments of the dive towards the prey. In contrast, maintaining its hovering altitude by flapping flight gives the Osprey better opportunities for readjusting and waiting for the optimal diving situation. Hence, the mixture of flapping and gliding flight during hovers may be determined by a trade-off between increased fishing efficiency associated with flapping flight, and energy-saving combined with a gain in total hovering time associated with gliding flight.

Hovering in stronger winds

The hovering times of males reached a plateau and showed a very wide scatter at wind speeds exceeding 7 m/s, suggesting that there was no longer any important limitation in hovering technique associated with wind speed. Although hovering times of females showed a similar increase in scatter with increasing wind speed, there was a difference between the sexes in the mean hovering time, which continued to increase in stronger winds for the females but not for the males.

This difference is unexpected and surprising. We predicted that females, because of their larger body size, (Table 1; perhaps with an additional but minor effect because of the possibly smaller aspect ratio among females) should be more seriously limited than males in their hovering at low wind speeds. This was also supported by the data, as discussed above. We also predicted that the females would escape these constraints at slightly higher wind speeds than males. However, we did not expect that the females would surpass the males in hovering performance under strong winds. We can think of at least three possible explanations for this surprising result. (a) The balance and trade-off between flapping and gliding flight during hovering may differ between the sexes because of the body size difference, with strong winds possibly facilitating gliding flight more for the heavier females than for the males (cf. Pennycuick 1989). Unfortunately we have no data on the exact flapping and gliding components during the hovering bouts to investigate this possibility. (b) It seems likely that the larger females hunt partly different prey than do the smaller males. Hunting of different types of fish, e.g. shoaling fish compared to solitary fish, may well be associated with different optimal hovering times, and a larger prey will generally be worth the investment of longer hovering expenditure than a smaller prey. (c) Females spend most of the breeding season at the nest, being dependent on the hunting effort of males (Poole 1989). This might influence both the foraging technique and fishing success in a negative direction, which would be most pronounced early in autumn migration, which was the time for our study period.

Hovering among juveniles

There are clear tendencies of differences between adult and juvenile Ospreys in hovering performance. The juveniles showed a lower mean, smaller scatter, and less increase in hovering time along the wind speed gradient. A great part of the fishing trips probably are better referred to as try outs than as trips with the aim to catch prey. Many hovers were followed by apparently uncontrolled dives with no definite target. No hovers occurred at wind speeds below 2 m/s and above 12 m/s, also indicating a more restricted use of the technique. Prevost (1982) showed that juveniles have a significant lower diving success than adults, up to the age of 6 months. The diving success is affected by the hovering skills, because dives initiated by hovering have been proven to increase the fishing success by 50% compared to dives without initial hovering (Grubb 1977a). Thus, the hovering technique probably requires experience to be performed with success and thereby could be an important selection factor for survival among juvenile Ospreys during their first autumn migration.

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Sammanfattning

Detaljerade studier av fiskgjusens födosöksbeteende är intressanta, eftersom resultaten kan ge oss bättre förståelse för hur begränsningar i födosöket kan påverka andra beteenden och livshistoriekaraktärer hos arten såsom flyttning, överlevnad och reproduktion. Tidigare studier av fiskgjusens födosök har visat att vindhastigheten påverkar både fisketeknik och fiskeframgång. Vi går steget längre och undersöker hur fisketekniken förändras gradvis i takt med att vindstyrkan förändras. Fiskgjusar jagar regelbundet med hjälp av ryttling, vilket innebär att fågeln håller en fast position i luften, relativt marken, innan den dyker ner i vattnet för att fånga fisk. Vanligen sker ryttling med hjälp av aktiv flykt, men gjusarna använder sig dessutom av både glidflykt eller en kombination av aktiv flykt och glidflykt för att stå stilla i luften. Fiskgjusar kan även jaga helt utan att ryttla, men ryttling ökar fångstchanserna avsevärt.

Att ryttla vid en viss vindhastighet är det samma som att flyga horisontellt framåt med motsvarande ”airspeed”, det vill säga den hastighet fågeln har i förhållande till omgivande luft vid vindstilla förhållanden. Det bör alltså bli lättare för en fiskgjuse att ryttla när vindstyrkan ökar, men bara upp till den vindhastighet där fågeln har sin maxkapacitet för ryttling enligt effektkurvan för aktiv flykt. Vid glidflykt är fågelns höjd beroende av glidhastigheten enligt en liknande U-formad kurva, där fågelns sjunkhastighet är minst vid en måttlig glidhastighet. En fågel kan alltså hålla sig stilla i luften med hjälp av ren glidflykt mot vinden om den glider med samma hastighet som vinden, men samtidigt tappar den höjd. Glidflykt är dock inte möjligt vid vindhastigheter som är lägre än fågelns minimala glidhastighet (vikningshastigheten). Glidflykt är inte så energikrävande som aktiv flykt, och därför förväntar vi oss att fiskgjusar infogar glidperioder i ryttlingarna vid högre vindstyrkor (överstigande minsta möjliga hastighet för glidflykt) för att spara energi.

Fiskgjusen är en relativt tung fågel (1,4–2,0 kg), vilket medför höga flygkostnader för ryttling när det är vindstilla eller svag vind. Vi förväntar oss alltså en ökad ryttlingslängd allteftersom vinden ökar i styrka, upp till en vindhastighet som ger minimal kostnad för ryttling. Eftersom honor är större än hanar, med viktförhållandet 1,26, förväntar vi oss dessutom skillnader mellan könen. Ryttlingseffekten vid låga vindhastigheter förväntas vara högre för honor, vilket innebär större ryttlingsbegränsningar än för hanar. Vi fann inga signifikanta skillnader mellan könen med avseende på vinggeometri (Tabell 1). Följaktligen förväntas bägge könen ha likvärdiga förhållande för glidflykt och aktiv flykt, vilket innebär att honor bör vara kapabla att ryttla vid något högre vindhastigheter, med faktorn 1,04, än hanar. För en typisk hona med vikten 1,81 kg, vingyta 0,35 m^2 och vingbredd 1,66 m (Tabell 1) beräknas lägsta energiförbrukning för aktiv flykt infinna sig vid 10,3 m/s, lägsta glidhastighet vid 7,2 m/s och lägsta sjunkhastighet vid 8,7 m/s i glidflykt.

Vidare förväntar vi oss skillnader mellan gamla och unga fåglar (under sin första levnadshöst), eftersom erfarenhet bör ge förbättrade fiskefärdigheter. Unga fiskgjusar är under första höstflyttningen fortfarande i en inlärningsfas när det gäller fiske och flygfärdigheter, och de blir inte lika skickliga på att fiska som gamla fåglar förrän de är ca 6 månader gamla. Detta bör innebära att de påverkas annorlunda av vinden än gamla fåglar.

Sammantaget leder detta till följande förväntningar rörande gjusarnas ryttling:

(1) Möjligheterna för ryttling blir mer och mer begränsade med minskande vindhastighet, dessutom i högre grad för honor än för hanar.

(2) Ryttling med glidflykt är inte möjlig vid vindhastigheter lägre än 7 m/s.

(3) Ryttlingen har minst begränsningar vid vind-

hastigheter runt 9–11 m/s då kraftbehovet är som lägst.

(4) Ryttlingen är bättre anpassad och effektivare i relation till vinden hos gamla jämfört med unga fåglar.

Fältarbetet utfördes vid Hammarsjön, Skåne under perioden 1 augusti–30 september 2003. Totalt spenderades 277 timmar (50 dagar) vid sjön med dagliga pass från 06:00 till 14:00 eller 11:00 till 19:00 lokal normaltid, med gradvis kortare dagar allteftersom antalet soltimmar blev färre. Dagar valdes efter väder och vind för att täcka in bra sträckdagar och så många olika vindhastigheter som möjligt. Fisketurer registrerades för så väl sträckande som lokalt häckande fiskgjusar. Så långt det var möjligt köns-, ålders- och individbestämdes de fiskande gjusarna. Fyra olika fisketekniker urskiljdes: (1) fiske utan ryttling, (2) fiske med ryttling innefattande endast aktiv flykt mot vinden, (3) fiske med ryttling innefattande både aktiv flykt och glidflykt mot vinden och (4) fiske med ryttling innefattande endast glidflykt mot vinden. Fisketurer klockades från det att en fiskgjuse sågs börja fiska tills att den fångade en fisk, satte sig vid sjökanten eller försvann ur sikte (lämnade sjön). Vindhastighet uppmättes i samband med varje fisketur, samt när en vindförändring uppmärksammades. Den uppmätta vindhastigheten korrigerades till den beräknade vindhastigheten på 20 meters höjd med korrektionsfaktorn 1,2. Detta för att ge den egentliga vindhastigheten för den höjd där majoriteten av gjusarna fiskade. Förhållandet mellan ryttlingslängd och vindhastighet undersöktes med hjälp av linjär och kvadratisk regression, samt genom multivariat analys i en generell linjär modell (GLM) med ryttlingslängd som beroende variabel, vindhastighet som oberoende variabel i kombination med kön-ålder som oberoende kategorivariabel, samt individ som slumpmässig faktor. Vidare användes en GLM för att identifiera könsskillnader i ryttlingsbeteende vid olika vindhastigheter för fyra gamla hanar och tre gamla honor som klockats för fler än 50 ryttlingar.

Totalt noterades 161 fiskgjusar vid Hammarsjön under studieperioden. Fisketurer noterades för 109 av dessa gjusar och totalt 300 fisketurer observerades. Under 278 av fisketurerna klockades så många ryttlingar som möjligt, och för 262 av turerna noterades även fiskeframgången. Mer än en fisketur utfördes av 27 individer och tolv av dessa stannade mer än en dag vid sjön. Totalt bokfördes 3480 minuter (58 timmar) fiske, varav 1500 min. för hanar, 1294 min. för honor och 324 min. för ungfåglar. Fiskehöjden varierade mellan 8 och 50 m (medelhöjd = 18,9, standardavvikelse (SD) = 5,5). Fisketekniken var beroende av vindhastigheten (Figur 1). Vid vindar upp till ca 1 m/s fiskade gjusarna helt utan ryttling. Ryttling med bara aktiv flykt dominerade vid vindtyrkor på 3–8 m/s, och när vinden var starkare än 8 m/s infogades även glidmoment i ryttlingarna. Ungefär 13% av ryttlingarna innehöll glidmoment i de 61 fisketurer som då noterades. Två fisketurer, som utfördes vid vindhastigheter nära 14,5 m/s, innefattade enbart ren glidflykt helt utan aktiv flykt i ryttlingarna. När vindstyrkan ökade ytterligare, >14,5 m/s, sågs inget fiske överhuvudtaget.

Totalt klockades 2065 ryttlingar utförda av 62 olika gjusar som identifierats till kön eller ålder. Den totala medelryttlingslängden för alla gjusarna var 4,2 sek. (SD = 3,1), med den maximala ryttlingslängden 40,6 sek. för hanar (medel = 4,4, SD = 3,3, n = 981), 28,3 sek. för honor (medel = 4,0, SD 3,1, n = 926) och 10,1 sek. för ungfåglar (medel = 3,1, SD 1,7, n = 158). Som ses i Figur 2, hade ryttlingslängden en likartad fördelning för hanar och honor, medan ungfåglarnas ryttlingslängd visade en mindre spridning. Majoriteten av ryttlingar varade i 2–5 sek. Endast 97 ryttlingar översteg 10 sek. Glidflykt förekom i ryttlingar som varade längre än 3,6 sek. Medellängden för dessa ryttlingar var 11,1 sek. (SD = 5,8, n = 91).

Ryttlingslängden för hanar, honor och ungfåglar är plottade i relation till vindhastigheten i Figur 3. Vid svaga vindar ökade ryttlingslängden snabbare för hanar än för honor, och hanarnas ryttlingar var något längre vid låga vindhastigheter. Medelryttlingslängden vid vindhastigheter lägre än 3,0 m/s var för hanarna 2,04 sek. (SD 0,82, n = 136) och för honorna 1,81 sek (SD 0,75, n = 111; t-test; p = 0,022). Den maximala ryttlingslängden för hanar uppnåddes vid 10,5 m/s, medan honor ökade sin ryttlingslängd längs hela den uppmätta vindstyrkeskalan. Detta medförde att honorna ryttlade längre än hanarna vid vindhastigheter från ca 10 till 12 m/s (medelryttlingslängd för hanar = 5,77 sek., SD 0.26, n = 177, honor = 6,65 sek., SD 0,30, n = 160; t-test; p = 0,026). Relativt få ryttlingar klockades för ungfåglar, och de var korta, oregelbundna och förändrades inte nämnvärt när vindhastigheten förändrades. Regressionsanalyser av ryttlingslängd mot vindhastighet visade att hanarnas ryttling bäst förklarades med ett kvadratiskt förhållande till vinden medan honor och ungfåglar hade ett linjärt förhållande (Figure 3, Tabell 2). Vindhastigheten var en stor bidragande faktor till variansen i ryttlingslängd för hanar och honor till skillnad från ungfåglar enligt r2-värden i Tabell

2. Vi fann signifikanta skillnader i vindberoende interaktionseffekter mellan hanar och honor, men inte mellan något av könen jämfört med ungfåglar (Tabell 3). Analysen av de sju adulta fåglar som hade flest klockade ryttlingar bekräftade att det fanns en könsskillnad i förhållandet mellan ryttlingsbeteende och vindstyrka. Analyserna gav dock inga individuella skillnader inom könen (inga signifikanta interaktionseffekter mellan vind och individ). Analyserna visar att skillnaden mellan könen i förhållandet vindstyrka och ryttlingslängd verkligen är könsbunden och inte beroende av individuella variationer. Ingen signifikant vindeffekt på fiskeframgång (lyckade eller misslyckade fisketurer) kunde påvisas. Fiskeframgången skiljde inte heller mellan de tre dominerande fisketeknikerna. Ren glidflykt mot vinden noterades endast vid två tillfällen utan lyckat fiskeresultat.

Observationerna stödde förväntningarna angående ryttlingens begränsningar vid låga vindhastigheter. Vid vindstyrkor upp till 1 m/s användes inte ryttling alls, och ryttlingarna var betydligt kortare vid låga jämfört med måttliga vindhastigheter. Vid låga vindhastigheter ryttlade hanarna längre än honorna och hanarnas ryttlingslängd ökade även snabbare i relation till vindökningen. Detta stöder våra förväntningar om att honor, beroende på högre kroppsvikt, är mer begränsade i sitt ryttlingsbeteende vid låga vindhastigheter än hanar. Den storleksrelaterade skillnaden i ryttlingsteknik kan få ekologiska, beteendemässiga och/eller evolutionära konsekvenser. Fiskgjusarna kan förhindras att fiska effektivt tidigt på morgonen när vinden oftast är svag, vilket stöds av att den energisparande strategin att ”sittfiska” är vanlig tidigt på morgonen vid sjöar med tillgång på lämpliga träd för spaning efter fisk. Under flyttningen använder fiskgjusarna mestadels termikkretsflykt, vilket sker under den delen av dagen när termiken utvecklas (ca 08:00–17:00). Detta ger en del tid över till morgon- respektive kvällsfiske. Men om gjusarna vid dessa tidpunkter förhindras att fiska effektivt på grund av svaga vindar, förväntar vi oss att de delvis får lösa bränslebehovet för flyttningen på annat sätt. En möjlighet är naturligtvis att de laddar upp med allt bränsle de behöver under hela flyttningen redan innan de ger sig iväg. En annan möjlighet är att avbryta flyttningen och förlägga en eller flera dagar på en lämplig fiskeplats för att bygga upp energireserverna. En tredje variant är att göra korta avstickare för att fiska när de träffar på lämpliga vatten längs rutten, med andra ord kombinera fiske med aktivt sträck. Satellitsändarstudier visar att fiskgjusar ofta stannar på vissa platser i flera dagar eller till och med veckor under flyttningen. Dessutom finns det observationer av att fiskgjusar ofta kombinerar aktivt sträck och fiske, vilket visar att även denna strategi kan vara viktigt under både höst- och vårflyttningen.

En alternativ förklaring till begränsningar i ryttlingsutförande vid låga vindhastigheter, förutom storleksrelaterade inskränkningar, kan vara att fisket under blåsiga förhållanden är svårare och kräver längre ryttlingar. Detta skulle i så fall innebära att fiskeframgången skulle vara högre vid låga vindhastigheter. Detta motsägs dock av de observerade ryttlingsbegränsningarna vid låga vindhastigheter och att vi inte fann några uppenbara skillnader i fiskeframgång vid olika vindhastigheter.

Som förväntat använde sig inte gjusarna av glidflykt under ryttlingarna när vindstyrkan var lägre än 7 m/s. Vid vindstyrkor över 7 m/s dominerades ryttlingstekniken av aktiv flykt med kortare glidmoment infogade. Glidmomenten bidrog till att förlänga ryttlingarna, men trots detta var kortare ryttlingar med enbart aktiv flykt vanliga vid högre vindhastigheter. En förklaring till varför gjusarna inte använder glidflykt som dominerande teknik vid vindhastigheter över 7 m/s är förmodligen att glidflykt automatiskt medför att de tappar höjd (med åtminstone 0,6 m/s), vilket ger dem mindre tid till att sikta in ett dyk mot ett specifikt byte. Om de däremot kan hålla höjden med hjälp av aktiv flykt under ryttlingen, så ger det bättre förutsättningar för att justera och vänta in rätt dyktillfälle. En blandning av aktiv flykt och glidflykt i ryttlingarna kan alltså vara en kompromiss mellan ökad fiskeframgång genom aktiv flykt och energibesparning/längdökning genom glidflykt i ryttlingarna.

Hanarnas ryttlingslängd nådde en platå och visade stor spridning vid vindhastigheter över 7 m/s (Figur 3). Vid vindhastigheter över 7 m/s finns alltså troligen inga betydande ryttlingsbegränsningar som har med vindhastigheten att göra. Även honornas ryttlingslängd visade en likartad spridning som hanarna. Skillnaden gentemot hanarna var emellertid att honornas medelryttlingslängd fortsatte att öka vid höga vindhastigheter. Vi förväntade oss att de större och tyngre honorna (Tabell 1) var begränsade vid lägre vindhastigheter, vilket även bekräftades av observationerna. Vi förväntade oss även att honor begränsas upp till något högre vindhastigheter än hanar, men inte att honor överglänser hanar i ryttlingsutförande vid höga vindhastigheter. Resultatet kan möjligen förklaras med att (a) kompromissen mellan aktiv flykt och glidflykt vid ryttling kan skilja mellan könen beroende på skillnaden i kroppsstorlek, där högre vindhastigheter gör det möjligt för de tyngre honorna att använda glidflykt i större utsträckning, (b) honor och hanar kan ta olika byten på grund av storleksskillnaden, och olika bytesstorlek och/eller art kan medföra skillnader i optimal ryttlingslängd på grund av olika beteende hos bytet, (c) eftersom honor mest sitter på och vid boet under häckningssäsongen och överlåter åt hanen att fiska, kan deras fisketeknik och fiskeframgång påverkas negativt, vilket bör vara tydligt tidigt under hösten då vår studie utfördes.

De unga fiskgjusarnas ryttlingsbeteende skiljde sig från de gamla fåglarnas. Unga gjusar hade lägre medelvärde, mindre spridning och mindre ökning i ryttlingslängd längs vindstyrkegradienten. En avgörande del av de unga fåglarnas fiskeförsök var dock förmodligen snarare övningar i fisketeknik än fisketurer med avsikt att fånga något byte. Många ryttlingar åtföljdes av okontrollerade dyk utan något definitivt mål. Inga ryttlingar förekom vid vindhastigheter under 2 m/s eller över 12 m/s, vilket även det indikerar begränsningar i de unga fåglarnas fisketeknik.

Som tidigare nämnts har dyk utförda av fiskgjusar som är yngre än 6 månader sämre fångstframgång jämfört med dyk som görs av äldre fåglar. Detta borde åtminstone delvis bero på begränsningar i ryttlingsfärdigheterna, eftersom dyk initierade med ryttling ökar fiskeframgången med 50% jämfört med dyk utan ryttling. Med andra ord kräver troligen ryttlingen erfarenhet för att utföras framgångsrikt och kan därför vara en viktig selektionsfaktor för överlevnad hos unga fiskgjusar under sin första höstflyttning.