

HANDICAPPED AMERICAN KESTRELS: NEEDY OR PRUDENT FORAGERS?

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ABSTRACT.—To determine the role that individual predator attributes may play in prey selection, we studied the effect of morphological abnormalities of wild American Kestrels (*Falco sparverius*) on their predatory behavior. Because morphological abnormalities should affect foraging behavior, we classified individuals possessing these traits as handicapped. As a measure of predatory behavior, we used the latency to attack a trap baited with a relatively large and potentially dangerous prey item. Handicapped individuals may be needy because they are poor foragers and, therefore, by necessity would attack large and dangerous prey sooner than would controls. Alternatively, handicapped individuals may be ineffective predators and would, therefore, be prudent in their selection of prey and reluctant to attack. Consistent with the latter prediction, we found that latency to attack tended to be longer for handicapped than for control males, but there was no difference for females. For males, the reluctance to attack may be explained by either the low profitability or high risk presented by the prey. A difference in motivation to capture prey during the prelaying season may account for the different results for males and females.

KEY WORDS: *American Kestrel*; *Falco sparverius*; condition; foraging; handicaps; Saskatchewan.

Cernicalos lisiados: necesitados o prudentes a la hora de forrajear?

RESUMEN.—Para determinar el papel que juegan los atributos de los depredadores en la selección de presas, estudiamos el efecto de las anomalías morfológicas de cernicalos silvestres (*Falco sparverius*) en su comportamiento depredador. Debido a que las anomalías morfológicas deben afectar el comportamiento depredador, hemos clasificado a los individuos con estas características como lisiados. Como una medida del comportamiento depredador utilizamos el estado latente para atacar un señuelo con una presa relativamente grande y peligrosa. Los individuos lisiados pueden estar necesitados debido a que no son buenos al forrajear y por lo tanto por necesidad puedan atacar mas pronto a presas grandes y peligrosas que los de control. En forma alternativa, los individuos lisiados pueden ser depredadores ineficientes y por lo tanto ser prudentes en la selección de presas y reacios a atacar. Siendo consistentes con la última predicción, encontramos que el estado latente al atacar fue mas largo que en los machos de control, en cambio en las hembras no hubo diferencia alguna. En los machos el rechazo a atacar puede ser explicado por el bajo provecho o el alto riesgo representado por la presa. La diferencia en la motivación para capturar la presa antes de la estación reproductiva puede ser la explicación de los diferentes resultados para hembras y machos.

[Traducción de César Márquez]

Predatory behavior has been studied extensively using a variety of approaches. Typically, investigators have concentrated on characteristics of either food items or of the foraging predator. Most studies of prey items have centered around attributes of prey that elicit an attack response of a predator, such as movement (Ruggiero and Cheney 1979,

Ruggiero et al. 1979, Smallwood 1989, Sarno and Gubanich 1995), size (Marti and Hogue 1979, Smallwood 1989, Sarno and Gubanich 1995), novelty (Mueller 1971, Ruggiero and Cheney 1979, Ruggiero et al. 1979, Bryan 1984), as well as color and conspicuousness (Kaufman 1972, 1974). Specific search images (Mueller 1971) and prey densities (Collopy 1973, Korpimäki 1986) also have been implicated as important factors in prey selection.

Although a wealth of literature exists on characteristics of food items with regards to prey selec-

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tion, predator traits have received much less attention. Studies of predator characteristics have largely been concerned with differences in class characteristics such as age (Mueller and Berger 1970) and gender (Cade 1960, Selander 1966, Storer 1966). Predation responses are rarely considered in context of individual variation in predator attributes, although studies have addressed the roles of hunger (Mueller 1973, Marti and Hogue 1979), condition (Gorney et al. 1999), experience (Mueller and Berger 1970), and parasitism (Rau and Bird 1991). To ascertain the influence of individual variation in predator characteristics on prey selection, we used the novel approach of determining the impact of morphological handicaps on predatory behavior.

Abnormal morphological characteristics may alter foraging behavior and success, and could therefore be considered handicaps. We used the American Kestrel (*Falco sparverius*), a small falcon, as a model for studying the predatory behavior of naturally handicapped birds. Kestrels are known to eat insects, small mammals, birds, reptiles and amphibians (Bird 1988). When predators capture such a variety of prey sizes, representing a wide range of difficulties and risks, their motivation to select certain prey items may depend on their own ability, morphology and condition. Studies of naturally occurring handicaps may be of particular importance for biologists who are experimentally handicapping birds (Slagsvold and Lifjeld 1990, Whittingham et al. 1994, Weimerskirch et al. 1995) or studying potential handicaps of sexually selected traits (Zahavi and Zahavi 1997), but the behavioral consequences of naturally occurring handicaps are generally unknown.

Our approach was to present kestrels with a large and potentially dangerous prey item that was relatively difficult to capture and subdue. Our rationale was that birds with broken, missing or deformed toes or talons, or broken remiges and rectrices, would be impaired in their ability to capture or subdue prey. Both wing and foot attributes are critical determinants of foraging behavior in falcons (Cade 1982). Many raptors probably kill their prey by squeezing with their toes (Csermely and Gaibani 1998), and the talons are used to assist in grabbing prey and pinning it to the ground (Csermely et al. 1991). Similarly, recent studies of feather asymmetries imply that broken feathers would be a detriment. Increased wing asymmetry of European Starlings (*Sturnus vulgaris*) affects flight

performance (Swaddle 1997, Swaddle and Witter 1998) and experimental tail elongation in male Barn Swallows (*Hirundo rustica*) has aerodynamic consequences which affects foraging behavior (Møller and de Lope 1994). We believe that much larger asymmetries created by broken feathers are likely to be detrimental to foraging kestrels.

We made two mutually exclusive predictions as to how handicaps would affect the behavior, i.e., latency to attack (see Csermely et al. 1989, Csermely 1994), of kestrels. First, if handicapped birds are needy because they are poor foragers, they should be more motivated, by necessity, to attack a difficult prey item. We also tested the assumption that handicapped birds would be hungrier and in poorer condition than controls, and that latency to attack and condition would be positively correlated (Mueller 1973). Alternatively, handicapped birds are expected to be ineffective at capturing and subduing prey; therefore, they may be prudent in their selection of prey. Prudent predators may be less willing to either risk injury or waste energy in attacking a difficult prey species; therefore, handicapped birds may have a longer latency to attack.

METHODS

We studied American Kestrels from 1990–97 in the boreal forest region of northcentral Saskatchewan, Canada, near Besnard Lake (55°N, 106°W) (Bortolotti 1994, Gerard et al. 1996). Kestrels arrived on territories in mid-to late-April and began to lay eggs in mid-May. We captured kestrels prior to laying using bal-chatri traps (Berger and Mueller 1959). Typically, we set two traps each baited with two laboratory mice (*Mus musculus*) (Bortolotti and Iko 1992). Small mammals are a major food of kestrels, and we censused mammals by snap-trapping to determine the sizes of available prey (see Bortolotti et al. 1991, Dawson and Bortolotti 1997).

For each bird trapped, we recorded latency to attack, defined as the time elapsed (nearest min) between setting the trap and the time of first attack on the trap. We banded and weighed (nearest g) each bird, inspected its crop for food and measured the length of the unflattened wing chord (nearest mm). To control for body size, a condition index was derived by dividing wing chord length into mass. Mass and condition indices of birds with food in their crops were excluded from analyses. We inspected each bird for physical abnormalities and any with broken, missing or deformed talons or toes, or broken remiges or rectrices, were deemed to be handicapped. Individuals without such anomalies were used as controls. To control for potential variation in the trapping situation (e.g., year, time and weather), we paired each handicapped bird with a control bird of the same sex, that was the nearest capture in time, and trapped by the same person. We used only previously unbanded birds in analyses, as trapping experience could influence latency to attack.

According to Mueller and Berger (1970) and Mueller (1973), predation by raptors is a direct response to hunger, and hunger is a function of mass and time since the previous meal; therefore, we used body mass, condition index and the presence of crop contents as indicators to determine the effects of hunger on latency to attack. The relationships between indices of hunger and latency to attack were analyzed for handicapped and control birds both separately and combined. To test the prediction that handicapped birds were needy, we also compared hunger and condition indices between handicapped and control birds. To determine effects of handicaps on latency to attack, we compared handicapped birds to control birds. If handicapped kestrels were needy then latency to attack would be shorter for handicapped birds. Conversely, if handicapped kestrels were prudent predators then latency to attack would be longer for handicapped birds.

Behavior of male and female kestrels differ during the prelaying season (Balgooyen 1976, pers. obs.), so we expected them to differ in their motivation to capture prey. Males, for example, may be highly motivated to capture food items, as they must procure food for both themselves and their mates (Balgooyen 1976). Therefore, we analyzed data for males and females separately. Means are presented ± 1 SE. Analyses were performed on SPSS (Norušis 1993) and all tests were two-tailed.

RESULTS

Small mammals available to the kestrels included red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), jumping mice (*Zapus hudsonicus*), least chipmunks (*Eutamias minimus*) and shrews (*Sorex* spp.). The smallest available prey were shrews (5.8 ± 0.6 g, $N = 13$) and the largest prey were chipmunks (43.9 ± 0.8 g, $N = 108$). Generally, red-backed voles (19.0 ± 0.3 g, $N = 247$) were the main prey of kestrels (Iko 1991, Dawson 1999). We did not weigh the lures used in this study, but mice from the same source weighed an average of 37.0 ± 0.5 g ($N = 192$) which is approximately one-third the mass of an adult kestrel. Therefore, the bait was relatively large compared to naturally available prey.

We captured 1120 American Kestrels on bal-chatri traps and 5.9% of these were handicapped. When we presented kestrels with mice, we found that hunger was not a factor in latency to attack. Overall, 15% (10/66) of handicapped and 17% (11/66) of control birds had food in their crops, indicative of recent meals. We found no difference in latency to attack between birds with food in their crops and those with empty crops (Mann-Whitney U test: males: $U = 59$, $N_1 = 34$, $N_2 = 4$, $P = 0.64$; females: $U = 597$, $N_1 = 73$, $N_2 = 17$, $P = 0.80$). We did not find any significant correlations between latency to attack and mass (handicapped

Table 1. Latency to attack (mean $\pm$ SE) of handicapped and control American Kestrels to bal-chatri traps, 1990–97.

SEX	STATUS	N	LATENCY TO ATTACK	RANGE
			(min)	
Male	Handicap	17	7.3 ± 2.3	0–32
	Control	17	3.8 ± 1.2	0–19
Female	Handicap	45	3.5 ± 0.6	0–19
	Control	45	3.2 ± 0.4	0–14

and controls pooled, Spearman rank correlation: males: $r_s = 0.19$, $N = 34$, $P = 0.28$; females: $r_s = -0.10$, $N = 73$, $P = 0.40$), or condition (males: $r_s = 0.22$, $N = 34$, $P = 0.20$; females: $r_s = -0.04$, $N = 72$, $P = 0.74$). Similarly, no significant correlations were detected between latency to attack and mass for handicapped birds alone (males: $r_s = 0.14$, $N = 15$, $P = 0.64$; females: $r_s = 0.04$, $N = 37$, $P = 0.84$), or for control birds alone (males: $r_s = 0.31$, $N = 19$, $P = 0.20$; females: $r_s = -0.24$, $N = 36$, $P = 0.16$). We also did not detect significant correlations between latency to attack and condition for handicapped (males: $r_s = 0.29$, $N = 15$, $P = 0.30$; females: $r_s = 0.17$, $N = 36$, $P = 0.34$), or for control birds (males: $r_s = 0.21$, $N = 19$, $P = 0.38$; females: $r_s = -0.19$, $N = 36$, $P = 0.28$). Contrary to the prediction that handicapped birds would be in poor condition, we could not detect a difference in mass (Wilcoxon signed-ranks test: males: $z = -0.68$, $N = 18$, $P = 0.50$; females: $z = -0.74$, $N = 32$, $P = 0.46$) or condition (males: $z = -0.76$, $N = 18$, $P = 0.44$; females: $z = -0.60$, $N = 32$, $P = 0.56$) between control and handicapped birds.

As hunger indices were unrelated to latency to attack and handicap status, the prediction that handicapped birds were needy became less plausible. However, consistent with the prediction that handicapped birds were prudent predators, we found that handicapped males tended to take longer to attack the traps than did controls (Wilcoxon signed-ranks test: $z = -1.83$, $N = 17$, $P = 0.06$), but we could not detect such a difference for females ($z = -0.05$, $N = 45$, $P = 0.96$; Table 1).

DISCUSSION

Previous studies have suggested that predatory behavior of some raptor species was directly related to condition or hunger (Mueller 1973, Marti and

Hogue 1979, Gorney et al. 1999; but see Nunn et al. 1976), although some results were sex- and age-specific (Mueller and Berger 1970). In contrast, our results did not support the idea that handicapped birds were needy predators, as there were no differences in hunger indices between the two groups. Similarly, we found no indications that condition or any measures of hunger were related to latency to attack. Although hunger may be important to individual birds supporting themselves, during the prelaying period kestrels in our study may have been motivated outside of hunger; males must procure food for their mates and it therefore made sense that latency to attack and hunger were not related.

The prediction that handicapped birds are prudent predators was weakly supported by the trend for longer latency to attack by handicapped compared to control males, but there was no difference for females. For males, this reluctance to attack may be explained by either the potentially low profitability or high risk presented by the prey. Predators must detect and capture food items with enough efficiency that they do not expend more energy than they obtain (Bryan 1984, Balgooyen 1989). If handicapped birds are less adept predators, the energetic demands of capturing and subduing a large and dangerous prey item may be prohibitive. Therefore, handicapped birds may be reluctant to attack large prey such as the ones we presented. Handicapped birds may exploit alternative food resources, such as insects. Møller and de Lope (1994) found evidence for a shift in prey selection by experimentally handicapped male Barn Swallows. Similar results were obtained by Wright and Cuthill (1989, 1990) with experimentally handicapped European Starlings. Marti and Hogue (1979) found that Eastern Screech Owls (*Otus asio*) consistently chose several smaller mice over fewer larger mice. They postulated that selection of smaller prey may be advantageous as smaller individuals are younger, less experienced, and more vulnerable. Conversely, larger prey were assumed to be stronger, and more experienced, and were therefore perceived as risky prey by the owls. Thus, the energy expended on catching and killing such large prey may not be worth risking if larger prey are better able to escape.

Marti and Hogue's (1979) results are also consistent with the predictions of the dangerous prey hypothesis (Forbes 1989), which was developed to explain interspecific differences in foraging behav-

ior on dangerous prey items. The risk of injury may be greater with larger prey as they may be able to effectively defend themselves from predators. Therefore, risky prey items pose an energetic risk, as well as a risk of immediate physical harm, to the predator.

Regardless of the possible reasons for the behavioral differences of handicapped birds, these behaviors could affect reproduction if foraging behavior affects the quantity or type of prey procured. Although handicapped birds did not appear to be in poor condition, their mates may have been. As males are providing their mates with food in the prelaying period, resources available for egg laying may be reduced for mates of handicapped males. Similarly, a shift from a preferred prey to suboptimal prey likely would have detrimental effects on reproduction. Korpimäki (1986), for example, found that the number of breeding pairs of Eurasian Kestrels (*Falco tinnunculus*) and the average clutch size correlated positively with the percent of voles, the preferred prey, in the diet. Similarly, Balgooyen (1989) found that female American Kestrels in southwestern Venezuela did not produce eggs if there were too few lizards, their preferred prey, in the diet. In our study area the number of small mammals is an important correlate of several reproductive variables (Wiebe and Bortolotti 1992, Bortolotti et al. 1991, Dawson 1999). Presumably, handicapped birds that use alternate prey items may suffer reduced reproductive success.

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