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THE PAINTED REDSTART (*MYIOBORUS PICTUS* L.) SEARCH RATE OF A CRYPTIC *VERSUS* CONSPICUOUS PREY: A FIELD TEST OF OPTIMAL SEARCH MODELS

ABSTRACT: Models of optimal search rates predict that predators increase the search rate when availability of conspicuous prey increases relative to cryptic prey. I tested this prediction by comparing foraging hop rates by 19 Painted Redstarts (*Myioborus pictus*) – insectivorous birds in Arizona, USA. Redstarts often use flashy displays of open wings and tail to flush their prey and to subsequently chase the prey in air. Such flush-displays make the prey conspicuous and easy to detect. Hence, foraging mode affects relative availability of conspicuous *versus* cryptic prey: birds foraging with frequent flush-displays encounter conspicuous prey more often than birds foraging with infrequent flush-displays. As predicted, the hop rates during foraging with infrequent flush-displays were lower than hop rates during foraging with frequent displays.

KEY WORDS: search rates, foraging, flush-pursue, *Myioborus pictus*

Predators may respond to changes in availability of conspicuous prey by optimizing foraging speed (search rate) (Gendron and Staddon 1983, 1984, Gendron 1986) or allocation of attention (Dukas and Ellner 1993). If abundance of the conspicuous prey increases relative to abundance of the cryptic prey, then the search rate and the proportion of conspicuous prey in total prey capture should increase (Gendron and Staddon 1983). These predictions are rela-

tively robust. For example, in models maximizing the net rate of energy gain, the effect of energetic costs of foraging can be regarded negligible for most natural situations (Gendron and Staddon 1983). In food intake rate maximization models, differences in handling time (which represents “costs” of a single prey capture in the models) between prey types affect the optimal search rate only when handling times are large relative to inter-catch interval (Gendron and Staddon 1983). Even then the search rate for the conspicuous prey is predicted to be faster than for the cryptic prey. I tested this prediction using insectivorous birds, for which the duration of a capture attempt is usually much shorter than inter-catch interval (e.g. Jabłoński 1999).

Prey of insectivorous birds can be generally divided into two groups according to their antipredatory behavior: those that rely mostly on camouflage and crypticity and stay put on the substrate in response to approaching predators (for example many caterpillars) and those that escape by flying or jumping away in response to approaching predators (for example leafhoppers, treehoppers, flies; Edmunds 1974, Green 1989, Evans and Schmidt 1990). Certain insectivorous birds, classified as flush-pursuers (*sensu* Remsen and Robinson 1990) are specialized in exploiting the latter group of prey, although

their diet includes both prey types (Jabłoński 1996, 1999, Barber *et al.* 2000, Jabłoński *et al.* – unpublished). Flush-pursuers are morphologically well adapted to efficiently chase and capture escaping insects (Keast *et al.* 1995). Painted Redstart (*Myioborus pictus*) is such a flush-pursuer. Redstarts often use visual displays of fanned tail and spread wings to evoke prey escape responses and to increase the number of conspicuously escaping insects, which are then available for aerial chase (Jabłoński 1999, 2001, Barber *et al.* 2000, Jabłoński and Strausfeld 2000, 2001). The flashy display behavior helps birds in foraging by increasing the number of conspicuous prey available for chase in air. Hence, flush-displays change the relative proportion between the number of conspicuous prey in air and cryptic prey on substrates around a foraging bird. Therefore redstarts are good organisms to test predictions from a model of optimal search rate in response to changes in proportion of conspicuous *versus* cryptic prey (Gendron and Staddon 1983). The prediction is that an increase in the availability of the conspicuous prey should result in the increased search rate. Inter-specific comparisons confirmed this prediction (Jabłoński 2002). Here, I test this prediction using intra-specific comparisons of painted redstarts (*Myioborus pictus*).

Redstarts were observed in the Cave Creek Canyon, Chiricahua Mountains (Arizona, USA) in the breeding seasons (May, June) of 1992–1995. I followed nineteen individually marked Painted Redstarts and recorded the number of hops, pecks and chases performed during foraging. The observations were recorded on an audio-recorder and later transcribed and timed from the recording (281–1244 seconds per individual; $n = 19$ individuals). I tested the hypothesis that redstarts have higher search rates during foraging with frequent displays than during foraging with infrequent flush-displays. Hop rate was used as an index of search rate in accordance with the methods used previously (Jabłoński 2002). The distribution of the frequency of flush displays during foraging is bimodal (Fig. 1): approximately 30% of recorded foraging time consisted of hop sequences, in which more than 90% of hops were with the flush display (spread tail and wings), and 15% of foraging consisted of sequences that at most had 10% of hops with a flush-display (Fig. 1). Therefore I compared

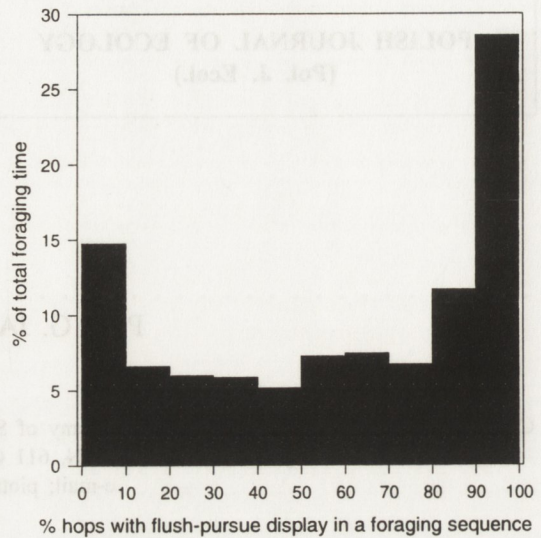


Fig. 1. Distribution of foraging sequences according to the proportion of hops with open tail and wings in a sequence (proportion of display foraging). Proportion of time in the total time of observations is used as a measure of the frequency of foraging with a given percentage of hops with display. Observations of 19 birds resulted in 976 sequences of foraging hops for total of 14955 seconds (duration of a sequence: 5–140 seconds).

the two extreme ends of this bimodal distribution. For each bird I compared hop rate during “non-display foraging”, which contained less than 25% of hops with open tail and wings (pooled sequences for each individual), with search rate during display foraging, which contained more than 75% of hops with open tail and wings. I chose the 25% range, rather than a narrower one, in order to have larger sample size. Wilcoxon Matched Pairs test was used (Zar 1999) for this comparison. Additionally, because I expected an increase in search rate due to the increase in conspicuous prey availability, the significance level was calculated according to the procedure for directed tests (Rice and Gaines 1994). All remaining tests are two-tailed. I used the sequential Bonferroni procedure (Rice 1989) to correct for double comparison used in testing the model predictions (search and attack rate). Additionally, I compared the two foraging modes of redstarts with regard to attack rate components, peck and chase rates, and also with respect to the proportion of attacks by chasing. Bonferroni correction with $k = 3$ was applied to the P -values in this case. Sample size is 19 for all comparisons.

During foraging with mostly spread tail and wings redstarts moved faster (Wilcoxon Matched Pairs test, $z = 2.05$, $P = 0.025$, $P_B = 0.05$; P_B denotes significance level after Bonferroni correction) than during foraging with mostly closed tail and wings (Fig. 2), indicating that birds use higher search rates when their major foraging mode is based on flushing and chasing conspicuously escaping prey. The attack rates did not differ between the two foraging modes (Fig. 3A; $z = 0.48$, $P = 0.629$, $P_B = 0.629$), but the chase rate was significantly larger ($z = 1.97$, $P = 0.049$, $P_B = 0.049$) during display foraging than during non-display foraging (Fig. 3B). Simultaneously, the peck rate decreased ($z = 1.97$, $P = 0.043$, $P_B = 0.086$) during the display foraging (Fig. 3C), and consequently the proportion of attacks by chasing during the display foraging (91.9%, 66.7–100%; medium, minimum-maximum) was higher ($z = 2.68$, $P = 0.008$, $P_B = 0.024$) than during the non-display foraging (71.2%, 0–100%).

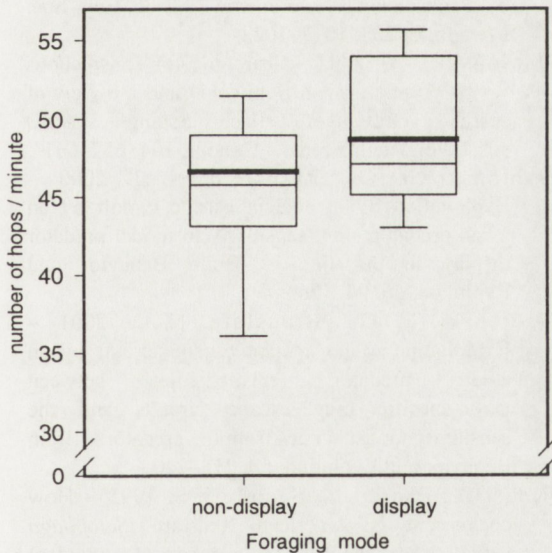


Fig. 2. Comparison of search rates between non-display and display foraging modes for 19 birds. Thick horizontal lines represent means. Thin horizontal lines represent medians. Boxes represent upper and lower quartiles and vertical lines (whiskers) represent 95% intervals.

Unlike in artificial situations created in the laboratory, I reported effects of increased availability of conspicuous prey in conditions, in which prey abundance and characteristics remain at the levels naturally experienced by birds. Detailed analysis of diversity and abundance of arthropod fauna at

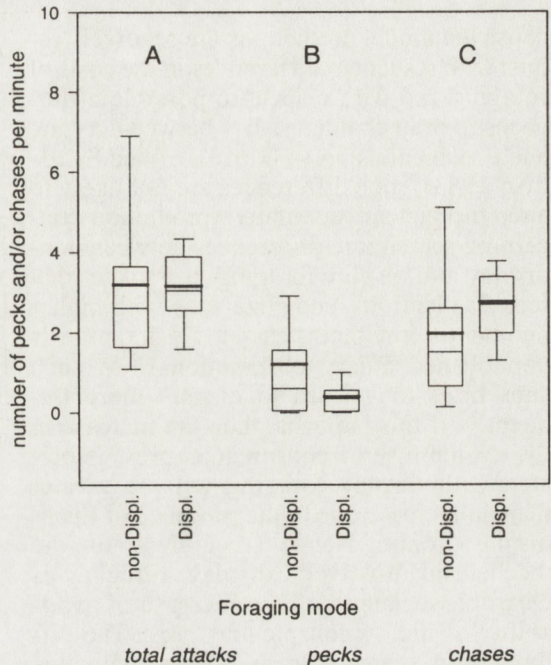


Fig. 3. Comparison of non-display *versus* display foraging of 19 birds with respect to attack rate (A: sum of pecks and chases/minute), peck rate (B: number of pecks/minute), and chase rate (C: number of chases/minute). Thick horizontal lines represent means. Thin horizontal lines represent medians. Boxes represent upper and lower quartiles and vertical lines (whiskers) represent 95% intervals.

the study site can be found in Green (1989), and the composition of redstart diet can be found in Barber *et al.* (2000). These natural conditions, unlike laboratory ones, might have influenced the evolution of foraging behavior of redstarts and other insectivorous birds. Therefore, the results are especially relevant to the evolution of forager's reactions to changes in prey conspicuousness. By showing that reactions of birds in the natural conditions are consistent with predictions from optimization models, I suggested that evolution towards optimal foraging efficiency might have shaped redstart reactions to changes in prey conspicuousness.

Unlike in laboratory tests, an observer does not have control over prey size and abundance in this natural situation. However models showed that an increase of availability of conspicuous prey rather than other prey characteristics is the main factor influencing the foraging rate in majority of situations (Gendron and Staddon 1983). Chasing is energetically more costly, may take more handling time and may be less successful than pecking the prey off the substrate. Be-

cause the model predictions are relatively robust with respect to differences in the costs of foraging and with respect to possible differences in prey characteristics between cryptic and conspicuous prey (Gendron and Staddon 1983), such differences are not likely to alter the general qualitative prediction concerning search rate differences between non-display and display foraging. It is likely that redstarts learn to recognize sites with higher number of prey that is easy to flush (author's unpublished aviary observations). At such sites birds may learn to display more frequently. If this happens, then the increase in the availability of conspicuous prey associated with display foraging will be greater than an increase due to the presence of flush-displays only. Hence, regardless of the mechanism involved, display foraging is clearly associated with an increase of availability of highly conspicuous prey. The difference in search rate associated with this increase is consistent with the expectations from theoretical models and with interspecific comparisons (Jabłoński 2002).

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