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Flycatching behaviour in some passerines during the late breeding season at Ammarnäs, Swedish Lapland

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Abstract

Many passerines have been recorded flycatching in the late breeding season in northern Swedish forests. In this paper, I analyze how flight energy costs according to Minimum Energy Power (sensu Pennycuick 1989) correlated with flycatching behaviour. Species included are (with increasing rank of flight energy cost): Spotted Flycatcher *Muscicapa striata*, Whinchat *Saxicola rubetra*, Yellow Wagtail *Motacilla flava*, Reed Bunting *Emberiza schoeniclus*, Brambling *Fringilla montifringilla*, and White Wagtail *Motacilla alba*. On average, birds performed 0.6–2.3 flights/30s and captured from 0 up to 10 prey per flight. Number of prey captured per flight varied significantly among species (from 0.8 to 1.1 prey). The efficiency of capturing prey (percentage of successful single capture flights) also varied between species, from 72% in the Whinchat to 97% in the White Wagtail. The percentage of multi-capture flights did not, however, vary. In two species, the multi-capture flights significantly reduced the time spent flying per prey. Flight energy costs were positively correlated with flycatching rate and number of prey captured per flight. The extensive use of flycatching is interpreted as an opportunistic response to local super-abundance of highly rewarding prey, mostly insects *Isoperla grammatica*, O. Plecoptera, during a period of presumed high energetic demands by birds.

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Introduction

It is generally assumed that food searching methods and feeding techniques used by birds tend to maximize the net energy intake rate (i.e. energy gained through food minus energy costs of searching and capturing, see Krebs & Cowie 1976, Alatalo 1982, Stephen & Krebs 1986). To achieve that, birds may select, in each situation, the most rewarding feeding technique according to their morphology, physiological stage and the local availability of food resources (Hutto 1981, Rabenold 1978, Norberg 1990).

Flycatching is a common foraging technique that includes manoeuvres in which the prey is pursued and captured during the flight after a variable searching time from an exposed perch (sensu Fitzpatrick 1980). Because of the high energy costs (cf. Pennycuick 1989, Norberg 1990), flycatching is mainly used by small-sized and well-adapted species (e.g. Holmes et al. 1979, Alatalo & Alatalo 1979, Fitzpatrick 1980, Alatalo 1982, Niemi 1985, Järvinen 1986, Svensson 1987). Flycatching has been recorded for many different species during the breeding season in northern Scandinavian forests (see references above). In this paper, I describe the flycatching behaviour of White and Yellow Wagtail *Motacilla alba* and *M. flava*, Brambling *Fringilla montifringilla*, Reed Bunting *Emberiza schoeniclus*, Whinchat *Saxicola rubetra* and Spotted Flycatcher *Muscicapa striata* during periods of extreme abundance of emerging flying insects at a river in Lapland (northern Sweden). Since these species are morphologically different, i.e. in wing shape, wing length and body mass (Table 1), I analyzed the effects of different flight energy costs on flycatching to test the assumptions that higher energy costs should be correlated with: 1) a lower flycatching rate (number of attempts/time), 2) lower efficiency in capturing the prey (percentage of successful attempts) and 3) a lower number of prey taken per flight.

Methods

My study site was at Tjulån, a torrent river in the subalpine birch forest in Swedish Lapland (7 km

Table 1. Basic morphological characteristics of species at Ammarnäs. All the individuals included in the analysis were adult, non-moulting birds. Power calculations are according to Pennycuick (1989). Air density at the study area was corrected for in the Power calculations.

Morfologiska data för de studerade arterna i Ammarnäs. Alla individer som tagits med i analysen är adulta fåglar som inte påbörjat ruggning. Beräkningen av "Minimum Power" enligt Pennycuick (1989). Korrigering har skett för luftens täthet på platsen.

	Body mass *Vikt* (g) $\bar{x}$±s.d.	Wing length *Vinglängd* (mm) $\bar{x}$±s.d.	Wing span *Vingspann* (m) $\bar{x}$	Minimum Power (W) $\bar{x}$
Spotted Flycatcher *Grå flugsnappare*	15.6±0.8	90.2±1.2	0.24	0.243
Whinchat *Buskskvätta*	15.4±1.2	75.0±2.5	0.22	0.261
Yellow Wagtail *Gulärla*	16.5±0.6	84.8±1.3	0.24	0.262
Reed Bunting *Sävsparv*	18.1±1.5	82.0±1.7	0.24	0.298
Brambling *Bergfink*	21.8±1.5	93.2±1.7	0.27	0.340
White Wagtail *Sädesärla*	21.4±1.7	89.3±3.0	0.25	0.360

west of Ammarnäs, 65° 58' N, 16° 06' E, 570 m a.s.l.). The surrounding vegetation was mainly composed of Birch *Betula pubescens*, 3–6 m tall on average, with occasional Norwegian Spruce *Picea abies* and Juniper *Juniperus communis*. The understore vegetation consisted mainly of different *Salix* spp. together with *Aconitum septemtrionale, Angelica archangelica, Equisetum* spp. and *Epilobium angustifolius*, which formed a luxuriant vegetation on the riversides. For a more detailed description of the area see Enemar et al. 1984, Arvidsson & Klaesson 1984, and for a detailed map of the study site see Ulfstrand (1968).

I recorded flycatching during a net total of 70 h during the late breeding season of three summers: 1988 (from 18 July to 10 August), 1989 (from 15 July to 3 August) and 1990 (from 15 July to 3 August). I pooled the observations from the three seasons since the time periods were quite similar and I got no impression of any behavioural difference between years. Observations were performed during 1–3 hrs/day sessions between 0800 to 1200 h on clear days. These sessions were evenly distributed between these hours. The observation sessions were carried out at several prominent sites along the river side (N=7, ca. 2.5 km long) with ample visibility (ca. 150 m of river). All the locations were visited every work day. I recorded as many flycatching sequences as possible of actively flycatching birds at each site. An observation sequence was defined as starting immediately after the detection of a focal individual searching from an exposed perch (e.g. a tree or an emergent rock) and ended when the bird landed after capturing either no prey (unsuccessful flights), one (single flights), or more than one prey (multi-capture flights). I did not include in the analysis those sequences where the bird changed to a new perch without making any capturing attempt and then, having waited unsuccessfully for some time for prey. Data on different species were recorded during the same session. Only one sequence (i.e. data for one bird) was recorded at the same time. When more than one bird was flycatching at the same time, I alternatively switched the sequence from one bird to another, trying to distribute evenly the flycatching sequences. Anyhow, no more than two sequences per bird were recorded at each location. I used a continuously running tape recorder for each flycatching sequence. Data recorded include: species, total time recorded per sequence, flight time (both in seconds) and type of flight (unsuccessful, single or multi-capture). Flycatching rates (measured as number of attempts/30 s, hereafter), were estimated on actively flycatching birds (N=3–5 individuals of each species) during periods of 3–4 min. in every field work session.

The statistical analysis treated each flycatching sequence as an independent observation. Although I can not exclude the possibility that the same individuals were recorded several times at different field work sessions, the total number of birds on focus is likely to be high. According to the ringing activity performed at the same site (total number of birds ringed from 1988 to 1990 were: 85 White and 209 Yellow Wagtails, 369 Bramblings, 258 Reed Buntings, 32 Whinchats and 294 Spotted Flycatchers and less than 30% of them (range=9–29%, data pooled for each species) were recaptured within the same season (LUVRE project unpubl. data). Also the fact that observations were collected in three years makes it unlikely that repeat observations of the same individual could cause any serious effect. All the statistical analyses were performed with SYSTAT (Wilkinson 1988). Pearson correlations were used in all the cases. Values given are means (±sd).

Flight energy costs were calculated as the Minimum Energy Power (sensu Pennycuick 1989). I prefer Minimum instead of Maximum Energy Power (sensu Norberg 1981) as the latter is affected by variables such as mass specific muscle work, muscle size and wing-beat frequency (A. Hedenström pers. com.) which are difficult to measure. Instead, Minimum Energy Power is an unbiased estimator based only on aerodynamics.

Results

Flight energy cost

Species were ranked in an increasing order of flight energy cost according to the Minimum Energy Power (sensu Pennycuick 1989) as follows: Spotted Flycatcher, Whinchat, Yellow Wagtail, Reed Bunting, Brambling and White Wagtail (Table 1). Hereafter, the species rank order (from 1 to 6) was used in all the correlations.

Prey characteristics

Most of the prey captured were *Isoperla grammatica*, Poda, O. Plecoptera, a very large and conspicuous insect (head to abdomen size=10.8±1.0 mm and wing length=8.5±2.0 mm, N=12). This prey species reaches extremely high densities at northern latitudes from late July to mid-August (see Svensson 1966, Ulfstrand 1967) and should easily be located by the birds from distances up to 25 m (own observ.).

Flycatching behaviour

Flycatching rate (Table 2) significantly differed among species ($F_{5,151}$=11.0, p<0.001, ANOVA test). Thus, White Wagtail and Reed Bunting performed as much as three times more flycatching per time unit than Whinchat. Birds captured from 0 up to 10 prey per flight. I was able to observe a White Wagtail capturing 10 prey during a continuous 40 s flight. The maximum number of prey captured per flight also significantly varied among species (χ^2_{10}= 44.2, p<0.001), and ranged between 3 and 10 prey per flight (see Table 2). Consequently, the average number of prey captured per flight varied significantly from 0.8 in Whinchat to 1.1 in White Wagtail and Brambling (Table 2). These differences might be due to a different prey capturing efficiency and not to a different proportion of multi-capture flights, as the number of unsuccessful vs successful flights significantly differed among species (χ^2_5=33.2, p<0.001), but the number of single vs multiple capture flights did not (χ^2_5=4.9, p= 0.42). Flycatching efficiency (percentage of successful single capture flights) ranged from 72% for Whinchat to 97 % for White Wagtail (see Table 2).

Flight energy costs were positively correlated with the average number of prey captured per flight

Table 2. Basic description of the species' flycatching behaviour recorded at Ammarnäs. Data include flycatching rate (number of flights/30 sec), number of flights where different numbers of prey were captured, range and average.

Arternas flugsnapparbeteende i Ammarnäs. Uppgifterna omfattar flygfrekvens (antal flygningar per 30 sekunder), antalet flygningar med olika antal fångade byten samt spridning och medeltal för antal byten per flygning.

	Flycatching rate *Flygfrekvens*		Number of prey captured per flight *Antal byten per flygning*						
	N	x̄±s.d.	0	1	2	>3	Total	Range	x̄±s.d.
Spotted Flycatcher	35	1.0±0.6	7	108	5	2	122	0– 3	1.0±0.4
Whinchat	18	0.6±0.3	10	25	4	0	39	0– 3	0.8±0.5
Yellow Wagtail	25	1.3±0.9	5	67	5	3	80	0– 4	1.0±0.5
Reed Bunting	24	1.8±1.4	18	65	4	4	91	0– 3	0.9±0.6
Brambling	16	1.1±0.7	6	74	4	7	91	0– 5	1.1±0.8
White Wagtail	39	2.3±1.1	5	162	5	5	177	0–10	1.1±0.8

Table 3. Average flight time (in seconds) per captured prey while performing single vs. multiple capture flycatching (see definitions in methods). Differences were tested with a two-tailed t-test.

Genomsnittlig flygtid i sekunder per fångat byte vid flygningar med en resp. flera fångster. Skillnaderna testades med tvåsidig t-test.

	Single capture flights *Flygning med en fångst*		Multiple capture flights *Flygning med flera fångster*		Differences *Skillnader*
	N	$\bar{x}$±s.d.	N	$\bar{x}$±s.d.	
Spotted Flycatcher	63	4.7±2.3	51	3.0±1.7	t=4.4, p<0.001
Whinchat	20	4.2±1.8	11	4.9±2.0	t=1.0, N.S.
Yellow Wagtail	31	4.0±1.8	23	4.1±2.1	t=0.1, N.S.
Reed Bunting	59	7.4±3.7	14	6.2±1.3	t=0.9, N.S.
Brambling	75	6.1±2.5	80	4.2±1.6	t=5.7, p<0.001
White Wagtail	59	4.3±2.6	24	4.2±1.1	t=0.2, N.S.

(r=0.88, p=0.02), flycatching rate (r=0.77, p=0.07), maximum number of prey captured per flight (r=0.782, p=0.06), but not with flycatching efficiency (r=0.43, p=0.39, N=6 in all the cases).

Flight time per captured prey differed significantly among species both in single ($F_{5,280}$=10.6, p<0.001, ANOVA test) and multiple capture flights ($F_{5,197}$=9.4, p<0.001, ANOVA test, see Table 3). At least in the Spotted Flycatcher and Brambling, flight time per captured prey was significantly shorter in multiple than in single capture flights (two-tailed t-test, p<0.001 in both cases, Table 3).

Discussion

Although it is generally assumed that size and body mass negatively influence the use of expensive energy techniques (Alatalo 1982, Jacksick & Carothers 1985, Norberg 1990), my results suggest that species with high flight energy costs performed, on average, more flights per time unit and captured more prey per flight. This can be explained by assuming that heavier species such as Reed Bunting and White Wagtail may increase their flycatching rates by performing shorter flights and by capturing more than one prey per flight (see results).

Flycatching efficiency and energy costs were not correlated. The variation between species could be due to: 1) different flight abilities or 2) failure in capturing the prey as a consequence of competition for the same prey. This was the case in some situations when I recorded up to three different birds competing for the same prey. The extensive use of multi-capture flights may represent not only an efficient strategy to reduce the flight time per prey captured (see Results) but also an efficient way of reducing unsuccessful flights.

In late breeding season, there might be very high energetic demands due to feeding young, premigratory fattening or moulting. The type of prey captured must positively balance their energy demands at that time of the season. Indeed, the massive emergence of benthic insects occurring at torrent rivers of high latitudes (see Svensson 1966, Ulfstrand 1967, 1968) represents a profitable and highly rewarding source of prey (a 10.8 mm *I. grammatica* means ca. 15.5 mg of dry weight, according to Rogers et al. 1976), which should be easy to detect and easy to catch (i.e. poor flight manoeuvring abilities, own obs.).

Migratory birds species at northern latitudes are well adapted to exploit the seasonal availability of abundant food resources (see Gauthreaux 1982 for a review) by using more flexible feeding techniques than resident ones (see, for instance, Herrera 1978, Des-Granjes 1979, Fitzpatrick 1980). In such situations, flycatching might represent an opportunistic response to the availability of a highly rewarding prey. As the species considered in my analysis have also been recorded flycatching in some other situations when energy requirements are presumably very high (e.g. migratory fattening at stopover sites, Alatalo & Alatalo 1979, Draulans & Vessem 1982, Niemi 1985, Lindström per. comm., own obs.), I hypothesize that flycatching represents a flexible and opportunistic response to temporal abundance of highly rewarding insects during periods of extremely high energetic demands such as breeding, moult and premigratory fattening periods.

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Sammanfattning

Flugsnapparbeteende hos några tättingar under senare delen av häckningssäsongen i Ammarnäs, Lappland.

Det anses allmänt att fåglarnas metoder för att söka och fånga sin föda har utvecklats för att maximera nettotillförseln av energi, d.v.s. energiintaget minus energiåtgången för att söka och fånga födan. För att uppnå detta bör en fågel vid varje givet tillfälle använda den mest lönsamma metoden i förhållande till sin byggnad, sina fysiologiska behov och den lokala födotillgången.

Flugsnapparbeteende, eller flugsnappning, är en vanlig metod som innebär flygmanövrar då bytet förföljs och fångas i flykten sedan det efter en variabel söktid upptäckts från en utsiktspunkt. Metoden kostar mycket energi och används därför främst av små och för ändamålet välanpassade arter. I denna uppsats beskriver jag flugsnapparbeteendet hos sädesärla, gulärla, bergfink, sävsparv, buskskvätta och grå flugsnappare under perioder med extremt god tillgång på kläckande insekter.

Utgångspunkten var att dessa arter har olika vingform, vinglängd och vikt (Tabell 1). Jag ville testa antagandet att högre energikostnad skulle vara korrelerad med färre fångstförsök per tidsenhet, lägre andel lyckade fångstförsök samt färre fångade byten per flygning.

Undersökningen utfördes under perioderna 18 juli–10 augusti 1988 samt 15 juli–3 augusti 1989 och 1990. Platsen var Tjulån i Ammarnäs, en snabbt rinnande å i björkskogszonen. Jag genomförde observationer under sammanlagt 70 timmar, vilka var jämt spridda över perioderna och mellan kl 8 och 12. Eftersom jag inte noterade några uppenbara skillnader mellan säsongerna slog jag ihop alla årens material för analyserna. Jag gjorde registreringar från flera platser längs ån. Varje observationssekvens utgjordes av tiden från det jag upptäckte en sittande och spanande fågel tills dess den åter satt sig efter ett framgångsrikt eller misslyckat fångstförsök. Observation av en fågel som förflyttade sig från en utsiktspunkt till en annan utan att ha gjort något fångstförsök togs inte med i analysen. Jag gjorde aldrig mer än två observationssekvenser av samma fågel på samma plats. Energikostnaderna för flygningarna beräknades som "Minimum Energy Power" enligt Pennycuick (1989).

Resultat

Energikostnaderna för flygning ökade för de olika arterna i följande ordning: grå flugsnappare, buskskvätta, gulärla, sävsparv, bergfink och sädesärla (Tabell 1). De byten som ingick i fångsterna dominerades av den storvuxna *Isoperla grammatica*, en ca 11 mm lång bäcksländа som kläcker i mycket stora mängder från slutet av juli till mitten av augusti.

Antalet flugsnappningar per tidsenhet (lyckade och misslyckade tillsammans) skiljde sig mellan arterna (Tabell 2). Sädesärla och bergfink gjorde tre gånger fler flygningar än buskskvätta. Antalet fångade byten per flygning varierade mellan 0 och 10. Rekordet var en sädesärla som fångade 10 byten under en kontinuerlig flygning på 40 sekunder. Det högsta antalet byten per flygning varierade också mellan arterna, från 3 till 10 (Tabell 2). Detta innebär att det genomsnittliga antalet byten per flygning varierade mellan arterna, från 0,8 hos buskskvättan till 1,1 hos sädesärlan. Fångsteffektiviteten (antalet lyckade av alla försök) varierade från 72 % hos buskskvätta till 97 % hos sädesärla (Tabell 2).

Energikostnaden var positivt korrelerad med antalet byten per flygning, antalet flygningar per tidsenhet och högsta antalet byten per flygning, men inte med fångsteffektiviteten. Flygtiden per flygning skiljde sig också mellan arterna både för flygningar då bara ett byte fångades och flygningar då flera byten fångades (Tabell 3).

Diskussion

Trots att det allmänt antas att ökande storlek och vikt negativt påverkar användningen av kostsamma fångstmetoder visar mina resultat att arterna med hög energikostnad för flygning utförde fler flygningar per tidsenhet och fångade fler byten per flygning. Detta kan förklaras av att de tyngre arterna sävsparv och sädesärla aktivt ökade fångstintensiteten genom kortare flygningar och genom att ta fler byten per flygning.

Under senare delen av häckningssäsongen kan energibehoven vara mycket höga på grund av ungmatning, fettupplagring eller ruggning. Anledningen till att de undersökta arterna använder den energikrävande flugsnappningsmetoden är därför säkerligen kombinationen av detta höga energibehov och den extremt rika tillgången på föda. Flugsnappning är alltså ett flexibelt och opportunistiskt svar på tillfälligt hög tillgång på energirik föda och ett extra högt energibehov.