Possible relationships between morphology, territory quality, and skin color of American Kestrels[1]

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ABSTRACT. Carotenoid-based coloration of skin and plumage has been found to be correlated with individual quality in many species of birds during the breeding season. However, less is known about the possible role of these signals during the nonbreeding season, particularly among nonpasserines that defend winter territories. American Kestrels (*Falco sparverius*) are sexually dimorphic raptors that defend winter territories and possess carotenoid-based morphological features known to be correlated with individual quality. Much is known about winter territory use and habitat segregation by male and female kestrels, but possible relationships among morphological features, individual quality, and habitat quality have not been examined. Our objective was to examine possible relationships between morphology, territory quality, and skin color of American Kestrels. Male kestrels had brighter skin than females, and the skin color of male kestrels was positively correlated with size (wing chord and tail length) and territorial quality (hunting territories with less canopy and more grass cover). No such relationships were found for female kestrels. Skin color appears to be an honest indicator of quality for male American Kestrels and may serve both intersexual (territory acquisition) and intersexual (mate choice) functions during the breeding and nonbreeding seasons.

SINOPSIS. **Posible relación entre la morfología, calidad del territorio y el color del integumento en *Falco sparverius***

Se ha encontrado que la coloración de plumas e integumento, asociada a la ingestión de carotenoides, está correlacionada con la calidad de individuos en muchas especies, durante la época reproductiva. Sin embargo, se conoce poco sobre el posible rol de estas señales durante la época no-reproductiva, particularmente entre paserinos que defienden territorios durante el invierno. *Falco sparverius* es un tipo de falcón sexualmente dimorfico que defiende territorio durante el invierno y tiene estructuras morfológicas cuyo pigmento está basado en carotenoides los cuales, a su vez, están correlacionados con la calidad de los individuos. Se conoce bastante sobre el uso de territorios durante el invierno y segregación de hábitat por parte de ambos sexos, pero nos se ha estudiado la posible relación entre aspectos morfológicos, la calidad de los individuos y la calidad del hábitat utilizado. Nuestro objetivo fue examinar la posible relación entre morfología, calidad del territorio y color del integumento en los falcones. El macho de la especie tiene un integumento más brillante que la hembra y el color de este se correlacionó positivamente con el tamano (largo del ala y el rabo) y la calidad del territorio (territorio de caceria con poco docel y más áreas abiertas con yerbas). No se encontró un correlación similar en las hembras. El color del integumento parece ser un buen indicador de la calidad de los machos y pudiera servir para la adquisición de territorios y la selección de parejas tanto durante la época de reproducción como fuera de la misma.

Key words: carotenoids, *Falco sparverius*, individual quality, integument color, territory quality

Morphological features such as plumage and skin color have been found to be correlated with individual quality in several species of birds (Hill and Montgomerie 1994, Bortolotti et al. 1996, Keyser and Hill 1999). For example, the intensity of coloration (red, yellow, and orange) derived from carotenoid pigments was correlated with nutritional condition in House Finches (*Carpodacus mexicanus*; Hill 1991) and physical

condition in American Kestrels (*Falco sparverius*; Bortolotti et al. 1996, Negro et al. 1998). Because carotenoid pigments cannot be synthesized by vertebrates and must be ingested, Hill and Montgomerie (1994) hypothesized that male House Finches in better condition (i.e., brighter males) were better able to acquire foods rich in carotenoids than males in poor condition. These authors found a correlation between plumage brightness and tail feather growth rates, supporting their hypothesis that brighter plumage was correlated with nutritional condition.

Morphological indicators of quality can reduce intraspecific competition and influence mate choice. For example, Mateos and Carranza

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(1997) experimentally brightened and dulled the plumage of male Ring-necked Pheasants (*Phasianus colchicus*) equal in body weight, tarsus length, spur size, frequency of wattle displays, and rank. Dull male pheasants were subordinate to brighter individuals, suggesting that assessing a conspecific's fighting ability through plumage brightness allowed individuals to avoid confrontations (Mateos and Carranza 1997). Similarly, Studd and Robertson (1985) found that territorial Yellow Warblers (*Dendroica petechia*) evaluated the possible threat posed by a conspecific intruder by assessing the amount of brown streaking on an intruder's breast. Intruders with more brown streaking elicited aggressive responses from the territory holder, while those with less streaking did not. Such assessment allowed resident Yellow Warblers to determine if an intruder was a threat without wasting energy or risking possible harm by confronting a subordinate (Studd and Robertson 1985).

American Kestrels are sexually dimorphic raptors that defend winter territories and possess carotenoid-based morphological features shown to be correlated with individual quality (Bortolotti et al. 1996, Negro et al. 1998). Much is known about winter territory use and habitat segregation by male and female kestrels (Koplin 1973, Mills 1976, Smallwood 1987, 1988a, Ardia and Bildstein 1997), but possible relationships among morphological features, individual quality, and habitat quality have not been examined. For example, higher quality kestrels may obtain higher quality winter ranges and, thus, spend less time and energy hunting. Smallwood (1988b) found a correlation between the quality of kestrel foraging habitat and time spent hunting, with those in better quality habitat (hunting substrate containing grasses and weedy forbs <25 cm in height) producing pellets of greater mass by noon than birds in lower quality habitats (Smallwood 1988b). By days end, kestrels in higher and lower quality sites acquired similar quantities of prey, but Smallwood's (1987, 1988b) results indicate that habitat quality may have influenced daily activity budgets. That is, kestrels in better habitat may spend less time foraging and, perhaps, more time on nonhunting activities (e.g., resting). The objective of our study was to examine the possible relationship between habitat quality and individual quality in male and female American Kestrels in central Kentucky.

METHODS

Kestrels were studied from October 2000–April 2001 at the Blue Grass Army Depot (BGAD) and adjacent areas in Madison County, Kentucky. The BGAD consists of 5907 ha, primarily composed of pasture with trees and woodlands interspersed throughout. Male ($N = 19$) and female ($N = 18$) kestrels were captured from 17 November 2000 to 22 March 2001 using bal-chatri traps (Berger and Mueller 1959) baited with mice. Each kestrel captured was fitted with a numbered aluminum band and a unique combination of colored-plastic bands to permit individual recognition. Standard morphological measurements, including wing chord, tarsus length, tail length, and mass, were determined. In addition, one rectrix (fourth from the right) was plucked from each kestrel so the mean width of daily growth bars (a measure of nutritional condition; Hill and Montgomerie 1994) could be determined.

A technique similar to that described by Bortolotti et al. (1996) was used to score the color of unfeathered ceres, lores, and tarsi. This included a six-color chart consisting of Munsell color chips ranging from 1 (pale yellow) to 6 (red-orange). These colors were chosen because they best represent the increasing intensity in carotenoid coloration (Table 1). Munsell color chips are characterized by three aspects: (1) the hue defined as the quality by which the color is distinguished from other colors, (2) the value defined as the quality of the color by which light

Table 1. The six-color option chart used to score the color of the skin of the cere, lore, and tarsus of male and female American Kestrels.

Color score	Hue[a]	Value[b]/Chroma[c]
1	7.5y[d]	8.5/10
2	2.5y	8.5/12
3	1.25y	8.0/14
4	2.5y	7.0/12
5	10.0yr[e]	7.0/12
6	10.0yr	6.0/12

[a] Hue is defined as the quality by which one color is distinguished from another.

[b] Value is defined as the quality by which a light color is distinguished from a dark color.

[c] Chroma is defined as the quality that distinguishes the difference from a pure hue to a gray shade.

[d] y = yellow.

[e] yr = yellow-red.

and dark colors are distinguished, and (3) the chroma, or the color quality that distinguishes the difference from a pure hue to a gray shade. As the color score increases from pale yellow to red-orange, the values of the color chips increase (i.e., increasing brightness) as do the hues (i.e., tending toward red and away from yellow indicating increased carotenoid pigment), with increasing chroma scores indicating a more pure color. The scores for each body part were added together for a total score, with a high score indicating brightness (high quality) and a low score indicating dullness (low quality).

Observations of focal kestrels were conducted from January to April 2001. An observation began when a focal kestrel was located and lasted until the bird was lost from view or had been observed for 60–90 min. During each observation period, all hunting perches from which attacks were initiated were identified. Perch site analyses were conducted following the methods of Smallwood (1987). For each analysis a 1-ha circular plot was placed around a perch used by a focal kestrel. Within each 1-ha circular plot, 20 sites were divided evenly into four quadrants, and randomly distributed in each quadrant using a random number table and a numbered circular grid of the plot. The grid was numbered 1 through 9 for each quadrant both down and across. Numbers were chosen from the random number table by dropping two pieces of rice on the table and the numbers most covered by the rice were used. At each of the 20 sites a 1-m² quadrat was placed on the ground to assure the same size was measured for each site. For each, site the habitat was characterized using eight parameters: (1) type of ground vegetation (grass, forbs, woody vegetation, or no vegetation), (2) condition of ground vegetation (<33% dead, >33% but <67% dead, or >67% dead), (3) average height of ground vegetation, (4) presence of tree or shrub canopy directly over sample point (no canopy, on the edge of dense shrub (>1 shrub, above a meter)/woodlot opening, under solitary tree or shrub, or within dense shrub (>1 shrub, above a meter)/woodlot with closed canopy), (5) species of canopy plants, (6) condition of canopy plant (alive with foliage, dormant without foliage, or dead), (7) canopy height (any portion of a tree or trees ≥2 m over the plot; a clinometer was used to determine heights) and tree diameter, and (8) land use. Land-use categories included old field (presence of shrubs, trees, and grass >1 m), water, continually maintained vegetation (vegetation regularly mowed to keep vegetation ≤10 cm in areas such as roadsides near buildings), vegetation maintained annually (vegetation mowed once or twice a year in June, July, or August), vegetation maintained, but not annually (mowed in the past but not on an annual basis, vegetation >1 m high with a few or no trees >1 m tall), grazed (cattle present), woodlot (≥four trees ≥3 m in height in close proximity, with branches touching or overlapping), paved road, unpaved road, building (not including bunkers due to vegetation covering them), or some combination of these categories (such as grazed and maintained annually).

Relationships between feather growth rates and skin color were examined using correlational analysis, and Wilcoxon tests were used to examine differences in morphometric measurements, growth bar width, and total color score between male and female kestrels. Discriminant function analysis was used to determine if the characteristics of kestrel perch sites varied with skin color. Based on skin color, female kestrels were categorized as either dull or bright, and males as dull, medium, or bright. These categories were determined based on overall mean color scores for females and males, as well as gaps between scores. For males, the mean color score was 12.8 (range = 9–17) and no male had color scores of 11 or 15. Thus, color scores of 10 or less were categorized as dull, scores of 12–14 as medium, and 16 or more as bright. For females, the mean color score was 9.2 (range = 5–15) and no female had a color score of 11 and, therefore, color scores of 10 or less were categorized as dull and scores of 12 or more as bright. Variables important in discriminating between males and females in these categories were determined by a stepwise discriminant analysis (backward procedure). The cross-validation technique was then used to evaluate model classification efficacy (Williams et al. 1990). Cohen's κ and its Z value were calculated to test model performance (Titus et al. 1984). All analyses were performed using the statistical analysis system (SAS Institute 1999).

RESULTS

Male and female American Kestrels differed in the color of the skin on the cere, lore, and tarsus.

Table 2. Comparison of morphometric measurements of male and female American Kestrels.

Variable	z value[a]	P value	Male			Female		
			Mean	SE[b]	N[c]	Mean	SE	N[c]
Mass(gm)	4.08	<0.0001	113.2	2.1	18	132.2	2.2	17
Bill (mm)	3.48	0.005	12.2	0.2	19	12.9	0.2	18
Tarsus (mm)	0.82	0.41	42.2	0.3	18	42.5	0.2	18
Wing chord(mm)	3.70	0.0002	188.3	1.5	19	197.0	1.2	18
Tail (mm)	3.34	0.0008	120.4	1.5	19	127.8	1.2	18
Color score[d]	3.25	0.0011	12.8	0.7	18	9.2	0.6	18
Growth bar width (mm)	0.36	0.72	4.2	0.1	19	4.0	0.2	15

[a]Wilcoxon tests.
[b]Standard error.
[c]Sample sizes are unequal because we did not obtain all measurements for all individuals.
[d]Color score equals the sum of cere score + tarsus score + lore score.

Each of these areas was scored for each kestrel and the three values summed for an overall color score. The overall color scores for males ($N = 18$) and females ($N = 18$) differed significantly ($z = 3.25$, $P = 0.0011$), with a mean of 12.8 ± 0.7 (SE; range = 9–17) for males and 9.2 ± 0.6 (SE; range = 5–15) for females. In addition, female American Kestrels were larger than males, with females weighing significantly more than males and having significantly longer bills, wing chords, and tails (Table 2). However, male and female kestrels did not differ in either tarsus length or mean width of rectrix growth bars (Table 2).

We found few significant correlations between morphology and either growth bar width or skin color for female kestrels (Table 3). We found a significant correlation between cere score and wing chord ($r_s = 0.55$, $P = 0.018$). However, correlations between tarsus score and wing chord ($r_s = 0.22$, $P = 0.37$) and between lore score and wing chord ($r_s = 0.25$, $P = 0.31$) were not significant. We found no significant correlations between total color score and tail length ($r_s = 0.18$, $P = 0.48$), tarsus length ($r_s = 0.09$, $P = 0.74$), or mass ($r_s = 0.30$, $P = 0.25$), respectively.

For male kestrels (Table 4), the correlation between growth bar width and total color score approached significance ($r_s = 0.45$, $P = 0.059$). In addition, we found significant correlations between total color score and wing chord ($r_s = 0.65$, $P = 0.004$) and total color score and tail length ($r_s = 0.59$, $P = 0.0093$). Larger males

Table 3. Correlations between skin color and morphological characteristics of female American Kestrels.

Correlation (variable × variable)	r_s value	P value[a]
Color score[b] × wing chord	0.43	0.08
Color score × tarsus length	0.09	0.74
Color score × mass	0.30	0.25
Color score × tail length	0.18	0.48
Cere color score × rectrix growth rate	0.29	0.31
Cere color score × wing chord	0.55	0.02
Lore color score × wing chord	0.25	0.31
Tarsus score and wing chord	0.22	0.37
Rectrix growth rate × mass	0.19	0.52
Rectrix growth rate × color score	−0.006	0.98

[a]Bonferroni-corrected; significance accepted at $P \leq 0.005$.
[b]Color score equals the sum of cere score + tarsus score + lore score.

Table 4. Correlations between integument color and morphological characteristics of male American Kestrels.

Correlation (variable × variable)	r_s value	P value
Color score[a] × wing chord	0.65	0.004
Color score × tarsus length	−0.12	0.66
Color score × mass	0.20	0.43
Color score × tail length	0.59	0.009
Tarsus color score × rectrix growth rate	0.34	0.16
Tarsus color score × wing chord	0.55	0.019
Rectrix growth rate × mass	0.28	0.26
Rectrix growth rate × color score	0.45	0.059

[a]Color score equals the sum of cere score + tarsus score + lore score.
[b]Bonferroni-corrected; significance accepted at $P \leq 0.005$.

Table 5. Variables permitting best discrimination among hunting areas used by male American Kestrels with dull, medium, and brightly colored skin.

Habitat variable	Partial $R^{**}2$ value	F value	P value
% Grass	0.458	7.19	0.0055
% Woody vegetation	0.393	5.49	0.0145
% No canopy	0.497	8.41	0.0029
% Edge of dense shrubs/woodlot opening	0.594	12.43	0.0005
% Under solitary tree/shrub	0.568	11.18	0.0008
% Within dense shrubs/closed canopy	0.351	4.59	0.0255
% Live vegetation	0.497	8.40	0.0029
% Dead vegetation	0.406	5.80	0.0120
% Old field	0.649	15.74	0.0001
% Grazed woodlot	0.320	4.00	0.0377
% Maintained annually/grazed	0.863	53.69	0.0001
% Woodlot	0.640	15.74	0.0002
% Paved road	0.679	17.96	0.0001
% Unpaved road	0.393	5.49	0.0145
Mean vegetation height	0.420	6.15	0.0098

Color scores (sum of cere score + tarsus score + lore score) for each category: dull = 9 or 10, medium = 12–14, or bright = 16 or 17.

(based on wing chord and tail lengths) were brighter. Correlations between total color score and other possible measures of male size, tarsus length (r_s = -0.12, P = 0.66), and mass (r_s = 0.20, P = 0.43), were not significant.

We found no differences in the characteristics of areas used by hunting male and female American Kestrels (Wilk's λ = 0.44, $F_{29,38}$ = 1.66, P = 0.072). Similarly, there was no difference between dull (total score ≤10; N = 14) and bright (total score ≥12; N = 4) female kestrels in the characteristics of habitats used for hunting (Wilk's λ = 0.14, $F_{5,29}$ = 1.07, P = 0.52). For male kestrels, however, we found a significant difference (Wilk's λ = 0.01, $F_{14,52}$ = 2.31, P = 0.044) in the characteristics of habitats used by dull (total score of 9 or 10; N = 18), medium (total score of 12–14; N = 5), and bright (total score of 16 or 17; N = 12) individuals. Stepwise discriminant analysis revealed that 15 variables permitted best discrimination among habitats used by males in these three categories (Table 5). A model including all 15 variables correctly classified 86% of all hunting areas used by males into the appropriate category. This, however, was only 15% better than categorizing by chance alone (Cohen's κ Z = 1.70, P = 0.088). Most incorrect classifications were for medium individuals (only 2 of 5, or 40% were correctly classified). Excluding those five males

from the analysis, all 12 bright males and all 18 dull males were correctly classified (100% better than chance alone; Cohen's κ Z = 5.29, P < 0.0001). Examination of these 15 variables indicates that areas used by brighter male kestrels tended to be grazed and maintained (mowed) habitats with more grass cover and less canopy than areas used by dull individuals.

DISCUSSION

Male American Kestrels in our study had brighter skin than females. Similarly, Negro et al. (1998) reported that male American Kestrels exhibited brighter skin color than females during both the breeding and nonbreeding seasons and, further, that skin color became brighter during the breeding season. Male Eurasian Kestrels (*Falco tinnunculus*) were also found to have brighter skin color than females during the breeding season (Casagrande et al. 2006). Such seasonal variation would be expected in a sexually selected trait and, further, suggests that kestrels may have the ability to regulate their skin color (Negro et al. 1998).

The skin color of male American Kestrels in our study was correlated with measures of both individual and territorial quality, with brighter males and hunting in areas with more, but shorter, grass cover and less canopy cover. Skin

color is likely an accurate indicator of current condition (Johnson et al. 1993, Bortolotti et al. 1996). Johnson et al. (1993) suggested that carotenoid pigmentation in the skin of birds was an indicator of short-term changes in physiological condition because birds generally do not store carotenoid pigments in the skin due to the lack of chromatophores (Brush 1990). Even though feathers may contain carotenoid pigments, these pigments have been deposited and are not stored in a way that allows them to change as result of short-term changes in physiological condition (Brush 1990).

The correlation between skin color of male American Kestrels and rectrix growth rates in our study approached significance, suggesting that male skin color may be an honest indicator of nutritional condition and, perhaps, individual quality. Previous studies have revealed that rectrix growth rates are positively related to nutritional condition in a number of species (e.g., Grubb 1989, Jenkins et al. 2001), and the relationship between condition and carotenoid-based coloration has also been demonstrated in a wide variety of species (Horak et al. 2001, Saks et al. 2003). In American Kestrels Bortolotti et al. (1996) found a significant correlation between plasma carotenoid levels and plasma protein levels, suggesting a relationship between carotenoid levels and a kestrel's condition. In addition, Casagrande et al. (2006) found that the skin color of male Eurasian Kestrels was correlated with the number of prey delivered to the nest, suggesting that males with brighter skin were better hunters.

We found that male American Kestrels with brighter skin hunted in areas with more, and shorter, grass and with less canopy cover than did males with duller skin. Areas with these characteristics are likely higher quality hunting sites because shorter vegetation increases prey detectability (Bechard 1982, Toland 1987). Toland (1987) found that American Kestrels preferred disturbed grasslands (mowed, grazed, and harvested) because the shorter vegetation increased detectability of prey. Similarly, Bechard (1982) found that Swainson's Hawks (*Buteo swainsoni*) favored habitats with less vegetative cover (harvested crop fields) because less cover increased the chances of prey detection. Vegetation cover may be more important than prey density in the selection of foraging sites by Swainson's Hawks (Bechard 1982). If areas with shorter vegetation

are also important for kestrels, the presence of brighter male kestrels in such areas further suggests that skin color of males is an indicator of quality. Male kestrels with brighter skin may be dominant to those with duller skin and, therefore, might be able to obtain and defend higher quality hunting sites.

Although we found a position correlation between skin color and apparent quality of hunting sites for male American Kestrels, no such correlation was found for female kestrels. One possible explanation for such results is that female kestrels are dominant to males, regardless of skin color, and, as a result, must compete only with other females for access to hunting areas. Male kestrels, on the other hand, would then compete with each other for access to the remaining areas. If so, female kestrels are more likely to be observed hunting in higher quality areas. In support of this conclusion, Aborn (1989) found that female American Kestrels did tend to dominate males and, in addition, that heavier kestrels tended to dominate lighter ones.

In summary, skin color of male kestrels appears to represent an honest indicator of quality (nutritional condition and size). As such, skin color could potentially serve both intrasexual (territory acquisition) and intersexual (mate choice) functions during the breeding and non-breeding seasons.

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