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Source: Folia Zoologica, 60(3) : 214-220

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v60.i3.a5.2011

Folia Zool. – 60 (3): 214–220 (2011)

Effects of recent experience and background features on prey detection of foraging American kestrels (*Falco sparverius*) in captivity

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Received 11 October 2010; Accepted 25 March 2011

Abstract. Predators activate a search image process for the most frequent prey type as a result of repeated chance encounters with that prey. In addition, selective attention to a limited subset of prey visual features should increase the precision with which the prey is discriminated from the background. In our experiment, we investigated the effects of multiple backgrounds on prey detection by captive American kestrels (*Falco sparverius*). We predicted that the background itself can serve to cue attention towards the prey type and that a most recent experience provided predictive information. As expected, we observed the effects of search image formation where the background was informative (familiar substrate). Nevertheless, search image effects disappeared with extended practice and kestrels rapidly increased the use of unfamiliar background where prey were completely non-cryptic. Our data suggest that short-term changes in prey detection of a predator cue with the background upon which this prey is found. We discussed the results in the light of related studies on neophobia, visual acuity and achromatic and chromatic contrasts.

Key words: predation, search image formation, associative cues, visual ability, cryptic prey

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Introduction

Optimal foraging models predict that between two patches containing the same prey at different densities, the higher density patch shall be exploited (Stephens & Krebs 1986, Krebs & Kacelnik 1991). Through the choice of the highest profitable patch, feeding organisms could maximize energy intake rate during resource exploitation (Krebs & Kacelnik 1991, Uiblein et al. 1995, Roche 1996). Nevertheless, prey availability varies in time and predators use their recent experiences to decide whether to leave the patch and overcome the effects of potentially sub-optimal conditions (Cuthill et al. 1990, Yosef & Grubb 1993, Valkama et al. 1995, Roche 1996). In addition, search effort, based on detectability, represents a variable cost for predators, especially for those that locate prey mainly by eyesight (Hirsh 1982, Uiblein et al. 1995). Thus, the bias of foragers on a familiar substrate is to collect during successive feeding periods a single prey type only (Tinbergen 1960). This temporary selection for specific prey features should improve the chances for a predator to distinguish prey from its substrate. In fact, selective attention to a limited subset of prey visual features should increase the precision with which the prey is discriminated from the background (Endler 1984, Kono et al. 1998).

Previous studies have shown that prey choice by predators tie in with visual prey features such as color, general morphology and movements (Mueller 1974, Ruggiero et al. 1979). Tinbergen (1960) suggested that foragers activate a search image process for the most frequent prey type as a result of repeated chance encounters with that prey. In addition, hunting by search image should increase with the degree of resemblance between prey and background. In fact, search image effects are evident when prey are cryptic but not when they are conspicuous (Bond 1983, Bond & Riley 1991, Reid & Shettleworth 1992). This search image formation implies that the encounter probability for a particular prey type is a function of its density (Morgan & Brown 1996). Field experiments conducted on wild Eurasian kestrels

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(*Falco tinnunculus*) demonstrated that patch choice should be influenced by prey density toward patches with unpredictable high prey profitability than stable steady patches (Valkama et al. 1995). Nevertheless, prey densities should vary among patches, and predators could be shifting between different patch areas (Dukas & Ellner 1993, Morgan & Brown 1996, Roche 1996). Background features define patch characteristics and presumably which food types might be present, which increase the bird's ability to exploit the best territory portions (Pietrewicz & Kamil 1979, Kono et al. 1998). In fact, search-image effects disappeared with extended practice in trained birds faced with ambiguous backgrounds (Kono et al. 1998). This suggests that patch choice and patch-leaving decisions should be linked to a short time period where the predator tracks the prey population (Norrdahl & Korpimäki 1996).

We investigated the effects of repeated presentations of a specific prey type upon backgrounds that differed in achromatic properties on prey detection of captive American kestrels (*F. sparverius*). In addition, we examined short-term changes in kestrels' ability to detect prey against search image formation. Our main aims were 1) to ascertain if the background itself served to cue attention towards the prey type and 2) the extended practice essentially removed search-image effects. We discussed the results in the light of related studies on neophobia, visual acuity and achromatic and chromatic contrasts.

Material and Methods

Subjects

We used six one-year old captive American kestrels, three males and three females, for testing prey detection (Bird 1982). Birds were housed in single pens (2.3 × 1.5 × 2.3 m) at the Avian Science and Conservation Centre of McGill University and weighed at the beginning and end of each experimental session. The experimental birds previously were housed in large flight pens (5.8 × 6.0 × 2.3 m) where daily food, i.e., frozen-thawed day-old yellow whitish cockerels, was placed upon white, wooden planks which was the only background used by these birds for feeding. Kestrels were maintained at natural photoperiod and temperature. Test subjects were observed through one-way glass windows to minimize disturbance.

Test apparatus

Backgrounds consisted of two parallel pine planks (50 × 50 × 2 cm) placed 105 cm apart and 5 cm above the floor of the cage. A green carpet covered one plank (unfamiliar), and the other one was white and bare (familiar). For the purposes of consistency in statistical analyses, we considered attacks made only from perched birds. We maintained a constant distance from planks and perch site.

Preliminary observations

We made preliminary observations to assess the influence of the caching behaviour and the latency time (time in trial to successful predation event) on foraging responses. For the experimental sessions, we did not use birds tested during the preliminary phase due to possible modifications of their foraging behaviour. Since we did not use highly trained individuals, feeding choice showed an ample time latency (Pietrewicz & Kamil 1979). Because kestrels do perform caching behaviour due to cold winter conditions in Quebec, we doubled the food availability to two cockerels on alternate days and we checked the preferred caching sites periodically. The time latency, as discussed in previous foraging studies (see Bombardier 1992), was replaced by the assessment of the first choice (Krause & Godin 1995). Also, this dependent variable best fitted with sit-and-wait behavioral patterns of wild birds (Varland et al. 1991).

Experimental procedure

Many studies on search-image effects have concentrated on the concept of learning to discriminate a familiar food in novel circumstances. Evidence of rapidly established and reversible improvements in predators' ability to detect targets should be addressed to selective attention to visual features of a prey. Nevertheless, Kono et al. (1998) demonstrated that search image effects were evident when the background was informative and several backgrounds or several prey types interfered with search image formation. In our experiment, we used two backgrounds (familiar and unfamiliar) and a single prey type (cockerels). Thus, upon the unfamiliar background, cockerels became completely non-cryptic according to low contrast sensitivity (CS) measured for the American kestrel (Gaffney & Hodos 2003, Ghim & Hodos 2006). We subdivided each sessions into two daily bouts. First, kestrels faced with both backgrounds each containing a prey item. During the second bout, we placed a prey item upon the unfamiliar background only. In each session, we evaluated 1) what backgrounds kestrels first used for feeding, 2) the number of cockerels eaten at the end of the session. After 14 days, kestrels performed seven complete trials. Prey encounters among substrates varied as follows: $E_f = b/2$ and $E_u = b$ where E is the prey encounter, f and u are,

Table 1. *Results from two-tailed binomial test comparing the observed frequencies for the variable "first choice" to the frequencies expected under a binomial distribution with a specified probability parameter. We distinct this dependent variable as 1) familiar and 2) unfamiliar backgrounds. The probability parameter for variables was 0.5. E is the prey encounter, f and u are, respectively, the unfamiliar and familiar backgrounds.*

Sessions	*Ef* (*n*) *Eu* (*n*)	Category	N	Observed Prop.	Test Prop.	Exact Sig. (2-tailed)
1	1	Familiar	12	1.00	0.50	0.000
	2	Unfamiliar	0	0.00		
2	2	Familiar	10	0.83	0.50	0.039
	4	Unfamiliar	2	0.17		
3	3	Familiar	10	0.83	0.50	0.039
	6	Unfamiliar	2	0.17		
4	4	Familiar	8	0.67	0.50	0.388
	8	Unfamiliar	4	0.33		
5	5	Familiar	2	0.17	0.50	0.039
	10	Unfamiliar	10	0.83		
6	6	Familiar	6	0.50	0.50	1.000
	12	Unfamiliar	6	0.50		
7	7	Familiar	6	0.50	0.50	1.000
	14	Unfamiliar	6	0.50		

Table 2. *Results from two-tailed binomial test comparing the observed frequencies of for the variable "prey eaten" to the frequencies expected under a binomial distribution with a specified probability parameter. We distinct this dependent variable as 1) one prey and 2) two prey. The probability parameter for variables was 0.5. E is the prey encounter, f and u are, respectively, the unfamiliar and familiar backgrounds.*

Sessions	*Ef* (*n*) *Eu* (*n*)	Category	N	Observed Prop.	Test Prop.	Exact Sig. (2-tailed)
1	1	Two prey eaten	2	0.33	0.50	0.688
	2	One prey eaten	4	0.67		
2	2	Two prey eaten	3	0.50	0.50	1.000
	4	One prey eaten	3	0.50		
3	3	Two prey eaten	6	1.00	0.50	0.031
	6	One prey eaten	0	0.00		
4	4	Two prey eaten	5	0.83	0.50	0.219
	8	One prey eaten	1	0.17		
5	5	Two prey eaten	3	0.50	0.50	1.000
	10	One prey eaten	3	0.50		
6	6	Two prey eaten	5	0.83	0.50	0.219
	12	One prey eaten	1	0.17		
7	7	Two prey eaten	6	1.00	0.50	0.031
	14	One prey eaten	0	0.00		

respectively, the unfamiliar and familiar backgrounds and *b* a bout. In the first session $E_f = 1$ and $E_u = 2$ and in the last one $E_f = 7$ and $E_u = 14$, prey encounters were two times more frequent upon the unfamiliar than familiar background. In this manner, we increased possible effects of associative cuing of background against search image formation. Thus, we predicted three possible results from this experiment. First, depending exclusively on visual features of prey, we expected that foraging kestrels visit indifferently both backgrounds and eat all available prey presented to them. Inversely, a search image formation, resulting from repeated encounters of a single prey type, drove kestrels towards more cryptic prey upon familiar background (Tinbergen 1960; dietary conservatism as in Marples & Kelley 1999). Finally, the background itself served to cue attention towards the prey type and the extended practice essentially removed search-image effects (Kono et al. 1998). Another key to the reading our results not involved search image formation but the neophobia (Greenberg & Mettke-Hofmann 2001, Greenberg 2003). According with previous studies, birds reared in controlled environments showed a higher level of neophobia toward novel situation than their wild counterparts (Greenberg 1992, 2003).

***Table 3.** Results from two-tailed binomial test comparing the observed frequencies for the variable "background shifting" to the frequencies expected under a binomial distribution with a specified probability parameter. We distinct this dependent variable as 1) no shifting and 2) shifting. The probability parameter for variables was 0.5. E is the prey encounter, f and u are, respectively, the unfamiliar and familiar backgrounds.*

Sessions	*Ef* (*n*) *Eu* (*n*)	Category	N	Observed Prop.	Test Prop.	Exact Sig. (2-tailed)
1	1	No shifting	12	1.00	0.50	0.000
	2	Shifting	0	0.00		
2	2	No shifting	10	0.83	0.50	0.039
	4	Shifting	2	0.17		
3	3	No shifting	12	1.00	0.50	0.000
	6	Shifting	0	0.00		
4	4	No shifting	6	0.50	0.50	1.000
	8	Shifting	6	0.50		
5	5	No shifting	6	0.50	0.50	1.000
	10	Shifting	6	0.50		
6	6	No shifting	8	0.67	0.50	0.388
	12	Shifting	4	0.33		
7	7	No shifting	6	0.50	0.50	1.000
	14	Shifting	6	0.50		

Statistical analysis

Each kestrel completed 7 sessions (bouts = 14 *per* bird, 12 *per* session). We excluded data from those sessions with ascertained caching behaviour. We used as dependent variables 1) the first choice, 2) the background shifting and 3) the total number of prey eaten at the end of a session. We ran a two-tailed binomial test to compare the observed frequencies of the two categories of a dichotomous variable (0, 1) to the frequencies expected under a binomial distribution with a specified probability parameter (Zar 1984, Uiblein et al. 1995). We defined groups for each dependent variable as follows: 1) familiar and unfamiliar backgrounds (first choice), 2) staying and leaving (background shifting) and 3) one prey versus two prey (i.e. prey eaten at the end of a session). The probability parameter for both groups of a variable was 0.5. Statistical tests in which the probability level is less than 0.05 are reported as significant. We made all analyses using SPSS statistical software ver. 11.0 (SPSS Inc., 2001, Chicago, Illinois, USA).

Results

Background choice

During the first session, search image effects were evident and thus, drove the behavioral choice of feeding kestrels toward the familiar background (Table 1, session 1). Although the use of the unfamiliar background increased during subsequent sessions, birds continued to visit the familiar one significantly so (Table 1, session 2-3). In the third session, all individuals ate prey from both backgrounds (Table 2, session 3). In the successive session the unfamiliar background became the first choice of kestrels (Table 1, session 5). Afterward, background decisions were unbiased (Table 1, session 6-7) and during the last session all prey available were eaten by kestrels (Table 2, session 7).

Background-leaving decision

Up until the third session, the kestrels avoided leaving the familiar background (Table 3, session 1-3). Afterward, influences of this background disappeared and associative cuing effects of the unfamiliar one influenced feeding decisions of kestrels (session 4-7).

Discussion

As expected, search-image effects disappeared with extended practice (Kono et al. 1998). Thus, visual clues such as background features were valuable sources of information for predators, suggesting to them the presence of prey (Mitchell 1989, Valone & Brown 1989, Valone 1991, Kono et al. 1998). In addition, when a predator has learned the association between prey and background, visits increased also when prey became completely non-cryptic (unfamiliar background; Table 1). Ultimately, kestrels seems to avoided an extremely conservative strategy (dietary conservatism) when searching for prey upon different backgrounds (Marples & Kelley 1999). In fact, predators collect pre-harvest foraging information by which they choose among alternative food places (Valone 1991, 1992). After selecting a new feeding background, prey capture rates provided direct evidence of profitability to the predator that left the familiar substrate to pursue prey on the unfamiliar substrate (Table 2, Valone 1991, 1992).

The assessment of prey presence should be made by the forager during current exploitation efforts but also based upon information acquired previously (Valone 1991). In our experimental foraging situation, kestrels did have knowledge about a predictable familiar background. In addition, test birds that kept choosing the prey on the familiar substrate were in concordance with the search image formation (Morgan & Brown 1996). Inversely, when individuals acquired practice and were also stimulated by the persistence of good profitability, they begun to exploit the new background as a stable food source based on current information (Table 2, Valone & Brown 1989, Yosef & Grubb 1993).

As shown in Tables 1 and 2, search-image effects disappeared after three sessions and kestrels gradually increased their visits to the new background. The possession of this information for prey assessment permitted them to shift to the other background for improved exploitation (Table 3). According to optimal foraging theory, foragers with no knowledge about patch quality spend equal efforts to obtain useful information (Iwasa et al. 1981). Consistent information from the new feeding background, as in our experiment, permitted the achievement of a sufficient experience which improved prey detection and feeding performance.

Another possible explanation for the their initial preference to white background could be a consequence of neophobia and the change in their behaviour could be caused by its deactivation due to the repeated contact with the novel situation. Neophobia is the aversion that an animal displays towards approaching a food item, object, or place simply because it is novel (Greenberg 2003). According with the dangerous niche hypothesis (DNH) the primary function of neophobia is to protect animals from the unknown potential dangers of new things rather than to maintain foraging specialization (Greenberg 2003). In particular, birds reared in similar and controlled environments (as in our experiment) showed the so-called intrinsic neophobia (Greenberg 2003). The intrinsic level of neophobia is higher in captive birds than their wild counterparts experienced with a more unpredictable array of habitats during the juvenile period (Greenberg 1992). Although our captive kestrels have a lifelong experience with white food planks, after three sessions only the presumed intrinsic neophobia for novel background has been disengaged (Table 1). In addition if we considered the number of prey eaten *per* session, some birds exploited food sources upon unfamiliar backgrounds since the first session and their number increased to an half in the second one (Table 2). Probably, the degree of discontinuity from the familiar background seems to be one of the main features that contribute to the variation in the initial neotic response as suggested by Thorpe (1956). Unfortunately, there are very few experiments on neophobia and its effects on captive birds (see Greenberg & Mettke-Hofmann 2001 – for a review) and our results should be useful for future comparisons.

Fox et al. (1976) described the American kestrel with the highest known visual acuity (160 c/deg). Thus, there is the possibility that our birds did not formed a search image at all since the prey was not cryptic for them on either background. Nevertheless, recent studies using the pattern electroretinogram and retinal configuration demonstrated that American kestrels acuity ranged only from 25.3 to 30.1 c/deg (Gaffney & Hodos 2003, Ghim & Hodos 2006). In fact, kestrels have a low contrast sensitivity (CS) hence a scarce ability to discriminate between adjacent stimuli (i.e. object and background) on the basis of their differences in relative luminosity (contrast) rather than their absolute luminances (Ghim & Hodos 2006). Probably, this predator may compensate for less than higher achromatic contrast sensitivity using UV (Ultraviolet radiation) vision mechanisms in cone systems (Ghim & Hodos 2006). In fact, many other birds may use UV cues of food items or of the environment for their foraging strategy (see Rajchard 2009 – for a review). Although we did not evaluate UV reflectance of prey, our experiment followed the eye model proposed by Vorobyev & Osorio (1998) where increasing contrasts (as chromatic aspect and achromatic aspects) between target and background increases detectability. In particular, UV-whitish cockerels were displayed upon two different background that strongly differed in achromatic properties. Recently, Cazetta et al. (2009) demonstrate that probability of detection was explained by the chromatic contrast between prey and their background not by the achromatic contrasts. This finding agree with our results where visits by kestrels increased also when UV-white prey became completely non-cryptic upon unfamiliar green background (chromatic contrast).

Acknowledgements

We are greatly indebted to I. Ritchie and P. Thomas of the Avian Science and Conservation Centre for their help and suggestions. We also thank J.A. Smallwood, G. L. Dell'Arte and two anonymous reviewers for useful comments and suggestions on the manuscript. G. L. benefitted of a grant from the University of Catania, Italy.

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