# Innate plasticity of a predatory behavior: nonlearned context dependence of avian flush-displays

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If a foraging adaptation comprises a signal for sensory exploitation of prey, does the behavior and its use develop through learning, like many foraging behaviors or does it depend on nonlearned stereotypical motor actions, like many signals for sensory exploitation? We asked whether the visually conspicuous motor pattern of body pivoting with spread tail and wings used by the painted redstart (*Myioborus pictus*) to flush insect prey is a nonlearned phenotypic trait. The motion pattern and the increase in these displays under branches (context dependence based on physical properties of the habitat) help the wild birds in foraging because prey that rest on substrates is visually stimulated, flushed into the air, and consequently chased in aerial pursuits. In unrewarded conditions in the aviary, both the foraging-experienced adults and the foraging-naive hand-raised fledglings increased the frequency of flush-displays at locations with substrates above birds, recreating the pattern of foraging observed in adults in their natural habitats. The results imply that parent–offspring cultural transmission or learning during foraging is not required for the development of both the display motion pattern and the adaptive context-dependent increase in display frequency. Such a nonlearned context dependence based on physical properties of the habitat is remarkable considering that avian foraging context-dependent plasticity is often based on learning. We hypothesize that this innate character of the signals may be a result of evolution to exploit universal properties of visually triggered escape behaviors of various insects that are predictably flushed from their resting sites in the habitat. *Key words:* behavioral evolution, flush-pursuer, foraging mode, innate behavior, *Myioborus pictus*, predator–prey, sensory exploitation. *[Behav Ecol]*

Determining which elements of a given behavioral phenotype are innate (nonlearned by imitation or by using the behavioral actions in the functionally relevant context, which is the only meaning of "innate" used in this paper) and which are learned is crucial for understanding the evolution of behavior (Lewontin 1974; West-Eberhard 2003). It is also important for understanding evolution of morphological features associated with performing the behavioral actions because behavior can modify or be modified by heritable morphological features (Grant 1986; Grant BR and Grant PR 1989; West-Eberhard 2003). Dependence on innate mechanisms is expected for behavioral responses to stereotyped predictable stimuli or situations, whereas learning is expected for behaviors in response to cues that are changing and unpredictable (Jonhston 1982; Tierney 1986; Stephens 1991; Dukas 1998). Although some basic motor actions for foraging may be nonlearned, numerous studies have suggested that context-dependent use of various foraging behaviors can be acquired through individual-experience learning associated with the assessment of the characteristics of food resources (Heinrich 1983; Greenberg 1985, 1987a; Stephens and Krebs 1986; Whelan 1989a, 1989b; Helfman 1990; Bell 1991; Krebs and Kacelnik 1991) or through social or socially enhanced learning that may involve imitation of conspecifics or heterospecifics

(Fisher and Hinde 1949; Klopfer 1961; Greig-Smith 1978; Werner and Sherry 1987; Giraldeau et al. 1994; Galef and Allen 1995; Terkel 1995; Shettleworth 1998). The resulting behavioral patterns can modify (or even mask) innate behavioral elements (Greenberg 1987a, 1987b; Honkavaara et al. 2004). Experience other than watching or imitating motor actions in adults may also affect development of these motor patterns in young (West and King 1988; King et al. 2005).

We studied avian flush-pursuers, which provide examples of evolutionary interactions between behavioral and morphological elements of a foraging adaptation. Therefore, the question of innateness of behavior has consequences for the evolution of a suite of behavioral and morphological characteristics. We studied the painted redstart (*Myioborus pictus*), which is an insectivorous passerine bird that uses displays of spread tail and wings, combined with extensive body pivoting, for flush-pursue foraging where birds visually trigger escapes in prey (Jabłoński 1999, 2001, 2002, 2003; Jabłoński and Strausfeld 2000, 2001; Mumme 2002; Galatowitsch and Mumme 2004; Jabłoński and McInerney 2005; Jabłoński and Lee 2006; Mumme et al. 2006). The escaping prey is subsequently pursued in air. During displays, a bird keeps its head down with half-spread wings and half-raised and fully spread tail (Figure 1), presenting white and black conspicuous plumage pattern toward substrates (branches, leaves, rocks, logs, etc.) located above and in front of a bird. Prey located on such substrates and adult birds in their natural habitats show context-dependent behavior: they adjust their foraging by an almost 2-fold increase of the display frequency from about 47% display-hops during random foraging

**Figure 1**
Foraging painted redstart (*Myioborus pictus*) in a flush-display pose. White and black plumage pattern is directed toward substrates in front of and above the bird, where majority of the flush-chased prey are located. Inset shows a single frame from a video of a hand-raised fledgling displaying in response to a hand above the bird. Photo by P.G. Jabłoński.

to about 86% when a bird focuses its visual attention on substrates that are present above the bird (Jabłoński 1999).

Plumage coloration in many birds (Price 2002; Roulin 2004), including flush-pursuers (Caughley 1969; Craig 1972), has strong genetic basis, and there is no reason to believe that the conspicuous plumage features of the *Myioborus* displays are different with this respect. An evolutionary mechanism that may lead to habitat-specific diversification of these heritable plumage patterns has been recently proposed (Mumme et al. 2006), suggesting that genetic evolution of plumage patterns may be affected by the presence of the flush-display motor actions. However, it is not clear whether these motor actions and their context dependence require learning. If learning is required, we anticipated that flush-displays, and their field-documented context-dependent use (Jabłoński 1999), will be absent in foraging-naive young individuals but present in adults that have had opportunities to learn how to use the displays (through individual assessment-based learning or by imitating more experienced conspecifics, such as their parents).

Different groups of prey, including Diptera, Homoptera, and Lepidoptera, increase their escapes in response to looming and translational motion of contrasting patterns (Jabłoński and Strausfeld 2000, 2001; Mumme 2002; Galatowitsch and Mumme 2004; PG Jabłoński, K Lasater, R Mumme, M Borowiec, JP Cygan, J Pereira, E Sergiej, unpublished data), which suggests that the basic visual parameters that trigger escapes in a variety of prey species may not be prey species specific. Therefore, there may be no need for the ability of flush-pursue predators to learn how to adjust the flush-display behavior to match sensitivities of different taxons of prey at different localities. Under this scenario, it is possible that the context dependence of the displays observed in the field (Jabłoński 1999) may be a nonlearned stereotypical response to the presence of a substrate above/near the bird, in a manner similar to innate triggering of bathing movements in birds by visual properties of a shiny surface of water (Mueller 1970). If the displays and their use do not require learning, we expected that the flush-display motor pattern and its context dependence, which is observed in the foraging-experienced adults, would also be present in hand-raised foraging-naive individuals (birds that had not seen displaying adults and had not foraged by themselves).

Here we compare behavior of foraging-naive hand-raised nestlings with foraging-experienced adults in an unrewarded experimental situation of birds exploring under-substrate and on-substrate locations. We ask whether the motor pattern of the flush-displays and its context-dependent use are innate (sensu nonlearned).

## METHODS

### Experimental subjects

Painted redstarts were studied near the Southwestern Research Station, Chiricahua Mountains, AZ (31°883′N, 109°203′W). Ten adult males and 6 hand-raised fledgling painted redstarts were used. Adult males were caught in mist nets in May to June 2000. Each adult bird was put into the experimental aviary, and after 1–2 days of acclimatization its behavior was videotaped for 1–3 days, 2–6 h daily. Afterward, a bird was released to its breeding territory, where it joined his mate in feeding the nestlings. Males were used in the experiment because removing them from the breeding territory for 2–4 days did not affect the survival of nestlings, which were fed by the female. Six hand-raised nestlings of unknown sex were tested in the aviary at the age of 30–45 days (about 2–3 weeks after such a display is observed for the first time in a young bird). The birds were hand raised since their 5th to 6th day of life. They were fed with mealworms and freshly killed crickets and occasionally with abdomens of moths caught in the natural habitat. A model of adult redstart with tweezers incorporated as the model's beak was used to feed the nestlings. The young birds did not have experience with live escaping insects before the tests, and they were not exposed to adult birds before the tests. After the experiments, 2 young birds were transferred to the Desert Museum, Tucson, where they were kept in a large aviary. The remaining hand-raised birds were released at the study site. Before release the birds were kept in the large aviary and live prey was given to them. After we saw that they learned how to pursue and capture prey, we released the birds in the vicinity of the aviary. They were observed foraging in the neighboring area for up to 10 days before moving away. All activities and procedures were approved by the appropriate Federal and State agencies (see acknowledgements for details) and were in accordance with the Animal Behavior Society/Association for the Study of Animal Behavior guidelines.

### Experimental setup

The birds were tested in the 10 × 4 × 3–m (width, length, height) aviary with 12 substrate surfaces and 3 sticks provided according to the setup in Figure 2. The setup was designed to imitate a variety of under-substrate and on-substrate situations, which resemble a wide range of natural locations used by wild birds as well as more artificial situations familiar to hand-raised birds. Therefore, in order to provide a variable habitat that promotes natural behavior in birds, 6 different types of substrate surfaces were used, each represented by two 30 × 80–cm boards: oak tree bark (oak bark attached to both sides of a wooden board), pine tree bark (pine bark attached to both sides of a wooden board), dry leaves (leaves between 2 layers of chicken wire to imitate dry leaves collected on exposed roots, caught between roots and sticks, etc.), plain wooden board with rough surface, dark semitransparent surface (made of black wire mesh spread on a wooden frame), and light semitransparent surface (made of a white wire mesh spread on a wooden frame). For the analysis, the data for all surface types were pooled together. Perches made of sticks were located on top (0–5 cm above the substrate) and 20 cm under each of the substrate surfaces (Figure 2). The
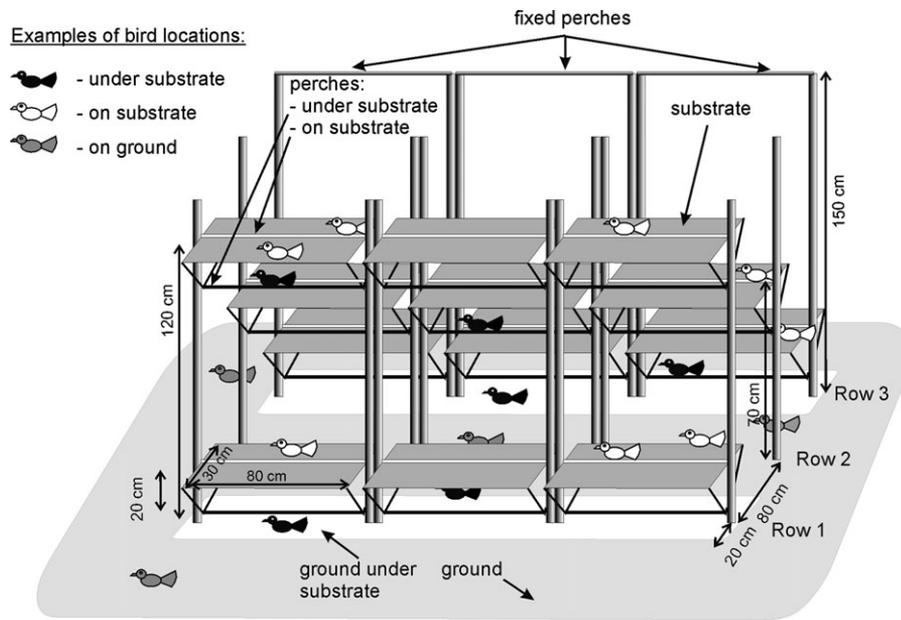
distance from a bird on a perch to any substrate other than a substrate associated with that perch was much larger than the range of distances at which the majority of redstart prey is flushed in natural habitats: 0–45 cm (Jabłoński 1999). Thus, a bird on a perch on top of an experimental substrate, or directly on a substrate, was considered as experiencing on-substrate situation even though there might have been another substrate about 1 m above the bird. A bird on under-substrate perch (i.e., a perch associated with a given substrate) was considered experiencing under-substrate situation. Each bird was tested with a different spatial arrangement (chosen randomly, without replications) of the substrates. Additionally, three naturally looking 80-cm-long sticks were horizontally provided in fixed locations (Figure 2; row 3 of substrates). The aviary walls were covered with fabric (to prevent insects from entering and to make the birds adapt faster to the captive conditions), and fresh twigs from the local trees were added (after insects were shaken off or brushed off the twigs) to create a situation in which the wild birds displayed normal exploratory behaviors. The roof was covered with transparent plastic. Videotaping was conducted for 2–4 h in the morning and for 2–4 h in the afternoon. Birds were fed ad libitum after the morning videotaping session and after the afternoon videotaping session, but no feeding was administered during the videotaping session. The birds were fed with crickets and mealworms on a tray on the ground in front of the experimental setup. No other food was provided. Water was available all the time for drinking and bathing. Only one bird at a time was present in the aviary, and no birds were present in the vicinity to prevent influences of other birds on the experimental bird.

Before the experiments the young birds were housed in small cages (1 × 1 × 1 m) where they were fed on a regular basis. There were several twigs (5–10 mm diameter) running across cage interior. For a test, a young bird was transported from the cage to the experimental aviary. Feeding regimen prevented young birds from gaining any foraging experience before the experiments.

## Data analysis

### Classification of behaviors
From the videotapes the following data were transcribed for each bird by a person who was not informed about the hy-potheses being tested: number of hops with open tail and wings (i.e., with the display) under a substrate, number of hops with closed tail and wings (i.e., without the display) under a substrate, number of hops with display on a substrate, number of hops without display on a substrate, number of hops with display on the ground (when not under substrate), and number of hops without display on the ground. "On ground" excludes hops on the ground when a bird was directly under a substrate in rows 1 and 3 (white areas in Figure 2)—these hops belong to the category "under substrate." In row 2 (Figure 2), substrates were about 70 cm above the ground, and hops were classified as "on ground." Among all the birds, there was no apparent general preference for any particular substrate, and birds that displayed more under one substrate also displayed more under any of the other substrates: correlation coefficients between display frequencies under various substrates (9 pairwise correlations) were positive (0.67 ± 0.14, [0.47–0.87]; mean ± SD [minimum–maximum]). For analyses the data were pooled across substrates to compare bird behavior at 3 general locations (under substrate, on substrate, and on ground) given the unconstrained choice by each bird among the 6 particular substrate materials.

Total number of hops recorded per bird averaged 2305 ± 592 (mean ± SE) with median equal to 1761 and a range between 119 and 8259 (minimum to maximum). For 14 out the16 experimental birds, the total number of recorded hops was larger than 450. Two birds contributed 119 and 188 recorded hops. To describe the tendency to use under-substrate locations, the number of hops at under-substrate location type by an individual was divided by the number of hops at all 3 location types by this individual. We applied arcsine transformation (arcsine(square root(proportion))) designed to normalize the data and to reduce the heterosce-dacity for the parametric analyses (Zar 1999). This transformed variable is referred to as *use of under-substrate locations* (Table 1). In order to study the use of displays at each of the 3 location types, we applied the following formula for each bird, for each location type separately: number of hops with display/(number of hops with display + number of hops without display). The resulting proportions were arcsine transformed and are referred to as *frequency of under-substrate displays*, *frequency of on-substrate displays*, and *frequency of on-ground displays* (Table 1).

**Table 1**

**Transformed variables used in the analysis**

| Name of the variable | Formula |
| --- | --- |
| *Use of under-substrate locations* | Arcsine (SquareRoot ($N_{us}/N$)) |
| *Use of on-substrate locations* | Arcsine (SquareRoot ($N_{os}/N$)) |
| *Frequency of under-substrate displays* | Arcsine (SquareRoot ($D_{us}/N_{us}$)) |
| *Frequency of on-substrate displays* | Arcsine (SquareRoot ($D_{os}/N_{os}$)) |
| *Frequency of on-ground displays* | Arcsine (SquareRoot ($D_{gr}/N_{gr}$)) |

$N$, number of all recorded hops; $N_{us}$, number of hops at under-substrate locations; $N_{os}$, number of hops at on-substrate locations; $N_{gr}$, number of hops on the ground; $D_{us}$, number of hops with flush-displays at under-substrate locations; $D_{os}$, number of hops with flush-displays at on-substrate locations; $D_{gr}$, number of hops with flush-displays on the ground.

*Effect of location on frequency of displays*

Two-factor repeated measures analysis of variance (ANOVA) was used to calculate the effect of location (under substrate, on substrate, on ground) and age (young vs. adult) on the frequencies of displays. All collected data were used in this analysis to increase the sample size for each individual. Each bird was tested in the morning, but in 5 adults and 2 young the morning sessions comprised less than 50% of the video time, whereas for the remaining 5 adults and 4 young the morning tests comprised more than 50% of the analyzed videos. To guard against a possibility that the apparent similarity between young and adults in response to location (Figure 3A in Results) might be a coincidental result of this somewhat uneven morning versus afternoon sampling between young and adults, combined with a possibility of a different effect of time of day on the effect of location on displays by young versus adults, we additionally run the ANOVA separately for morning and afternoon samples.

*Tendency to use under-substrate locations versus tendency to flush-display there*

Regression analysis was used to study relationships between the *use of under-substrate locations* and "frequencies of under-substrate displays." For some of the analyses the arcsine transformation did not remove the heterogeneity of variances among treatment groups, and we used the generalized linear models (GLZ, Statistica, version 4, Statsoft, Inc., Tulsa, OK) because they relax the requirement of homogeneity of variances typical for traditional linear models (McCullagh and Nelder 1989). Waldman statistics ($W$) in the generalized linear model with normal distribution and identity link was used to study the effect of age (young vs. adult) and *use of under-substrate locations* (continuous predictor) on the *frequency of under-substrate displays*. generalized linear models were also used to study whether the *frequency of on-substrate displays* is related to the *frequency of under-substrate displays* and whether bird age affects this relationship.

*Within-individual variation in behavior*

We calculated within-individual correlations between the *use of under-substrate locations* and the *frequency of under-substrate displays* by a bird during an observational session (1 session comprises one 2-h-long video recording). For each bird, we calculated linear regression coefficient using video observation sessions as separate data points. Using Student's *t*-statistics we tested the hypothesis that the average of these regression coefficients is larger than zero. We used generalized linear models (Statistica, Statsoft Inc.) to study the effect of *use of under-substrate locations* (continuous predictor) on the *frequency of under-substrate displays* while controlling for individ-
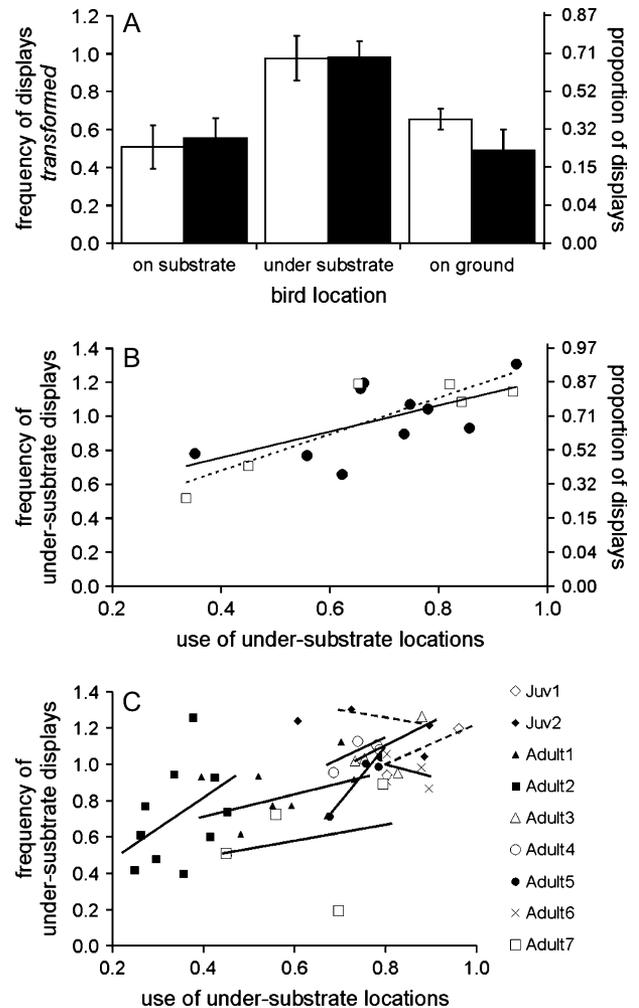


**Figure 3**

Foraging of young and adult redstarts. (A) Relationship between foraging location (on substrate, under substrate, or on ground) and the frequency of displays (left vertical axis: arcsine-transformed proportion of hops with displays in total number of hops in a given location) for adult (filled bars) and young (unfilled bars) painted redstarts in the experimental aviary (lines represent SE). The corresponding nontransformed proportions are shown on the right axis. (B) Relationship between the *use of under-substrate locations* (arcsine-transformed proportion of under-substrate hops in all hops in the aviary) and the *frequency of under-substrate displays* (arcsine-transformed proportion of display-hops in all under-substrate hops by a bird) for 6 young (open squares) and 10 adult (filled circles) birds. The corresponding nontransformed proportions are shown on the right axis. (C) Relationships between the *use of under-substrate locations* and the *frequency of under-substrate displays* for each of 9 birds with 4 or more observation sessions. Two fledglings (Juv1, Juv2; broken regression lines) and 7 adults were used (Adult1 to Adult7; solid regression lines).

ual identity (categorical predictor: 9 individuals). These analyses included 2 fledglings and 7 adults that were observed for 4 or more independent video sessions. In order to obtain individual regression coefficients based on at least 4 data points, birds with fewer taping sessions were not used.

*Effect of time of day*

Finally, to estimate if the time of day might be a factor underlying variation in the behavioral variables and if it may affect the *use of under-substrate locations* and the *frequency of*

under-substrate as well as on-substrate displays, we used 7 adult and 2 young birds with morning and afternoon video sessions recorded on the same day (total $N = 9$). We used paired $t$-tests to compare birds' behavior in the morning session, before they were given food, with their behavior in the afternoon session on the same day, when videotaping started within 1 h after the bird was fully fed. We did not use morning and afternoon observations from different days to avoid possible confounding effects. Although this may not disentangle the effect of time of day and hunger, it will provide insights as to the factors underlying the between- and within-individual variation in behavior.

## RESULTS

### Occurrence of tail displays in young birds

The displays by young hand-raised foraging-naive redstarts were observed at an age of 18–25 days, which corresponds to 5–12 days after fledging. The tail-spreading displays at this early age are not effective because the tail is not fully developed. Before the tests, we observed that in hungry fledglings there was a connection between the presence of any surface above the nestling (e.g., an experimenter's hand, face, and shoe) and the flush-displays. These displays were not triggered by a taxidermic model that was routinely used for feeding the nestlings. The displays were different from begging displays, which contained wing shaking, bird's vocalizations, and beak opening. The displays were also different from bird reactions to apparently perceived danger such as large birds flying over (when fledglings were observed outside). On such occasions the bird would stop moving and sit motionless without any elements of display-like pivoting or tail spreading.

### Effect of location on frequency of displays.

Wild-caught adult males ($N = 10$) and hand-raised fledglings ($n = 6$) did not differ in the frequency of displays at the 3 locations: on substrate, under substrate, and on ground (Figure 3A; interaction term between bird location and age in Table 2, a). The displays were used most often under substrates, and there was no effect of bird age on the use of displays (Table 2, a). After narrowing down the analysis to the 2 location classes of interest, the on-substrate and under-substrate locations, the lack of difference between young and adult birds in their frequencies of displays at both location types is evident in the almost identical bar heights in Figure 3A (nonsignificant interaction between bird location

**Table 2**
**Effects of bird location (on ground, on substrate, and under substrate; within-individual independent variable) and age (young vs. adult; between-individuals independent variable) on arcsine-transformed frequencies of displays (see Table 1)**

| Independent variable | df | $F$ | $P$ |
| --- | --- | --- | --- |
| (a) Location with 3 levels | | | |
| Location | 2 | 12.98 | 0.0002 |
| Age | 1 | 0.09 | 0.77 |
| Location × age | 2 | 1.18 | 0.32 |
| (b) Location with 2 levels | | | |
| Location | 1 | 28.76 | 0.0001 |
| Age | 1 | 0.07 | 0.80 |
| Location × age | 1 | 0.05 | 0.82 |

In (b) the independent variable "location" had only 2 levels (on substrate and under substrate). The analysis corresponds to Figure 3A.

and age in Table 2, b). The smallest effect size for which this conclusion of lack of interaction is statistically reliable (power = 0.80, alpha = 0.05) approximated 0.27 for the transformed frequencies of displays (power calculations for 2-way ANOVA interaction effect using Statistica software). Therefore, we can statistically reject the hypothesis that the increase of display frequency at under-substrate locations in young birds differed from such an increase in adult birds by 0.27 or more (in the units of the transformed variable). It corresponds to a change by 0.19–0.28 in terms of nontransformed proportions (right axis in Figure 3A) calculated across the range (minimum to maximum) of mean display frequencies for on-substrate and under-substrate locations in young and adult birds (for transformed variables this range of means was 0.51–0.98; Figure 3A). The analysis using only morning samples of bird behavior was similar to Figure 3A, with significant effect of bird location ($P < 0.006$) and nonsignificant effects of age ($P > 0.30$) and interaction between age and location ($P > 0.40$), regardless of whether both years or only 2000 was analyzed or whether all 3 or only 2 (under substrate, on substrate) locations were used. Similarly, separate analysis of the less numerous afternoon data resulted in significant effect of birds location ($P < 0.03$) and no difference between young and adults in the effect of location on the displays ($P > 0.59$). In 3-way repeated measures ANOVA, with time of day as an additional repeated measures factor, only the effect of location (3 location types) was significant ($F_{2,16} = 8.42$, $P = 0.003$), and the other single-variable or interaction effects were nonsignificant ($P > 0.20$). The similarities in the effect of location on display frequency between young and adult birds indicate that young and adult birds behaved in a similar manner.

### Tendency to use under-substrate locations versus tendency to flush-display there

The standardized regression coefficients between the use of under-substrate locations and frequency of displays at these locations (Figure 3B) were positive for young ($B = 1.07 \pm 0.28$ [mean $\pm$ SE], $t_4 = 3.834$, $P = 0.019$) and for adult ($B = 0.77 \pm 0.36$, $t_8 = 2.111$, $P = 0.068$) birds. The probability of obtaining these 2 positive relationships by chance is between 0.001 and 0.01 ($\chi_4^2 = 13.303$, $P < 0.01$; Fisher's combined test, using two probabilities 0.019 and 0.068), suggesting similarity between young and adult birds in this respect (regression for pooled data: $B = 0.93 \pm 0.22$, $t_{14} = 4.227$, $P = 0.0008$). Age (categorical predictor in GLZ analysis) indeed did not modify the significant effect of the use of under-substrate locations on the frequency of under-substrate displays (Table 3, a; Figure 3B).

Is this increase of the display frequency specific to the under-substrate location or is it associated with an increase of on-substrate displays as well? The frequency of under-substrate displays (continuous predictor) did not affect the frequency of on-substrate displays ($W_{1,12} = 0.672$, $P = 0.412$) regardless of age (interaction age × frequency of under-substrate displays: $W_{1,12} = 1.917$, $P = 0.167$), and the regression between the frequency of under-substrate displays (regressor) and frequency of on-substrate displays (response variable) was positive for young birds ($B = 0.564$, $t_4 = 1.422$, $P = 0.228$) and negative for adults ($B = -0.144$, $t_8 = -0.336$, $P = 0.746$). Consequently, there was no consistent age-independent effect of the use of under-substrate locations on the frequency of on-substrate displays (Table 3, b).

All these results indicate that, regardless of age, those birds that were observed more frequently under the substrates also used the flush-display foraging method more frequently there, regardless of the frequency of their on-substrate displays. In other words, in the unrewarded experimental situation foraging-naive birds did not differ from foraging-experienced adults in their under-substrate display strategy.

**Table 3**

**Effects of *use of under-substrate locations* (continuous predictor) and age (categorical predictor: young vs. adult) on the (a) *frequency of under-substrate displays* and on the (b) *frequency of on-substrate displays* analyzed by the generalized lineralized model**

| Independent variable | df | W | P |
|---|---|---|---|
| (a) Effects on under-substrate displays | | | |
| *Use of under-substrate locations* | 1 | 20.53 | <0.0001 |
| Age | 1 | 0.48 | 0.49 |
| *Use of under-substrate locations* × age | 1 | 0.57 | 0.45 |
| (b) Effects on on-substrate displays | | | |
| *Use of under-substrate locations* | 1 | 1.21 | 0.27 |
| Age | 1 | 4.64 | 0.03 |
| *Use of under-substrate locations* × age | 1 | 4.56 | 0.03 |

*W*, Waldman statistics. The analysis in (a) corresponds to Figure 3B.

### Within-individual variation in behavior

Does the age-independent positive relationship in Figure 3B result from inherent individual differences among birds or from temporary differences in the condition among individuals at the time of observations? Seven adults and 2 young birds were filmed on 4 or more sessions over the span of 1–3 days. Therefore, individual condition that results from changes in physiological state or motivation of an individual was probably different among these recording sessions. The standardized regression coefficients between the *use of under-substrate locations* (regressor) and the *frequency of under-substrate displays* (response variable), calculated for each bird separately, were between −0.476 and 2.832, with the mean ($0.884 \pm 0.365$, mean ± SE) significantly larger than zero (Student's *t*-test: $t_8 = 2.651$, $P = 0.0292$; see regression lines in Figure 3C). These results, combined with the significant effect of the *use of under-substrate locations* on the *frequency of under-substrate displays* (Table 4), together with lack of effect of individual identity on this relationship (interaction effect in Table 4), indicate that short-term changes in individual condition might have contributed to the age-independent relationship in Figure 3B. This suggests that such changes in individual condition may affect young and adult individuals in a similar way.

### Effect of time of day

The *use of under-substrate locations* was higher (Student's *t*-test for paired data; $t_8 = 3.540$, $P = 0.008$) in the morning ($0.778 \pm 0.067$; arcsine-transformed proportions) than in the afternoon ($0.672 \pm 0.071$). Within-individual difference between the morning and afternoon observations (morning minus afternoon) was $0.11 \pm 0.03$ (mean±SE). Equivalent tests for the *use of on-substrate locations* were not calculated: they would not have been independent because proportions of "under-

**Table 4**

**Effects of *use of under-substrate locations* (continuous predictor) and individual identity (categorical predictor: 9 individuals) on the *frequency of under-substrate displays* analyzed by the generalized linear model**

| Independent variable | df | W | P |
|---|---|---|---|
| *Use of under-substrate locations* | 1 | 4.42 | 0.04 |
| Individual identity | 8 | 8.36 | 0.40 |
| *Use of under-substrate locations* × individual identity | 8 | 7.49 | 0.49 |

*W*, Waldman statistics. The analysis corresponds to Figure 3C.

substrate" and "on-substrate" locations are inherently related with each other. The *frequency of under-substrate displays* was higher ($t_8 = 2.672$, $P = 0.028$) in the morning ($1.04 \pm 0.09$, $n = 9$) than in the afternoon ($0.89 \pm 0.09$, $n = 9$) of the same day, whereas the *frequency of on-substrate displays* did not differ ($t_8 = 1.390$, $P = 0.202$) between morning ($0.62 \pm 0.12$, $n = 9$) and afternoon ($0.51 \pm 0.10$, $n = 9$). The within-individual difference between morning and afternoon *frequency of under-substrate displays* was $0.16 \pm 0.06$, $n = 9$, and the same difference for the *frequency of on-substrate displays* was $0.11 \pm 0.09$, $n = 9$. These results suggest that hunger, or any other factor associated with time of the day, may modify the flush-display strategy.

## DISCUSSION

### Nonlearned motor pattern

Stereotypical foraging displays were observed in all foraging-naive hand-reared juveniles from the age of 18 to 25 days. In the wild, birds at this age are still dependent on their parents and the experimental birds displayed begging behavior, which is different from flush-displays (Marshall and Balda 1974; Barber et al. 2000). These birds had had no opportunity in their life to watch foraging adult birds. The displays of young birds were perceived by human observers as very similar (especially after correction for shorter tail is taken into account) to the displays by adult experienced birds. In a different flush-pursuer—the mockingbird (*Mimus polyglottos*), which is characterized by unique wing-spreading movements called "wing flashing" (Hailman 1960) the motor actions that produce the display appear early in life of the fledglings and seem to be nonlearned as well: hand-raised birds performed the stereotyped displays identical to the displays of foraging adults (Laskey 1962). No such *Myioborus*-like or *Mimus*-like displays have ever been mentioned in studies of behavior of hand-raised non–flush-pursuing warblers (*Dendroica pennsylvanica*, Greenberg 1984; *Helmitheros vermivorus*, Greenberg 1987b), which are relatives of *Myioborus* redstarts, or in hand-raised tits, Paridae (*Parus carolinensis*, Greenberg 1987b; *Parus ater*, Gruenberger and Leisler 1990) and Old World warblers (*Phylloscopous borealis*, Van Patten and Price 1990). Although these researchers did not specifically pay attention to the occurrence of such display motor patterns, the lack of record of this relatively conspicuous behavior may imply that the displays of flush-pursuing birds may be species-specific motor patterns, and our results show that parent–offspring cultural transmission or learning through individual foraging experience is not required for development of the displays.

The context-dependent increase in the use of the displays by young and inexperienced birds exploring the aviary was indistinguishable from the use of displays by adult wild-caught birds that had opportunities to learn various associations between their foraging mode and their foraging success that exist in nature. This suggests that the context-specific (in terms of presence or absence of substrates above the bird) use of displays is a nonlearned (innate) phenotypic trait. Because 2 nestlings in 1999 and 3 in 2000 were housed together (these birds were of similar age and at a similar stage of acquiring the display behaviors), we cannot exclude some effects of one nestling's behavior on the development of display behavior in others. Even if such an effect existed, it does not preclude the conclusion that the appearance of the display in at least the first nestling in a group occurred in the absence of imitation learning.

The similarity between foraging-experienced and foraging-naive birds searching for food in the aviary could be explained if the young birds, as they grow into adulthood, continue to

use the stereotypic innate context dependence (observed in foraging-naive fledglings) regardless of its efficiency. Such rigid behavioral rules would be unusual in comparison to the typically learning-based plasticity of avian foraging behaviors (Klopfer 1961; Heinrich 1983; Greenberg 1985, 1987b; Palameta and Lefebvre 1985; Werner and Sherry 1987; Whelan 1989a, 1989b; Giraldeau et al. 1994). Alternatively, the adult and experienced birds may apply learning-modified context dependence based on the present and past foraging performance, but in the artificial aviary conditions they reverted to the rules characteristic for young birds. Comparisons between field and aviary observations of adult birds could be used in evaluating these hypotheses. However, field data from foraging painted redstarts (PG Jabłoński, unpublished data) and observations of similar tree-foraging flush-pursuers such as *Setophaga ruticilla* (Lovette and Holmes 1995; Sherry and Holmes 1997), *Myiobius* sp. (Fitzpatrick 1980, 1985; Sherry 1982, 1984), or *Rhipidura* sp. (Ude Shankar 1977; Cameron 1985; McLean 1989) do not contain proper records because they lack classification of the bird's positions with regard to the location of immediate substrates.

Although the experiment was not designed to study how the innate context-dependent displays change in response to variable prey availability and distribution or in response to internal factors, the results suggest that factors related to the temporary variation in individual condition, such as hunger, might affect the context dependence based on the presence of substrate above the birds. The results suggest that such effects may be similar in foraging-experienced adults and in foraging-naive young birds. Mumme's (2002) observation of more frequent use of flush-displays in *Myioborus miniatus* during the time of high demands for feeding the nestlings is consistent with the view that this specific context dependence may be affected by nutritional demands in general.

### Why innate (nonlearned)?

Foraging and searching behaviors are known for their high plasticity, variability, and adaptability to local conditions (Stephens and Krebs 1986; Helfman 1990; Shettleworth 1998; Ydenberg 1998; West-Eberhard 2003), and they provide classic examples of cultural transmission of new behaviors (Fisher and Hinde 1949; Klopfer 1961; Greig-Smith 1978; Palameta and Lefebvre 1985; Giraldeau et al. 1994). Even some invertebrate predators, such as *Portia* spiders, can actively learn how to design signals to efficiently exploit a variety of signaling and sensory systems in their diverse prey (Jackson and Wilcox 1990, 1993a, 1993b). Why does the avian flush-pursuer's use of sensory-exploitative signals appear to be based on stereotyped and innate motor actions? We hypothesize that simplicity and similarity of the properties of insect escape reactions among a variety of redstart prey might have promoted innateness of this stereotyped context-dependent use of motor displays for exploitation of prey escape responses. Behavioral mechanisms of escape reaction appear to be evolutionarily conserved across different prey taxa such as Orthoptera and Diptera, which both initiate escapes when a certain value of the angular velocity of the approaching object is reached (Simmons and Rind 1992, 1997; Rind and Simmons 1997, 1999; Jabłoński and Strausfeld 2001; Gabbiani et al. 2002; PG Jabłoński and SD Lee, unpublished data). If most prey are visually sensitive to the same key features of the stimuli, learning of various forms of flush-display by the predator would not be necessary: the display elements required for effective foraging could have a stereotypic nonlearned form regardless of prey species.

In summary, our results suggest that redstarts have a non-learned (innate) mechanism of triggering flush-displays in response to the physical structure of the habitat. We hypothesize that this nonlearned character might be a consequence of evolution to match and exploit universal simple properties of evolutionarily conserved visually sensitive escape circuits of insects that are predictably flushed from substrates near foraging birds. Further studies must be carried out to determine the degree of flexibility of the nonlearned flush-display motor action under influence of variable prey distributions.

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