Energetic consequences of sex-related habitat segregation in wintering American kestrels (*Falco sparverius*)

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Abstract: Behavioural dominance can cause individuals to use less-preferred habitats, with potentially important life-history consequences. In the American kestrel, *Falco sparverius*, females exclude males from preferred open areas; I hypothesized that this sex-related habitat segregation leads to energetic consequences for males. I predicted that males would show decreased body condition over winter, while females would not, and that females would maintain larger net-energy surpluses than would males. Working in southeastern Pennsylvania, between 1991 and 1995, I conducted 150 behavioural observations and measured body condition of 235 wintering kestrels. Male kestrels maintained a lower body condition (residuals of a regression of mass vs. size) than did females and showed a decrease in mean body condition over winter, which females did not. I estimated that females had larger daily energy expenditures than did males (248 vs. 195 kJ per bird per day, ratio 1.27) but also had larger daily energy intakes (537 vs. 322 kJ/day, ratio 1.67). Females had larger net energy surpluses than did males (288 vs. 126 kJ/day, ratio 2.27), particularly when temperatures were <0°C. I conclude that differences in energetics are due in part to habitat differences and that males may suffer consequences by being forced to use less-preferred habitats.

Résumé : La dominance comportementale peut pousser des individus à utiliser des habitats autres que ceux qu'ils préfèrent, ce qui peut influencer fortement leur biologie. Chez la crécerelle d'Amérique, *Falco sparverius*, les femelles excluent les mâles des zones ouvertes, généralement préférées; j'ai posé en hypothèse que cette ségrégation reliée au sexe avait des conséquences énergétiques pour les mâles. Les mâles, mais pas les femelles, seraient en moins bonne condition physique pendant l'hiver et les femelles auraient des surplus d'énergie nette plus importants que ceux des mâles. Dans le sud-est de la Pennsylvanie, entre 1991 et 1995, j'ai mené à bien 150 observations de comportements et mesuré la condition physique de 235 crécerelles en hiver. Les mâles avaient un coefficient de condition physique plus faible (résidus de la régression de la masse en fonction de la taille) que les femelles et ils ont subi une baisse de leur condition physique moyenne durant l'hiver, ce qui n'était pas le cas chez les femelles. Les femelles avaient des dépenses énergétiques plus grandes que celles des mâles (248 vs. 195 kJ par oiseau par jour, rapport de 1,27), mais elles consommaient aussi plus d'énergie que les mâles (537 vs. 322 kJ/jour, rapport de 1,67) . Les femelles avaient des surplus énergétiques nets plus grands que ceux des mâles (288 vs. 126 kJ/jour, rapport de 2,27), particulièrement quand les températures étaient <0°C. Les différences de bilan énergétique sont donc en partie attribuables aux différences d'habitat et les mâles peuvent en subir les conséquences en étant forcés d'utiliser des habitats qui leur conviennent moins.

[Traduit par la Rédaction]

Introduction

Competition can influence habitat use both within and among species, where competitively inferior individuals are forced to use less-preferred habitats (Holbrook 1979; Ward and Seely 1996; Herremans 1997). Long-term interactions of life-history traits may constrain development of adaptations to these less-preferred habitats (Gould and Lewontin 1979; Stearns 1992). Therefore, when dominance interactions occur, there may be no set of conditions where subordinate individuals are able to avoid lower relative returns (Cresswell 1998; Donazar et al. 1999; Ruxton 1999), higher rates of predation, or reduced breeding effort (Högsted 1980; Sherry and Holmes 1988; Marra et al. 1993). Herein, I report on sex-related differences in nonbreeding foraging energetics in the American kestrel, *Falco sparverius*, and examine whether these differences lead to consequences for males, the subordinate sex.

Sex-related differences in winter-habitat use in the small falcon, the American kestrel (*F. sparverius*), have been reported in many parts of the species range (Koplin 1973; Mills 1976; Meyer and Balgooyen 1987; Smallwood 1987), including this study site (Ardia and Bildstein 1997, 2001). Generally, females, which are larger than males, occupy open areas mostly devoid of woody vegetation, while males inhabit semi-open areas containing more woody cover. Some researchers have suggested that males and females have their highest relative survival in the areas in which they are

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observed and consequently maintain separate habitat preferences (Koplin 1973; Meyer and Balgooyen 1987). However, work done at this study site has demonstrated that female kestrels are preferentially able to occupy mutually preferred open areas (Ardia and Bildstein 1997) and that male kestrels use open areas when they are available (Smallwood 1988; Arnold and Martin 1991), suggesting that males may be excluded from using open habitats.

Given this sex-related competitive difference in ability to occupy preferred sites, I tested the hypothesis that this observed habitat segregation causes males to maintain lower energy surpluses than females beyond those expected by mass differences alone. Further, if males maintain smaller energy surpluses, I predicted that males would suffer consequences and exhibit decreases in body condition over winter. Energy balances have been used to compare fitness consequences of behavioural choices such as foraging and habitat selection (Wolf and Hainsworth 1971; Arnold 1988; Hixon and Carpenter 1988; Krebs and Kacelnik 1991; Hall et al. 1992). The energetics and behaviour of American kestrels are strongly influenced by climatic conditions, in part because American kestrels lose and gain heat rapidly through changes in ambient temperature, wind speed, and solar radiation (Hayes and Gessaman 1980). In addition, weather variables, especially wind speed, affect foraging mode and capture success in kestrels (Bildstein and Collopy 1987). Accordingly, I incorporated weather variables in my analyses.

Materials and methods

Study site

The study was conducted from 1991 to 1995 in Berks and Lehigh counties, southeastern Pennsylvania (centered on 40°55′N, 75°75′W). During this period, migratory movements of kestrels in the region were limited (Stotz and Goodrich 1989), and kestrel density was constant for the study period (0.14 ± 0.02 kestrels/km (mean ± SE); D.R. Ardia, unpublished data). The total study area of approximately 800 km² comprised a patchwork of rolling hills and farmlands, consisting primarily of cut agricultural land (corn, *Zea mays*; soybean, *Glycine max*; alfalfa, *Medicago sativa*; and pasture) separated by small woodlots and orchards. The study area is bordered by the southeastern ridge of the central Appalachian Mountains on the northwest and the Atlantic Coastal Plain on the southeast. Each year between 70 and 100 pairs of American kestrels nest in the area in nest boxes erected for their use (Apanius 1991; Rohrbaugh and Yahner 1997).

Kestrel body condition

Two hundred and thirty-five unique wintering kestrels (130 female, 105 male) were captured between 1991 and 1995 using a wire bal-chatri trap (Berger and Mueller 1959) baited with two house mice, *Mus musculus*. Wintering kestrels were located by driving secondary roads at a speed of 15–45 km/h. Kestrels captured twice were not used in these analyses. Kestrels were weighed to the nearest gram with Pesola scales and sexed by plumage; the longest primary feather and central tail rectrix were measured with a ruler calibrated in 0.1-cm increments. To estimate body condition, I combined wing and tail lengths in a principal component analysis (PCA). The score of the first principal component

Table 1. Summary statistics (1991–1995) of weather conditions observed on the study site in Berks and Lehigh counties, southeastern Pennsylvania.

	Mean	SD	Minimum	Maximum
Temperature (°C)	5.3	5.2	−8.0	21.6
Wind speed (m·s⁻¹)	4.4	2.6	0	14.4
Cloud cover (%)	51.5	16.1	0	100

(PC1) was used as an index of body size. I then regressed body mass against PC1 and used the residuals from this regression as an estimate of body condition.

Foraging behaviour

I recorded foraging activity during one hundred and fifty 20-min observations of 150 unique individual (75 male and 75 female) American kestrels from November 1994 to February 1995. I distributed observations over all daylight hours and weather conditions to minimize bias, and conducted each observation from an automobile at least 100 m from each bird, using 8× binoculars and a 15–45× spotting scope. Behaviour was recorded on a microcassette recorder and transcribed at a later time. If a kestrel was lost from sight for longer than 30 s ($n = 21$), the observation was terminated and not included in the analysis.

During each observation, I recorded the frequency and duration of the following behaviours: perching, preening, flight-hunting, changing perches, hovering, successful prey capture, unsuccessful prey capture, flying with prey, and eating. I also recorded perch type and height, the distance traveled between perches, the type of prey captured (earthworm, orthopteran, unknown invertebrate, mammal, frog, snake, or bird), and the distance traveled to capture prey (measured using a metre tape).

Weather data

I measured ambient temperature with a sling psychrometer and wind speed with a hand-held cup anemometer and estimated cloud cover visually. I measured weather at 1-h intervals on 57 of 120 days during winter and obtained weather data collected at the Allentown–Bethlehem–Easton Airport (35 km from the center of the study site; National Climatic Data Center (NCDC) 1994, 1995) for other days. To correct these NCDC data for differences from my study site, I used linear regression of site-measured versus NCDC data to derive correction equations; I then used these correction equations to correct all NCDC data for differences from my site and used corrected data to calculate energy budgets (summary statistics, Table 1). In analyses, I divided weather data into categories that correlate with kestrel winter foraging behaviour (Bildstein 1987): temperatures <0°C, between 0 and 6°C, or >0°C; wind speed <2.23 m·s⁻¹, between 2.23 and 4.46 m·s⁻¹, between 4.46 and 6.69 m·s⁻¹, or >6.69 m·s⁻¹; cloud cover <50%, between 50 and 90%, or >90%.

Energy budgets

I calculated winter energy budgets of kestrels by integrating the field observations of male and female kestrel behaviour (activity budgets, predation success, prey selection) reported in this paper with published equations of the energy costs of

flight and thermoregulation of American kestrels (Gessaman and Haggas 1987), a technique applied to free-living American kestrels (Koplin et al. 1980; Gessaman and Haggas 1987) and other closely related species (Eurasian kestrels, *Falco tinnunculus*, Masman et al. 1988; ferruginous hawks, *Buteo regalis*, Wakeley 1978; bald eagles, *Haliaeetus leucocephalus*, Stahlmaster 1983).

I calculated American kestrel energy budgets in two discrete parts: daily energy expenditure (DEE; kJ per bird per day) and daily energy intake (DEI; kJ per bird per day) (see Appendix A). Calculations were made using a program written in FORTRAN (Fortran Powerstation 4.0, Microsoft Corporation, Redmond, Washington).

DEE, the total energy expended in a 24-h period, is the sum of energy expended for basal metabolism, thermoregulation, and flight activity during the day, or basal metabolism and thermoregulation while roosting at night. Each component comprised an activity-specific mass-sensitive metabolic rate measured on captive American kestrels in a laboratory (Gessaman and Haggas 1987) and a time budget, both of which are sensitive to temperature, wind speed, and cloud cover. DEI per 24-h period was calculated using an equation from Koplin et al. (1980). The number of prey captured per hour was derived from behavioural observations and is influenced by temperature, wind speed, and cloud cover. Energetic calculations are described in Appendix A.

Statistical analyses

I compared kestrel time budgets using ANOVA and Wilcoxon's ranked-sum tests on raw data (seconds or frequency per 20-min observation). I used χ^2 and Fisher's exact tests to determine male versus female differences in predation success and diet composition. All behavioural analyses were conducted as a function of weather conditions, because prey availability to kestrels varies with environmental conditions (Bildstein 1987). I averaged predatory movements (number of perch changes, distance between perches) for each observation and made comparisons using t tests. I compared male and female body condition changes using ANOVA. Because I intended my model to make relative rather than absolute predictions, I present a ratio of female value/male value, whenever absolute model output is given.

Results

Predatory behaviour and body condition

The measure of body condition, viz. the residual of a regression of body mass against body size, was larger for female than for male kestrels (females, 6.337 ± 1.05 (mean ± SE), n = 130; males, −1.941 ± 1.137, n = 105; $F_{[7,226]}$ = 29.50, $P < 0.001$). Male kestrels captured later in the winter had a lower average body condition value than did males captured earlier, while female kestrels showed no change in average body condition value over winter (month, $F_{[3,227]}$ = 4.55, P = 0.004; sex vs. month interaction, $F_{[3,227]}$ = 3.01, P = 0.03; Fig. 1).

Two low-energy activities, perching and preening, together comprise the majority of daytime activities for both males and females (>81% for both sexes); however, males spent slightly more time in flight than did females (Table 2). Males and females showed similar patterns for time flying through-

Fig. 1. Changes in body condition of American kestrels, *Falco sparverius*, captured during November–February 1991–1995 on the study site in Berks and Lehigh counties, southeastern Pennsylvania.
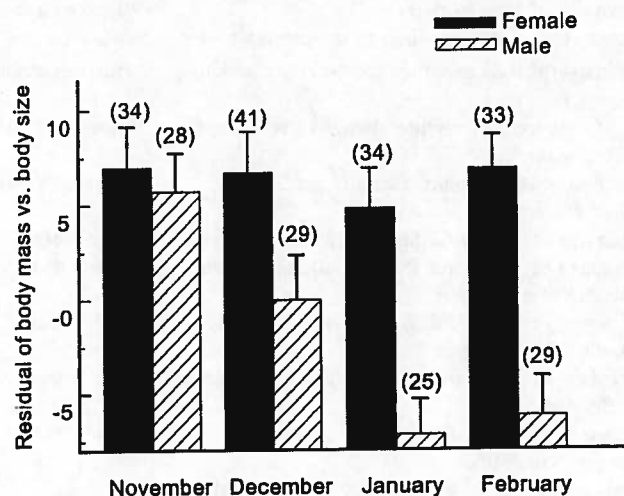
out the day, with peaks of activity in morning and evening (sex vs. time interaction, $F_{[1,146]}$ = 0.68, P = 0.61). Flight time decreased with decreasing temperature for both sexes ($F_{[1,146]}$ = 4.47, P = 0.04), with males exhibiting a greater decline than females when temperatures dropped below 0°C (Table 2). Flight activity decreased in both sexes as cloud cover increased ($F_{[3,142]}$ = 2.98, P = 0.03). Females spent more time hovering than did males when wind speeds were greater than 16 km·h^{-1} ($F_{[1,148]}$ = 4.58, $P < 0.01$).

Time spent in predatory behaviour (flight-hunting, hovering, and predation attempts) did not vary throughout the day, with changes in temperature, or between the sexes (Fs < 2.08, all Ps > 0.12). However, female kestrels spent more time unsuccessfully attacking prey and had more unsuccessful capture attempts per 20-min observation than did males (Table 2). There were no sex-related differences in time spent successfully capturing prey (P > 0.10) or in the number of successful capture attempts (Table 2).

Predation success varied with environmental conditions ($\chi^2_{[2]}$ = 16.1, P < 0.001), with males showing a decrease in capture success when invertebrates were no longer available (e.g., when temperatures were below 0°C). Overall, males were more successful at capturing prey than were females; males were especially more successful at capturing prey from perches than were females; and both sexes were equally successful at capturing prey from hovers (Table 2).

Females and males had different diets ($\chi^2_{[2]}$ = 8.312, P = 0.01, N = 54). Females captured more small mammals (primarily voles, *Microtus* spp.) than did males; males captured more invertebrate prey (primarily orthopterans and annelids) than did females. Invertebrate prey are easier for kestrels to capture and handle than are small mammals (Bildstein and Collopy 1987), and differences in prey selection and availability may have influenced capture success. Sexes differed most in capture success during midday hours (Table 2), presumably when invertebrates are most active. In temperatures below 0°C, when invertebrates are not active, there was no difference between males and females in capture success (Table 2). I detected no difference between males and fe-

Table 2. Comparisons of behaviour of male and female American kestrels, *Falco sparverius*, measured during behavioural observations.

Variable	Test	Female[a]	Male[a]	Test statistic	P
Percentage of time in flight	Wilcoxon's ranked-sum	9 (1)	6 (1)	$Z = 1.484$	0.07
Percent change in flight time in temperatures <0°C	ANOVA	−61.2	−49.3	$F_{[1,146]} = 3.15$	0.04
Percentage of time spent unsuccessfully attacking prey	Wilcoxon's ranked-sum	1.4 (1)	0.6 (1)	$Z = 2.23$	0.03
No. of unsuccessful capture attempts per 20-min observation	Wilcoxon's ranked-sum	0.95 (0.17)	0.51 (0.11)	$Z = 2.10$	<0.05
No. of successful capture attempts per 20-min observation	Wilcoxon's ranked-sum	0.26 (0.07)	0.45 (0.15)	$Z = -0.207$	0.84
Percentage of successful foraging attempts	Fisher's exact	22	47		<0.001
Percentage of successful foraging attempts while hunting from a perch	Fisher's exact	22	48		<0.001
Percentage of successful foraging attempts while hunting from a hover	Fisher's exact	23	25		0.48
Percentage of successful foraging attempts between 11:00 and 13:00	Fisher's exact	15	63		0.002
Percentage of successful foraging attempts in temperatures <0°C	Fisher's exact	12	17		0.46
Distance flown from perch to capture prey (m)	t	23.6 (2.76)	24.8 (2.80)	$t = 0.32$	0.76
No. of of perch changes per 20-min observation	t	4.03 (0.37)	3.49 (0.32)	$t = 1.09$	0.27
Distance moved between perches (m)	t	55.5 (5.28)	49.7 (4.21)	$t = 0.85$	0.39

Note: Values are given as the mean, with SE in parentheses.

males in the distance flown from perches to capture prey, in the distance moved from perch to perch, or in the number of times they changed perches per 20-min observation (Table 2).

Energy budgets

I calculated mean DEE to be 248 ± 2.1 kJ per bird per day (mean ± SE) for female kestrels and 195 ± 2.5 kJ per bird per day for male kestrels (female/male ratio 1.27). Overall and on a per gram mass basis, male and female kestrels exhibited differences in DEE and its components (Table 3). Owing to their smaller mass, male kestrels had a higher estimated nonflight metabolic rate (NFMR) than females (NFMR: females, 73.5 kJ·h⁻¹·kg⁻¹, males, 76.7 kJ·h⁻¹·kg⁻¹; ratio 0.95).

Differences in energy expenditure were greater than expected by differences in mass alone. Males spent less time flying per hour than did females (females 9.9 ± 0.2% (mean ± SE) time flying/h; males 3.5 ± 0.01% time flying/h), which led to lower flight energy expenditure (FEE) and higher nonflight energy expenditure (energy expended during daylight hours while not flying; hereinafter NFEE) for males than for females. When identical masses for males and females are used in calculations to control for mass differences (135 g), energetic differences are still seen in all components except nighttime energy expenditure (hereinafter NEE) (male/female ratio: DEE, 1.16; NFEE, 0.93; FEE, 3.2).

I estimated mean DEI to be 537 ± 16 kJ per bird per day (mean ± SE) for females and 322 ± 8 kJ per bird per day for males (ratio 1.67). Both sexes received most of their DEI from small mammals (females >99%, males 92%). Overall, and on a per gram mass basis, males received more energy from invertebrates than did females (females <0.01%, males 8%). Intake from small mammals captured from perches increased as temperature increased, with females experiencing a greater increase than males (Table 3). Intake from invertebrates captured from perches increased with increasing tem-

perature, with males experiencing a greater increase than females (Table 3).

Energy from small mammals captured while hover-hunting increased as wind speed increased (Table 3). Females began increasing hover-hunting intake in wind speeds above 2.2 m·s⁻¹, while males did not increase intake until wind speeds reached 4.5 m·s⁻¹. Females showed no change in hover-hunting intake with increasing temperatures, while males decreased hover-hunting intake by 33%, likely owing to a shift to capturing invertebrates. On some days, prey captured from hover-hunting comprised 50% of female DEI, but hover-hunting never contributed more than 22% to DEI for males.

Females maintained a higher energy surplus on a per gram mass basis (females, 288 ± 16 kJ/day (mean ± SE); males, 127 ± 8 kJ/day, ratio 2.27; Table 3). Overall, males and females showed a difference in the number of days with a negative energy deficit (females 11%, males 15%). However, when mean daily temperatures are below 0°C, males are more likely to experience a negative energy deficit than are females ($\chi^2_{[1]} = 8.3$, $P < 0.01$). Female kestrels maintained a larger positive energy surplus relative to daily energy expenditures on more days than did males ($\chi^2_{[5]} = 14.534$, $P = 0.013$).

As temperature increased, net energy surplus increased for both sexes. In temperatures below 0°C, male intake and expenditure were approximately equal, while females maintained a positive energy surplus (Table 3). Increasing wind speed caused an initial rise in energy surplus owing to increased returns from hover-hunting, but leveled off as thermoregulatory demands in high winds equalized gains in foraging efficiency.

Discussion

I found support for the prediction that female kestrels would maintain energy surpluses larger than those expected by body-mass differences alone. This sex-related difference

Table 3. Estimates (kJ per bird per day) of energy expenditure and intake of nonbreeding American kestrels (*Falco sparverius*) from energetics calculations.

Component[a]	Female	Male	Ratio[b]
Daily energy expenditure	248.43	194.87	1.27
Nighttime energy expenditure	82.06	72.89	1.12
Nonflight energy expenditure	103.20	102.07	1.01
Flight energy expenditure	63.24	19.89	3.17
Daily energy intake	536.81	321.72	1.67
From vertebrates while hunting from a perch	440.24	251.04	1.75
Temperature $\leq 0°C$	317.94	155.31	2.05
$0°C <$ temperature $\leq 6°C$	339.28	214.72	1.58
Temperature $>6°C$	619.65	328.61	1.89
From invertebrates while hunting from a perch	10.21	26.11	0.39
Temperature $\leq 0°C$	2.38	3.77	0.63
$0°C <$ temperature $\leq 6°C$	9.96	22.26	0.45
Temperature $>6°C$	12.59	37.45	0.34
From vertebrates while hunting from a perch	86.32	44.56	1.93
Wind speed ≤ 2.23 m·s^{-1}	37.49	1.80	20.83
2.23 m·s^{-1} < wind speed ≤ 4.46 m·s^{-1}	85.48	22.22	3.85
4.46 m·s^{-1} < wind speed ≤ 6.69 m·s^{-1}	84.31	76.61	1.10
Wind speed >6.69 m·s^{-1}	78.62	95.06	0.82
Net energy surplus or deficit	288.37	126.85	2.27
Temperature $\leq 0°C$	141.34	−3.45	40.97
$0°C <$ temperature $\leq 6°C$	181.70	81.36	2.23
Temperature $>6°C$	482.71	226.63	2.13

[a]See the text for a description of energetic component.
[b]Female value / male value.

in energetics appears to be due primarily to an interaction of behaviour, ecology, and habitat. Females spend more time in flight than males, so that even when mass is equal in energetic calculations, females still expend more energy. However, this behavioural difference is moderated by differential access to high-quality habitat. On average, areas used by females have a higher quantity and quality of foraging habitats than do areas used by males (Ardia and Bildstein 2001). Thus, even though females invest more energy in foraging (e.g., spend more time in flight), they generate larger foraging returns and, consequently, have larger net energy surpluses than do males.

The magnitude of the male–female difference in energy balance varies depending on temperature. When temperatures are high, both males and females maintain energy surpluses because thermoregulatory demands are low and prey is sufficiently available. Males eat both invertebrate and vertebrate prey but females have higher returns from vertebrate prey and, consequently, have larger net energy balances. In lower temperatures (<0°C), when invertebrates are unavailable, males respond behaviourally by expending more energy, but they have lower foraging returns on investment than do females and, consequently, males have much smaller net energy surpluses. This is particularly exacerbated when wind speeds are low, because females begin hover-hunting at lower wind speeds than males.

In this study, I found support for the hypothesis that sex-related behavioural dominance can lead to energetic consequences for the subordinate sex. In a previous study, I found that male American kestrels used less-preferred areas as wintering habitat, in part because females exclude them from more-preferred areas (Ardia and Bildstein 1997). Here, I found that males may suffer energetic consequences due to

this behavioural dominance by females. Over the course of five winters, mean body condition values were lower for male than for female kestrels and, more importantly, the mean body condition of male kestrels decreased over winter while that of females did not.

This suggests that if energy returns are based solely on habitat, males are always generating lower returns than females and may have lower over-winter survival rates from a higher risk of starvation and predation than do females. If males are suffering consequences, an adaptive response to these suboptimal conditions may be constrained by the need to balance many factors: nonbreeding survival and condition, breeding site and mate acquisition, and foraging ability. Males are under pressure to winter farther north to secure breeding sites and may be forced to accept less-preferred nonbreeding habitats to maximize breeding opportunities (Ketterson and Nolan 1983).

However, because males and females are influenced by different life-history pressures (e.g., mate attraction, territory defense, parental effort), the fitness effect to males of female dominance is unclear. Because males need to attract mates, and many winter residents also breed at my study site, males may be decreasing body condition to signal quality to females. In addition, male raptors are generally more efficient hunters than females (Temeles 1985); males may be able to or may need to maintain a lower ratio of mass to body size than do females. Thus, the seasonal decrease in body condition in males may be an adaptive response for breeding, whereas for females, it would not be (Witter and Cuthill 1993). However, adaptive mass loss seems unlikely; low energy returns may negatively affect early breeding condition and plumage characters in males, both of which affect reproductive success (Bortolotti and Iko 1992; Wiehn 1997). In

addition, the immediate trade-offs among winter condition, survival, and timing of breeding would most likely overwhelm strong selection on reproductive condition. The critical experiment to test whether the body condition of males is affected by habitat use would be a territorial removal experiment similar to that in Ardia and Bildstein (1997), in which individual males and females were followed through time in open and less-open habitats.

One conundrum of this research is that if females are generating such large surpluses, why did I not observe large increases in body condition in female kestrels? One possible explanation is that kestrels cache vertebrate prey, although I rarely observed kestrels retrieving cached prey. Given that the energetics model assumes that all of a prey item is consumed, it may overestimate intake, as many prey items may not be completely consumed. Also, the body-condition measure reported here is not from changes in individual birds over time, rather it is from the sample of birds available to be captured within a given month. Individuals showing increases in body condition may move away from the study area or may be less likely to be captured. Thus, females may indeed be translating energy surpluses into body-condition increases but, owing to the resolution of my study, I was unable to detect it.

My study illustrates that competition between the sexes leads to important ecological consequences. Differences in fitness among individuals and habitats due to behavioural dominance may have important life-history consequences (Morton et al. 1987; Marra and Holberton 1998). Yet within the constraints of counteracting selection pressures, individuals may be acting optimally for a given habitat type. However, when dominance and competitive interactions are between the sexes, trade-offs and consequences become more complicated, and the long-term effects on sex ratio and population regulation are only beginning to be elucidated (Marra and Holmes 2001).

Acknowledgements

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Appendix A

Energy budgets were calculated in two discrete parts: daily energy expenditure (DEE; kJ per bird per day) and daily energy intake (DEI; kJ per bird per day). DEE was estimated using responses of kestrel behaviour measured empirically in this study, combined with published equations of energy costs from Gessaman and Haggas (1987). DEI was estimated using prey capture rates measured empirically in this study and a modification of Koplin et al. (1980).

Calculations were made for each hour of winter and were driven by the following weather input variables: ambient temperature, wind speed, cloud cover, and solar radiation. In addition to affecting thermal budgets, weather conditions determined the percentage of time not flying and prey captures per hour for each sex. Parameters used in the model are given in Table A1.

DEE was calculated using the following equations:

$$[A1] \quad \text{DEE}_{\text{hour}} = (M)[(T_{\text{NF}})(\text{NFMR}) + (T_F)(\text{FMR}) + (T_R)(\text{RMR})]$$

where M is mass (kg), T_{NF} is time not flying (min·h^{-1}), T_F is time flying (min·h^{-1}), T_R is time roosting (min·h^{-1}), NFMR is nonflight metabolic rate (kJ·h^{-1}·kg^{-1}), FMR is flight metabolic rate (kJ·h^{-1}·kg^{-1}), and RMR is resting metabolic rate (kJ·h^{-1}·kg^{-1}).

$$[A2] \quad \text{NFMR} = 104.569 - 204.6M - 1.2837T - 19.9677Q + 4.8903U^{0.5}$$

where M is mass (kg), T is ambient temperature (°C), Q is solar flux (kJ·cm^{-2}·min^{-1}), and U is wind speed (m·s^{-1}).

$$[A3] \quad \text{RMR} = -1.1046T + 55.69M$$

where M is mass (kg) and T is ambient temperature (°C).

DEI was calculated using the following equations:

$$[A4] \quad \text{DEI}_{\text{hour}} = (N_i)(C_i)(\text{DM}_i)$$

where N_i is the quantity of prey (prey items/h), C_i is the caloric content of prey (kJ·g dry mass^{-1}), and DM$_i$ is dry mass consumed (g dry mass/prey item).

$$[A5] \quad \text{DM}_i = (\text{WM}_i)(P_i)(A_i)(R_i)$$

where WM$_i$ is wet mass of prey (g/prey item), P_i is the percentage of prey consumed, A_i is assimilation efficiency, and R_i is the ratio of wet to dry mass.

Table A1. Energetic parameters used in energy-budget calculations.

Parameter	Description	Value	Source
FMR_{male}	Flight metabolic rate ($kJ \cdot h^{-1}$)	46.8	Gessaman and Haggas 1987
FMR_{female}	Flight metabolic rate ($kJ \cdot h^{-1}$)	53.1	Gessaman and Haggas 1987
C_{mam}	Energy content of mammalian prey ($kJ \cdot g$ dry mass^{-1})	19.7	Cumins and Weycheck 1971
C_{inv}	Energy content of invertebrate prey ($kJ \cdot g$ dry mass^{-1})	20.9	Cumins and Weycheck 1971
WM_{mam}	Wet mass of mammalian prey (g/individual)	33.0	Ingraldi 1992
WM_{inv}	Wet mass of invertebrate prey (g/individual)	3.3	Meyer and Balgooyen 1987
P_{mam}	Percentage of mammalian prey consumed	0.80	Ingraldi 1992
P_{inv}	Percentage of invertebrate prey consumed	0.85	Koplin et al. 1980
A_{mam}	Assimilation efficiency eating mammalian prey	0.76	Koplin et al. 1980
A_{inv}	Assimilation efficiency eating invertebrate prey	0.86	Koplin et al. 1980
R_{mam}	Ratio of dry to wet mass, mammals	0.2	Unpublished data
R_{inv}	Ratio of dry to wet mass, invertebrates	0.1	Unpublished data