# Sex-related differences in habitat selection in wintering American kestrels, *Falco sparverius*

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**Abstract.** The American kestrel, *Falco sparverius*, has sex-related differences in habitat use during the non-breeding season, with females occupying more open habitats than males. Two competing hypotheses have been proposed to explain this phenomenon: (1) males and females prefer different habitats, and (2) males and females prefer similar habitats, but larger females exclude smaller males from preferred areas. This study experimentally investigated habitat selection in wintering kestrels by temporarily removing kestrels from areas, and then observing the numbers and sex of the kestrels that occupied vacated areas. The home ranges of 20 birds (10 males and 10 females) were mapped and their occupants removed. Areas vacated in early winter (November 1994) were filled more quickly than those vacated in late winter (February 1995). Areas previously held by females were reoccupied more frequently than were those previously occupied by males. Female kestrels reoccupied vacated female areas more than vacated male areas. Male kestrels reoccupied vacated female and male areas equally. The results demonstrate that (1) high-quality kestrel habitat may be limited in the non-breeding season, (2) vacated areas are more likely to be reoccupied in the early winter than in late winter, (3) female kestrels appear at an advantage relative to males in occupying scarce and competed-for areas, and (4) male kestrels will use female areas when female occupants have been removed. It is hypothesized that open habitats are preferred over less open habitats because the former offer reduced risk of predation from bird-eating hawks.

Differences in the ecological and reproductive roles of males and females frequently lead to differences in both foraging behaviour (e.g. spiders, *Phidippus audax*: Givens 1978; weasels, family Mustelidae: Erlinge 1979; ambush bugs, family Phymatidae: Mason 1986; Gulf Coast fiddler crab, *Uca panacea*: Caravello & Cameron 1987; moose, *Alces alces*: Bartosiewicz 1987) and predation risk (Selander 1972; Power 1980; Shine 1989). These differences can cause males and females to use different habitats (birds: Selander 1966; reptiles: Schoener 1977; isopods, *Idotea baltica*: Jormalainen & Tuomi 1989; snowshoe hares, *Lepus americanus*: Litvaitis 1990, fallow

deer, *Dama dama*: Thirgood 1995). Either can result because the two sexes are adapted to different habitat types (Hulscher & Ens 1992; Whitehead & Tschirner 1992) or because one sex forces the other to occupy sub-optimal habitats (Peters & Grubb 1983; Hepp & Hair 1984; Carpenter et al. 1993).

Sex-related differences in habitat use are well studied in the smallest North American falcon, the American kestrel, *Falco sparverius* (Koplin 1973; Mills 1975, 1976; Stinson et al. 1981; Bildstein 1987; Meyer & Balgooyen 1987; Smallwood 1988). Kestrels frequently maintain areas of exclusive use in the winter (Cade 1955; Smallwood 1987; personal observation). Although both males and females occupy agricultural and grassland habitats, females usually use more open areas than do males. The amount of woody vegetation contained within male and female habitats

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appears to be the major difference in habitat types used. Two hypotheses have been proposed to explain the phenomenon of differential winter habitat use by male and female kestrels: (1) males and females prefer different habitat types (Koplin 1973; Meyer & Balgooyen 1987); (2) males and females prefer the same habitat type, but females, which are larger than males, exclude the latter from preferred sites (Mills 1976; Smallwood 1988).

Female kestrels are 10–15% heavier than males (Bird 1988). This difference, which may contribute to ecological and energetic differences between the sexes, has been used to support the hypothesis that male and female kestrels prefer different winter habitats (Koplin 1973; Meyer & Balgooyen 1987). Size dimorphism may have initially evolved for reasons other than differential habitat use, however (Snyder & Wiley 1976; Bildstein 1992).

In the present study, both female and male kestrels foraged mainly over vegetation less than 25 cm high (>97.5% of capture attempts for both sexes), as is true for wintering kestrels elsewhere (Smallwood 1987; see summary in Bildstein & Collopy 1987). Open areas used by female kestrels contain a larger proportion of suitable short vegetation for hunting, leading some workers to suggest that such areas are of higher quality than the semi-open areas used by male kestrels. Open areas also may provide an advantage independent of hunting substrate. Kestrels are vulnerable to predation from larger raptors (McAtee 1935; Kirkpatrick 1980; Bird 1988). Sympatric species such as Cooper's hawks, *Accipiter cooperi*, are common along field edges and shelterbelts (Rosenfield 1988), which are frequently also used by male kestrels. Kestrels in open areas probably come in contact with fewer of these stealth-hunting predators, and should be able to detect them better in open areas as well. On the other hand, woody vegetation may benefit wintering male kestrels. Male kestrels eat more birds than do female kestrels (Mills 1976; Bildstein & Collopy 1987), and semi-open areas may provide cover from which to ambush small birds. Semi-open areas also may provide a more suitable winter microclimate for the smaller males.

If open areas are of higher quality to both sexes, either because of increased prey availability or reduced predation risk, both males and females should prefer such areas. Female birds of prey often dominate their male counterparts

(Gauthreaux 1978; Mueller & Meyer 1985), and female kestrels dominate male kestrels in experimental settings as adults (Cade 1955) and as nestlings (Sherman 1913; Roest 1957). Habitat segregation may thus occur through females actively excluding males from high-quality areas (Mills 1976; Smallwood 1988).

On the other hand, differential timing of migration may result in habitat segregation in winter (Smallwood 1988). In central Florida, kestrels that arrive earliest on the wintering grounds occupy the highest quality areas, and, in general, females arrive earlier than do males (Smallwood 1988; see also Stotz & Goodrich 1989). A similar explanation for observed differences in habitat use has been proposed for dark-eyed juncos, *Junco hyemalis* (Ketterson & Nolan 1983). If males and females have similar habitat preferences, female kestrels may exclude males simply by arriving earlier. When Smallwood (1988) released 'intruder' kestrels into areas already occupied by kestrels, he found that the occupants, regardless of their sex, were able to expel the intruder. Although Smallwood's experiment does not directly replicate a natural situation, it does support the notion that prior occupancy may be important in habitat use.

Experimental removals have been used to examine sex-related differences in habitat use in hooded warblers, *Wilsonia citrina* (Morton et al. 1987), downy woodpeckers, *Picoides pubescens* (Peters & Grubb 1983), and American redstarts, *Setophaga ruticilla* (Marra et al. 1993). Here we report the results of a similar experiment with American kestrels. We conducted our removal experiments in both early and late winter to determine whether the likelihood of reoccupation following creation of a vacancy decreased over the course of the winter.

Our protocol was designed to test for differences within and between time periods and between the sexes to distinguish between two hypotheses: that males and females prefer different habitat types, or that males and females prefer similar habitat types but females exclude males from preferred areas. A pattern of only females occupying vacated females areas and only males occupying vacated males areas would support the first hypothesis. A pattern of both males and females using vacated female areas and no females using vacated male areas would support the second hypothesis.

## METHODS

### Removal Experiment

We conducted our experiments in early winter (November 1994) and late winter (February 1995) in farmlands in Berks, Lehigh and Schuylkill counties, southeastern Pennsylvania, U.S.A. The 800-km² study area, which is bordered by the southeastern ridge of the central Appalachian mountains on the northwest and the Atlantic coastal plain on the southeast, comprised a patchwork of rolling hills and farmland consisting primarily of cut agricultural land (corn, *Zea mays*, soybean, *Glycine max*, and alfalfa, *Medicago sativa*) broken by small woodlots and orchards.

Between 70 and 100 pairs of kestrels nest annually in the area in approximately 200 nest boxes that have been erected for their use (Apanius 1991; Rohrbaugh 1994). In winter, the study area is inhabited by both year-round residents and winter visitors (C. J. Robertson & S. Robertson, unpublished data). The sex ratio of wintering kestrels in the area approximates unity (173 females and 194 males seen on 3060 km of roadside counts over 60 days in winter 1994–1995). Data collected as part of a concurrent study and in previous years indicate that, by November, kestrels overwintering in the area have established areas of winter use (D. Ardia, unpublished data; C. J. Robertson & S. Robertson, unpublished data)

For the purposes of our removal experiment, kestrels were encountered by driving around rural roads at 15–45 km/h. Individual birds were observed from an automobile with × 8 binoculars and a × 15–45 telescope to map their areas. Areas where kestrels spent time, including perches, were recorded on maps denoting major landmarks and vegetative features. If a bird was lost from sight for more than 10 min, the observation was aborted and the data were not used in our analyses. We observed 20 birds for at least 4 h ($\bar{X} \pm$ SE $= 270.5 = 6.0$ min, $N=20$). We classified areas by the sex of the occupant, and refer to such areas as 'male' areas and 'female' areas. Sizes of home ranges varied from 2 to 6 hectares.

As soon as possible after the minimum 4 h observation period, birds were captured using a wire bal-chatri trap (Berger & Mueller 1959) baited with two house mice, *Mus musculus*. Birds were transported to Hawk Mountain Sanctuary, Pennsylvania, U.S.A., where they were main-tained in separate cages for up to 7 days. Birds were fed and watered daily. All birds were released at their site of capture. The home ranges of the 20 captured kestrels were mapped in early winter 1994 (5 males, 5 females) and late winter 1995 (5 males, 5 females). Birds observed and captured in early winter were not captured again in late winter.

We visited vacated areas twice daily, once between 0800 and 1200 hours, and again between 1300 and 1700 hours for 30 min during each visit. All visits took place while the previous occupant was held in captivity. The location and sex of kestrels seen on or near vacated areas was noted. Kestrels that occupied vacated areas were observed on subsequent visits for two or more days, and individuals observed on vacated areas were captured and colour-banded to facilitate identification. Vacated areas were classified as occupied if another kestrel was seen within its boundaries.

### Statistical Analysis

Data were analysed using the SAS statistical program (SAS Institute 1988). Seasonal and sexual differences were analysed using Fisher's exact tests (Zar 1984). Time to occupancy was analysed with a Wilcoxon rank-sum test (Zar 1984). Areas that remained vacant were not included in the rate of occupancy analysis. All tests were conducted at a significance level of 0.05.

## RESULTS

We rejected the null hypothesis that male and female areas are equally likely to be reoccupied once a kestrel has been removed from them. Our results support the alternative hypothesis that female areas are more likely to be used than are male areas.

The five areas from which females were removed in early winter were reoccupied by four females and three males. Non-overlapping portions of two of the vacated female areas were used simultaneously by two males, and a male and a female, respectively. Three areas from which males had been removed in early winter were reoccupied by three male kestrels. There was no significant difference between the number of

**Table I.** Number of American kestrels that occupied areas from which kestrels had been removed in early winter (November 1994) and late winter (February 1995)

| Time of removal | Sex of previous occupant | Number of vacated areas | | P* |
| | | Reoccupied | Not reoccupied | |
| --- | --- | --- | --- | --- |
| Early winter | Male | 3 | 2 | 0.22 |
| (N=10) | Female | 5 | 0 | |
| Late winter | Male | 0 | 5 | 0.02 |
| (N=10) | Female | 4 | 1 | |
| Early and late winter | Male | 3 | 7 | 0.01 |
| combined (N=20) | Female | 9 | 1 | |

*P*-values are the result of two-tailed 2 × 2 Fisher's exact tests.
Vacated areas were observed following removals for 7 days.

**Table II.** Number of male American kestrels that occupied areas from which kestrels had been removed in early winter (November 1994) and late winter (February 1995)

| Time of removal | Sex of previous occupant | Number of vacated areas | | P* |
| | | Reoccupied by males | Not reoccupied by males | |
| --- | --- | --- | --- | --- |
| Early winter | Male | 3 | 2 | 0.50 |
| (N=10) | Female | 2 | 3 | |
| Late winter | Male | 0 | 5 | 0.22 |
| (N=10) | Female | 2 | 3 | |
| Early and late winter | Male | 3 | 7 | 0.83 |
| combined (N=20) | Female | 4 | 6 | |

*P*-values are the result of 2 × 2 one-tailed Fisher's exact tests developed by a priori predictions that both females and males prefer vacated female areas over vacated male areas.
Vacated areas were observed following removals for 7 days.

vacated male and female areas reoccupied in early winter (Table I). Four female areas vacated in late winter were reoccupied by two females and two males. None of the five male areas vacated in late winter were reoccupied (Table I). Overall, nine kestrels used vacated female areas, and three kestrels occupied vacated male areas (Table I).

We rejected the null hypothesis that both male and female areas are equally likely to be used by both sexes. Our results support the alternative hypothesis that female areas are used by both sexes, but male areas are not. Male kestrels occupied both male and female areas equally (Table II). Female kestrels occupied only female areas (Table III).

Eight areas (five female, three male) were reoccupied in the early winter, but only four vacant areas (all female) were reoccupied in late winter (Table IV).

We rejected the null hypothesis that vacated areas are equally likely to be reoccupied as quickly in early winter as in late winter. Our results support the alternative hypothesis that, in early winter, vacated areas are reoccupied more quickly than they are in late winter. We were unable to reject the null hypothesis that male areas are reoccupied as quickly as are female areas.

Vacated areas were filled more quickly in the early winter than in the late winter (early winter: $\bar{X} \pm$ SE$=1.50=0.76$ days until area reoccupied, $N=8$; late winter: $3.25 \pm 1.26$, $N=4$; Wilcoxon signed ranks test: $Z=2.24$, $N=12$, $P<0.05$). No difference was detected in the time until reoccupation between vacated female and male areas (days until area reoccupied: vacated female areas$=2.11 \pm 0.45$, $N=9$; vacated males areas$=2.00 \pm 0.58$, $N=3$; Wilcoxon signed ranks test: $Z=0$, $N=12$, $P=0.99$).

Table III. Number of female American kestrels that occupied areas from which kestrels had been removed in early winter (November 1994) and late winter (February 1995)

| Time of removal | Sex of previous occupant | Number of vacated areas | | P* |
| | | Reoccupied by females | Not reoccupied by females | |
| --- | --- | --- | --- | --- |
| Early winter | Male | 0 | 5 | 0.02 |
| (N=10) | Female | 4 | 1 | |
| Late winter | Male | 0 | 5 | 0.22 |
| (N=10) | Female | 2 | 3 | |
| Early and late winter | Male | 0 | 10 | <0.01 |
| combined (N=20) | Female | 6 | 4 | |

*P-values are the result of 2 × 2 one-tailed Fisher's exact tests developed by a priori predictions that both females and males prefer vacated female areas over vacated male areas.
Vacated areas were observed following removals for 7 days.

Table IV. Number of American kestrels that occupied areas from which kestrels had been removed in early winter (November 1994) and late winter (February 1995)

| Sex of occupant | Time of removal | Number of vacancies | | P* |
| | | Reoccupied | Not reoccupied | |
| --- | --- | --- | --- | --- |
| Male and female | Early winter | 8 | 2 | 0.09 |
| combined (N=20) | Late winter | 4 | 6 | |

*P-value is the result of one-tailed 2 × 2 Fisher's exact tests based on a priori predictions that areas vacated in early winter are more likely to be reoccupied than those areas vacated in late winter.
Vacated areas were observed following removals for 7 days.

## DISCUSSION

Kestrels reoccupied 12 of 20 vacated areas within 1–6 days in our study site, suggesting that winter habitat availability is limited in southeastern Pennsylvania. That areas vacated in early winter were filled faster than those vacated in late winter suggests that kestrel density is higher in early than in late winter, since birds that remain in the study site throughout the winter generally remain in the same location (D. Ardia, unpublished data; C. J. Robertson & S. Robertson, unpublished data).

Vacated female areas were reoccupied more frequently than were vacated male areas, and female kestrels were more likely to occupy vacated female areas than were male kestrels. Taken together, these results suggest that female areas are more valuable to both male and female kestrels than are male areas, and that females are able to exclude males from such sites.

Although our experiments support the hypothesis that sexual differences in winter habitat use in American kestrels results from females excluding males from preferred habitat types, they do not explain why females exclude males from such sites. Smallwood (1987, 1988) suggested that open habitats might be preferred sites for both male and female kestrels because of the greater hunting opportunities afforded therein. We were, however, unable to detect any differences in the activity budgets of male and female kestrels in the area over the winter of 1994–1995 (D. Ardia, unpublished data). Therefore, female and male areas do not appear to differ greatly in prey availability.

American kestrels are probably less vulnerable to predation by larger bird-eating raptors when in open habitats than when in closed habitats. Cooper's hawks, sharp-shinned hawks, *A. striatus*, and northern goshawks, *A. gentilis*, all of which are more common in edge habitats than in more

open areas (Rosenfield 1988), prey on American kestrels (McAtee 1935; Kirkpatrick 1980; Bird 1988; E. Henckel, personal observation). American kestrels actively avoid these species (Bird 1988). The extent to which these predators affect habitat use in American kestrels has been unexplored.

Our results suggest that predation risk may be important in determining habitat choice in American kestrels. The importance of reducing predation risk varies as a function of predator density and interacts with trade-offs in foraging efficiency (Gilliam & Fraser 1987). If males and females differ in their susceptibility to predation or their ability to reduce the risk of predation, then male and female differences in habitat use may be observed (Power 1980; Slatkin 1984; Jormalainen & Tuomi 1989). In cases where one sex initially forces the other into sub-optimal areas, the subordinate sex may eventually adapt to a less preferred habitat. Our results suggest that this has not yet occurred in American kestrels.

## ACKNOWLEDGMENTS

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deer, *Dama dama*: Thirgood 1995). Either can result because the two sexes are adapted to different habitat types (Hulscher & Ens 1992; Whitehead & Tschirner 1992) or because one sex forces the other to occupy sub-optimal habitats (Peters & Grubb 1983; Hepp & Hair 1984; Carpenter et al. 1993).

Sex-related differences in habitat use are well studied in the smallest North American falcon, the American kestrel, *Falco sparverius* (Koplin 1973; Mills 1975, 1976; Stinson et al. 1981; Bildstein 1987; Meyer & Balgooyen 1987; Smallwood 1988). Kestrels frequently maintain areas of exclusive use in the winter (Cade 1955; Smallwood 1987; personal observation). Although both males and females occupy agricultural and grassland habitats, females usually use more open areas than do males. The amount of woody vegetation contained within male and female habitats

appears to be the major difference in habitat types used. Two hypotheses have been proposed to explain the phenomenon of differential winter habitat use by male and female kestrels: (1) males and females prefer different habitat types (Koplin 1973; Meyer & Balgooyen 1987); (2) males and females prefer the same habitat type, but females, which are larger than males, exclude the latter from preferred sites (Mills 1976; Smallwood 1988).

Female kestrels are 10–15% heavier than males (Bird 1988). This difference, which may contribute to ecological and energetic differences between the sexes, has been used to support the hypothesis that male and female kestrels prefer different winter habitats (Koplin 1973; Meyer & Balgooyen 1987). Size dimorphism may have initially evolved for reasons other than differential habitat use, however (Snyder & Wiley 1976; Bildstein 1992).

In the present study, both female and male kestrels foraged mainly over vegetation less than 25 cm high (>97.5% of capture attempts for both sexes), as is true for wintering kestrels elsewhere (Smallwood 1987; see summary in Bildstein & Collopy 1987). Open areas used by female kestrels contain a larger proportion of suitable short vegetation for hunting, leading some workers to suggest that such areas are of higher quality than the semi-open areas used by male kestrels. Open areas also may provide an advantage independent of hunting substrate. Kestrels are vulnerable to predation from larger raptors (McAtee 1935; Kirkpatrick 1980; Bird 1988). Sympatric species such as Cooper's hawks, *Accipiter cooperi*, are common along field edges and shelterbelts (Rosenfield 1988), which are frequently also used by male kestrels. Kestrels in open areas probably come in contact with fewer of these stealth-hunting predators, and should be able to detect them better in open areas as well. On the other hand, woody vegetation may benefit wintering male kestrels. Male kestrels eat more birds than do female kestrels (Mills 1976; Bildstein & Collopy 1987), and semi-open areas may provide cover from which to ambush small birds. Semi-open areas also may provide a more suitable winter microclimate for the smaller males.

If open areas are of higher quality to both sexes, either because of increased prey availability or reduced predation risk, both males and females should prefer such areas. Female birds of prey often dominate their male counterparts

(Gauthreaux 1978; Mueller & Meyer 1985), and female kestrels dominate male kestrels in experimental settings as adults (Cade 1955) and as nestlings (Sherman 1913; Roest 1957). Habitat segregation may thus occur through females actively excluding males from high-quality areas (Mills 1976; Smallwood 1988).

On the other hand, differential timing of migration may result in habitat segregation in winter (Smallwood 1988). In central Florida, kestrels that arrive earliest on the wintering grounds occupy the highest quality areas, and, in general, females arrive earlier than do males (Smallwood 1988; see also Stotz & Goodrich 1989). A similar explanation for observed differences in habitat use has been proposed for dark-eyed juncos, *Junco hyemalis* (Ketterson & Nolan 1983). If males and females have similar habitat preferences, female kestrels may exclude males simply by arriving earlier. When Smallwood (1988) released 'intruder' kestrels into areas already occupied by kestrels, he found that the occupants, regardless of their sex, were able to expel the intruder. Although Smallwood's experiment does not directly replicate a natural situation, it does support the notion that prior occupancy may be important in habitat use.

Experimental removals have been used to examine sex-related differences in habitat use in hooded warblers, *Wilsonia citrina* (Morton et al. 1987), downy woodpeckers, *Picoides pubescens* (Peters & Grubb 1983), and American redstarts, *Setophaga ruticilla* (Marra et al. 1993). Here we report the results of a similar experiment with American kestrels. We conducted our removal experiments in both early and late winter to determine whether the likelihood of reoccupation following creation of a vacancy decreased over the course of the winter.

Our protocol was designed to test for differences within and between time periods and between the sexes to distinguish between two hypotheses: that males and females prefer different habitat types, or that males and females prefer similar habitat types but females exclude males from preferred areas. A pattern of only females occupying vacated females areas and only males occupying vacated males areas would support the first hypothesis. A pattern of both males and females using vacated female areas and no females using vacated male areas would support the second hypothesis.

## METHODS

### Removal Experiment

We conducted our experiments in early winter (November 1994) and late winter (February 1995) in farmlands in Berks, Lehigh and Schuylkill counties, southeastern Pennsylvania, U.S.A. The 800-km² study area, which is bordered by the southeastern ridge of the central Appalachian mountains on the northwest and the Atlantic coastal plain on the southeast, comprised a patch-work of rolling hills and farmland consisting primarily of cut agricultural land (corn, *Zea mays*, soybean, *Glycine max*, and alfalfa, *Medicago sativa*) broken by small woodlots and orchards.

Between 70 and 100 pairs of kestrels nest annu-ally in the area in approximately 200 nest boxes that have been erected for their use (Apanius 1991; Rohrbaugh 1994). In winter, the study area is inhabited by both year-round residents and winter visitors (C. J. Robertson & S. Robertson, unpub-lished data). The sex ratio of wintering kestrels in the area approximates unity (173 females and 194 males seen on 3060 km of roadside counts over 60 days in winter 1994–1995). Data collected as part of a concurrent study and in previous years indi-cate that, by November, kestrels overwintering in the area have established areas of winter use (D. Ardia, unpublished data; C. J. Robertson & S. Robertson, unpublished data)

For the purposes of our removal experiment, kestrels were encountered by driving around rural roads at 15–45 km/h. Individual birds were observed from an automobile with × 8 binoculars and a × 15–45 telescope to map their areas. Areas where kestrels spent time, including perches, were recorded on maps denoting major landmarks and vegetative features. If a bird was lost from sight for more than 10 min, the observation was aborted and the data were not used in our analy-ses. We observed 20 birds for at least 4 h ($\bar{X} \pm SE = 270.5 \pm 6.0$ min, $N=20$). We classified areas by the sex of the occupant, and refer to such areas as 'male' areas and 'female' areas. Sizes of home ranges varied from 2 to 6 hectares.

As soon as possible after the minimum 4 h observation period, birds were captured using a wire bal-chatri trap (Berger & Mueller 1959) baited with two house mice, *Mus musculus*. Birds were transported to Hawk Mountain Sanctuary, Pennsylvania, U.S.A., where they were main-tained in separate cages for up to 7 days. Birds were fed and watered daily. All birds were released at their site of capture. The home ranges of the 20 captured kestrels were mapped in early winter 1994 (5 males, 5 females) and late winter 1995 (5 males, 5 females). Birds observed and captured in early winter were not captured again in late winter.

We visited vacated areas twice daily, once between 0800 and 1200 hours, and again between 1300 and 1700 hours for 30 min during each visit. All visits took place while the previous occupant was held in captivity. The location and sex of kestrels seen on or near vacated areas was noted. Kestrels that occupied vacated areas were observed on subsequent visits for two or more days, and individuals observed on vacated areas were captured and colour-banded to facilitate identification. Vacated areas were classified as occupied if another kestrel was seen within its boundaries.

### Statistical Analysis

Data were analysed using the SAS statistical program (SAS Institute 1988). Seasonal and sexual differences were analysed using Fisher's exact tests (Zar 1984). Time to occupancy was analysed with a Wilcoxon rank-sum test (Zar 1984). Areas that remained vacant were not included in the rate of occupancy analysis. All tests were conducted at a significance level of 0.05.

## RESULTS

We rejected the null hypothesis that male and female areas are equally likely to be reoccupied once a kestrel has been removed from them. Our results support the alternative hypothesis that female areas are more likely to be used than are male areas.

The five areas from which females were removed in early winter were reoccupied by four females and three males. Non-overlapping por-tions of two of the vacated female areas were used simultaneously by two males, and a male and a female, respectively. Three areas from which males had been removed in early winter were reoccupied by three male kestrels. There was no significant difference between the number of

**Table I.** Number of American kestrels that occupied areas from which kestrels had been removed in early winter (November 1994) and late winter (February 1995)

| Time of removal | Sex of previous occupant | Number of vacated areas | | $P^*$ |
| | | Reoccupied | Not reoccupied | |
| --- | --- | --- | --- | --- |
| Early winter | Male | 3 | 2 | 0.22 |
| ($N$=10) | Female | 5 | 0 | |
| Late winter | Male | 0 | 5 | 0.02 |
| ($N$=10) | Female | 4 | 1 | |
| Early and late winter | Male | 3 | 7 | 0.01 |
| combined ($N$=20) | Female | 9 | 1 | |

*$P$-values are the result of two-tailed 2 × 2 Fisher's exact tests.
Vacated areas were observed following removals for 7 days.

**Table II.** Number of male American kestrels that occupied areas from which kestrels had been removed in early winter (November 1994) and late winter (February 1995)

| Time of removal | Sex of previous occupant | Number of vacated areas | | $P^*$ |
| | | Reoccupied by males | Not reoccupied by males | |
| --- | --- | --- | --- | --- |
| Early winter | Male | 3 | 2 | 0.50 |
| ($N$=10) | Female | 2 | 3 | |
| Late winter | Male | 0 | 5 | 0.22 |
| ($N$=10) | Female | 2 | 3 | |
| Early and late winter | Male | 3 | 7 | 0.83 |
| combined ($N$=20) | Female | 4 | 6 | |

*$P$-values are the result of 2 × 2 one-tailed Fisher's exact tests developed by a priori predictions that both females and males prefer vacated female areas over vacated male areas.
Vacated areas were observed following removals for 7 days.

vacated male and female areas reoccupied in early winter (Table I). Four female areas vacated in late winter were reoccupied by two females and two males. None of the five male areas vacated in late winter were reoccupied (Table I). Overall, nine kestrels used vacated female areas, and three kestrels occupied vacated male areas (Table I).

We rejected the null hypothesis that both male and female areas are equally likely to be used by both sexes. Our results support the alternative hypothesis that female areas are used by both sexes, but male areas are not. Male kestrels occupied both male and female areas equally (Table II). Female kestrels occupied only female areas (Table III).

Eight areas (five female, three male) were reoccupied in the early winter, but only four vacant areas (all female) were reoccupied in late winter (Table IV).

We rejected the null hypothesis that vacated areas are equally likely to be reoccupied as quickly in early winter as in late winter. Our results support the alternative hypothesis that, in early winter, vacated areas are reoccupied more quickly than they are in late winter. We were unable to reject the null hypothesis that male areas are reoccupied as quickly as are female areas.

Vacated areas were filled more quickly in the early winter than in the late winter (early winter: $\bar{X} \pm \text{SE}=1.50 \pm 0.76$ days until area reoccupied, $N$=8; late winter: $3.25 \pm 1.26$, $N$=4; Wilcoxon signed ranks test: $Z$=2.24, $N$=12, $P<0.05$). No difference was detected in the time until reoccupation between vacated female and male areas (days until area reoccupied: vacated female areas= $2.11 \pm 0.45$, $N$=9; vacated males areas=$2.00 \pm 0.58$, $N$=3; Wilcoxon signed ranks test: $Z$=0, $N$=12, $P$=0.99).

**Table III.** Number of female American kestrels that occupied areas from which kestrels had been removed in early winter (November 1994) and late winter (February 1995)

| Time of removal | Sex of previous occupant | Number of vacated areas | | P* |
|---|---|---|---|---|
| | | Reoccupied by females | Not reoccupied by females | |
| Early winter | Male | 0 | 5 | 0.02 |
| (N=10) | Female | 4 | 1 | |
| Late winter | Male | 0 | 5 | 0.22 |
| (N=10) | Female | 2 | 3 | |
| Early and late winter | Male | 0 | 10 | <0.01 |
| combined (N=20) | Female | 6 | 4 | |

*P-values are the result of 2 × 2 one-tailed Fisher's exact tests developed by a priori predictions that both females and males prefer vacated female areas over vacated male areas.
Vacated areas were observed following removals for 7 days.

**Table IV.** Number of American kestrels that occupied areas from which kestrels had been removed in early winter (November 1994) and late winter (February 1995)

| Sex of occupant | Time of removal | Number of vacancies | | P* |
|---|---|---|---|---|
| | | Reoccupied | Not reoccupied | |
| Male and female | Early winter | 8 | 2 | 0.09 |
| combined (N=20) | Late winter | 4 | 6 | |

*P-value is the result of one-tailed 2 × 2 Fisher's exact tests based on a priori predictions that areas vacated in early winter are more likely to be reoccupied than those areas vacated in late winter.
Vacated areas were observed following removals for 7 days.

## DISCUSSION

Kestrels reoccupied 12 of 20 vacated areas within 1–6 days in our study site, suggesting that winter habitat availability is limited in southeastern Pennsylvania. That areas vacated in early winter were filled faster than those vacated in late winter suggests that kestrel density is higher in early than in late winter, since birds that remain in the study site throughout the winter generally remain in the same location (D. Ardia, unpublished data; C. J. Robertson & S. Robertson, unpublished data).

Vacated female areas were reoccupied more frequently than were vacated male areas, and female kestrels were more likely to occupy vacated female areas than were male kestrels. Taken together, these results suggest that female areas are more valuable to both male and female kestrels than are male areas, and that females are able to exclude males from such sites.

Although our experiments support the hypothesis that sexual differences in winter habitat use in American kestrels results from females excluding males from preferred habitat types, they do not explain why females exclude males from such sites. Smallwood (1987, 1988) suggested that open habitats might be preferred sites for both male and female kestrels because of the greater hunting opportunities afforded therein. We were, however, unable to detect any differences in the activity budgets of male and female kestrels in the area over the winter of 1994–1995 (D. Ardia, unpublished data). Therefore, female and male areas do not appear to differ greatly in prey availability.

American kestrels are probably less vulnerable to predation by larger bird-eating raptors when in open habitats than when in closed habitats. Cooper's hawks, sharp-shinned hawks, *A. striatus*, and northern goshawks, *A. gentilis*, all of which are more common in edge habitats than in more