ECOLOGICAL CORRELATES OF MATE REPLACEMENT IN THE AMERICAN KESTREL[1]

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Abstract. During 1983 and 1984 one adult member of 20 pairs of breeding kestrels was removed from the wild during the third week of incubation. We measured several variables, e.g., relative prey abundance, female body condition, territory size, amount of adjacent habitat, and time of removal at each experimental territory. There was no relationship between the date of a removal and the probability of a lost mate being replaced, however, only pairs in which a replacement mate was found early in the season subsequently laid a clutch. Replacement occurred within small territories with high relative prey abundance, and large amounts of suitable, but undefended, habitat nearby. Replacements did not preferentially replace lost mates of females in good body condition. Significant negative correlations occurred between territory size and prey abundance, and between territory size and the amount of suitable, adjacent habitat. This suggests that surplus birds reside on the fringes of territories with high prey densities where competition with breeding birds for food is minimized. We suggest that surplus kestrels may not monitor territories to ensure replacement with the best potential for successful breeding, but that replacement occurs more frequently when mates are lost from territories where surplus birds forage nearby.

Key words: American Kestrel; Falco sparverius; *mate loss; mate replacement; removal experiment; surplus populations; breeding strategies.*

INTRODUCTION

The removal experiment has been an important manipulative tool in avian population studies (see review by Powers 1981). In most cases, only a proportion of the removed birds was replaced. In early removal experiments (Hensley and Cope 1951, Stewart and Aldrich 1951), rapid replacement by male but not female passerines was noted. After compiling anecdotal evidence on mate replacement in raptors, Newton (1979) concluded that most replacements were female, probably because more females were lost due to their greater vulnerability to shooting. Replacement, though, has been noted when either males or females were removed (Powers 1975, Village 1983a). In Red Grouse (*Lagopus lagopus*) differences in replacement rates were related to seasonal differences in removal dates, suggesting that lower winter survival rates by surplus grouse caused lower replacement rates in the spring (Watson and Jenkins 1968).

In most cases, no explanation has been given why only a proportion of those birds removed were replaced. Smith (1978) suggested that surplus birds, or floaters, may monitor such factors as territory quality, relationship to potential mate, and state of health of territorial birds before "deciding" to enter the breeding

system. Replacement of only a proportion of removed female Common Chaffinches (*Fringilla coelebs*) indicated that females could discriminate among the territories offered by the males or among the males themselves (Saether and Fonstad 1981). Dare (1961), however, felt partial replacement in Common Buzzards (*Buteo buteo*) was related to the proximity of potential replacements at the time of mate loss.

If floating birds monitor potential territories to ensure replacement with the best chance for successful breeding, they should evaluate those factors which influence future reproductive success, i.e., female body condition (Newton et al. 1983, Village 1983b), prey availability (Newton 1976, 1979), and time of breeding (Cavé 1968).

Village (1982) proposed that territory size in European Kestrels (*Falco tinnunculus*) depended on the number of floating birds attempting to settle nearby and their persistence in fighting residents. Because floating birds may inhabit suitable, but undefended habitat adjacent to breeding territories (Smith 1978), territory size, as well as its isolation from other territories may relate to the proximity of surplus birds.

Surplus populations of American Kestrels (*Falco sparverius*) are not likely to exist in the form of flocks (pers. observ.), but rather as individuals spending some time in the territories of breeding birds (Smith 1978). The goal of this study was to examine ecological correlates of mate replacement in kestrels. Specifically, to examine factors related to reproductive success and to the proximity of surplus

birds, and to determine their relationship to observed replacement patterns.

STUDY AREA AND METHODS

The study was conducted at the western end of Montreal Island, Ile Perrot, and the eastern sections of Vaudreuil County (45°25'N, 75°05'W) in southwestern Quebec. The predominant kestrel habitat was fallow agricultural fields interspersed with natural hedgerows and small areas of northern hardwoods.

During 1983 and 1984, one adult member of 20 pairs of breeding kestrels was removed from its territory. Removals occurred 23 May to 19 June during both years, and most removals were timed to coincide with the third week of incubation (for detailed methods see Bowman 1985).

During initial pair formation, observations were made to determine locations of both nests and areas where pairs were observed hunting frequently. To assess relative prey abundance at each territory, 5 lines of 10 Victor snaptraps were spaced 15 m apart at an observed hunting site. Trapping grids were placed in areas of similar cover types. Although invertebrate prey abundance was not sampled, small mammal estimates were made early in the breeding season (before 1 May), when most kestrels prey upon vertebrates, and invertebrates are not an important food source. In California, grasshoppers do not become a major dietary item until the third week of June (Balgooyen 1976); in Montreal, grasshoppers do not become abundant until early July. We assumed that vertebrate populations, primarily microtines, represented the most available prey for kestrels during mate replacement. Traps were baited with peanut butter and rolled oats and checked on five consecutive evenings. A relative index of abundance was calculated from snap-trapping according to the formula (U.S.D.I. 1979):

$$\begin{array}{c}\text{Number of} \\ \text{Captures Per} \\ \text{Hundred Trap} \\ \text{Nights}\end{array} = \frac{\text{(Captures)(100)}}{\begin{array}{c}\text{(Trap Nights)} \\ \text{− (Sprung \& Missing Traps)}\end{array}}$$

A bird from each pair was trapped one week prior to the removal of its mate. Each was weighed to the nearest gram using a Pesola 200 g scale and its tarsal length measured to the nearest 0.01 mm with Vernier calipers. Birds were color-banded for individual recognition and released within their territory. A body condition index was calculated by dividing the cubed root of weight by tarsal length (an index to linear measurement). Since female body condition may be important in determining future reproductive success (Newton et al. 1983), only body condition indices of females widowed during male removal experiments were used to test for relationships dealing with the probability of mate replacement.

Removal and replacement dates were measured as the number of consecutive days from the start of the experiments (1 May). For example, a removal effected on 2 June would be recorded as occurring on the 32nd day.

Home range was assessed mainly by spot observation; we noted the location of all kestrels when first seen during each nest visit. Occasionally, an individual was followed during long flights, and locations were noted whenever birds crossed geographic landmarks e.g., roads, fences, hedgerows. The site of the most distant perch used during such flights was observed and recorded. Locations of study birds were plotted on 1:10,000 scale aerial photographs. Home range was determined as the maximum polygon area (MPA) by connecting the outer locations to form a convex polygon (Odum and Kuenzler 1955). The MPA was then measured using either a dot-grid or a compensating polar planimeter.

Sizes of areas determined by these methods are influenced by sample sizes. Within limits, a greater number of plotted locations will yield a greater area (Odum and Kuenzler 1955). Village (1982) determined that for European Kestrels the rate of increase in territory area slowed after 20 locations were plotted. Thus areas calculated from 20 or more locations were assumed to be approaching final range size. To avoid a sample size bias, kestrels were located at least 20 times prior to mate removal.

To estimate the amount of undefended habitat potentially available to surplus birds near breeding territories, areas of suitable habitat were identified on 1:10,000 scale aerial photographs. We considered habitat suitable if it provided adequate foraging areas. Areas such as forest edge, broad expanses of water, and residential areas were considered as boundaries to suitable habitat (Balgooyen 1976). Next, all territories were plotted, including other kestrel pairs with territories known to be located within the study area, on a photo-mosaic of the study area. The amount of suitable, but undefended habitat within a 1 km radius of each territory was estimated using a planimeter.

In order to test significance between replacement and nonreplacement groups, yearly differences were first compared. Distribution functions of data from 1983 and 1984 were

TABLE 1. Sources of bias due to disturbance at different times during incubation: replacement vs. nonreplacement territories ($\bar{x} \pm$ SE).

| Category | Days of incubation prior to: | | Interval between trapping dates |
	Marking of nonremoval	Mate removal	
Replacement ($n = 9$)	10.49 ± 1.6	19.33 ± 2.9	9.0 ± 1.0
Nonreplacement ($n = 11$)	10.09 ± 1.6	19.64 ± 2.4	9.6 ± 2.4

compared using a means and moments program (Texas Instruments Inc. 1977), and means were compared using the Mann-Whitney U-Test (Siegel 1956). Where no differences were found, data from both years were pooled.

RESULTS

To assess the relationship between ecological correlates and the probability of a lost mate being replaced, it was necessary to standardize trapping chronologies at all nests to minimize a bias due to disturbance at different times during incubation (Fyfe and Olendorff 1976). Although all trapping was performed during the third week of incubation, there was some variation due to difficulties encountered trapping specific birds. Using the Mann-Whitney U-Test we found no significant difference in the number of days of incubation prior to the trapping and marking of the nonremoval bird ($U = 43$, $P > 0.05$) nor in the number of days of incubation prior to mate removal ($U = 52.5$, $P > 0.05$) between territories where replacement occurred versus those where it did not. Differences in the interval between marking of a bird and the subsequent removal of its mate may have influenced whether or not a widowed bird acquired a replacement, but we found no significant difference in the interval between marking and removal ($U = 51.5$, $P > 0.05$) at territories where removals resulted in replacement and those that did not (Table 1).

Though all removals occurred during the third week of incubation for each individual pair, the date of removal as it related to the

TABLE 2. Relationship of removal and replacement dates between a) replaced vs. nonreplaced mates and b) laying vs. nonlaying replacement pairs of kestrels ($\bar{x} \pm$ SE).

Category	Removal date (days since 1 May)	Replacement date (days since 1 May)
a) Replaced ($n = 9$)	30.6 ± 6.06	32.0 ± 5.83
Nonreplaced ($n = 11$)	34.9 ± 9.49	—
b) Laying replacements ($n = 4$)	24.8 ± 1.26	27.3 ± 2.63
Nonlaying replacements ($n = 4$)	$35.0 \pm 3.36*$	$36.8 \pm 3.50*$

$*P < 0.05$.

time in the breeding season varied considerably. The mean removal time (days since 1 May) for all birds was 33.0 ± 8.22 days and there was no significant difference ($U = 32.5$, $P > 0.05$) in removal date between territories where replacement occurred and those not experiencing replacement (Table 2). However, among territories where replacement occurred, mate removals made early in the season usually resulted in replacement pairs that laid new clutches, whereas replacements of later removals did not attempt to renest (Table 2). Since the time interval between mate removal and its subsequent replacement date was not significantly different ($U = 22.5$, $P > 0.05$) between replacement pairs subsequently laying (56.5 ± 58.0 hr) and those not laying (34.0 ± 2.83 hr), it follows that the seasonal date of replacement was significantly earlier ($U = 20.5$, $P < 0.05$) at nests where replacements laid a new clutch than where replacements did not (Table 2).

Differences in relative prey abundance and female body condition were tested for samples taken during 1983 and 1984. No significant differences were found in the distributions of the samples based on comparisons of mean variation, kurtosis, and skewness. There was no significant difference ($U = 30.5$, $P < 0.05$) between mean relative prey abundance (captures/100 trap nights) in 1983 (1.06 ± 0.22) and 1984 (1.20 ± 0.30). The female body condition indices were also similar ($U = 40$, $P > 0.05$) between years (1.30 ± 0.01, 1983; 1.32 ± 0.01, 1984). Thus pooling data from both 1983 and 1984 was justified.

Relative prey abundance was significantly higher ($U = 22.5$, $P < 0.05$) at replacement territories than at nonreplacement territories (Table 3). Prey trapped during censuses included meadow voles (*Microtus pennsylvanicus*), short-tailed shrews (*Blarina brevicauda*) and meadow jumping mice (*Zapus hudsonius*), all common prey items of the American Kestrel (Sherrod 1978). Female body condition indices varied only slightly during both years and there was no significant difference ($U = 44.5$, $P > 0.05$) in body condition between females that acquired replacements and those that did not (Table 3). A Spearman's rank correlation test on relative prey abundance and

TABLE 3.   Relationship of 4 ecological variables to mate removal in kestrels: replacement vs. nonreplacement ($\bar{x} \pm$ SE).

Variable	Replacement	Nonreplacement
Relative prey abundance index	1.42 ± 0.59 ($n = 9$)	0.92 ± 0.38 ($n = 11$)*
Female body condition index	1.30 ± 0.05 ($n = 8$)	1.33 ± 0.05 ($n = 8$)
Territory size (km²)	0.19 ± 0.03 ($n = 9$)	0.28 ± 0.10 ($n = 11$)*
Adjacent, suitable habitat (km²)	1.80 ± 0.71 ($n = 9$)	1.36 ± 0.45 ($n = 11$)*

* $P < 0.05$.

female body condition indicated a nonsignificant relationship ($r_s = 0.11$, $n = 16$, $P > 0.1$).

Territory sizes where replacement occurred were significantly smaller ($U = 18.5$, $P < 0.05$), than territories where lost mates were not replaced (Table 3). A Spearman's coefficient of -0.623 ($n = 20$, $P < 0.005$) indicated a highly significant negative correlation between relative prey abundance and territory size (Fig. 1). Territories where replacement occurred also had significantly larger ($U = 27$, $P < 0.05$) areas of suitable, undefended kestrel habitat adjacent to them than did nonreplacement territories (Table 3). A significant negative correlation ($r_s = -0.419$, $n = 20$, $P < 0.05$) also existed between territory size and the amount of adjacent suitable, but undefended kestrel habitat (Fig. 2).

DISCUSSION

Two theories may help explain the replacement of only a proportion of mates lost during removal studies. Either surplus birds cue in on factors influencing their future reproductive potential before "deciding" to replace (Smith 1978, Saether and Fonstad 1981), or replacement merely depends on the proximity of suitable recruits when a mate is lost (Dare 1961). If surplus birds employ the former strategy distinct differences in factors influencing the potential reproductive success of any newly forming pairs should exist between removals that result in replacement and those that do not.

Many breeding studies on raptors have reported a trend for late nesters to produce smaller clutches with fewer viable eggs and to be more prone to complete nest failure (Herbert and Herbert 1965, Cavé 1968, Newton 1976). Given this, surplus birds should invest more time in monitoring potential replacement sites early in the season. Moreover, female body condition may also influence reproductive success (Newton et al. 1983). If, as Smith (1978) suggests, surplus birds judge the state of health of potential mates, they should replace the lost mates of those females in better body condition more frequently. Since no significant differences in time of removal or female body condition existed between replaced and non-

replaced removals, surplus birds did not appear to cue in on these factors prior to replacing a lost mate. The extremely low variability in female body condition may have made this difficult for surplus kestrels to assess but it seems more likely they did not or were not able to assess it at all. Body condition may also allow adult birds to assess their future probability of survival and modify their behavior accordingly (Nur 1984). Variations in female behavior patterns after mate loss (Bowman and Bird, in press) may have influenced whether or not a female acquired a replacement mate, however, these behavioral variations appear unrelated to differences in body condition.

Relative prey abundance, however, was significantly higher within replacement territories. Supporting our findings, European Sparrowhawks (*Accipiter nisus*) had earlier laying dates, larger clutch and brood sizes, more young produced per nest, and greater nestling survival in areas with higher prey densities (Newton 1976, 1979). Surplus birds may have been using prey abundance as a measure of territory quality, or more simply, were trying to maximize their energy intake by residing near areas of abundant prey.

If nonbreeders do not actively monitor territories for replacement potential, their strategy may be to maximize their survival for a future chance at reproduction. Consequently, they should attempt to reach peak body condition by maximizing energy gain and minimizing energy expenditure. Rudolph (1982) reported that kestrels forage to minimize the costs of energy acquisition. Surplus birds should be expected to hunt in areas of high prey densities where they encounter little intraspecific competition from territorial breeders. Thus, breeding territories with high prey densities may have greater numbers of surplus birds nearby, hunting on the fringes of the territory. Since territories in which replacement occurred had higher vertebrate prey densities, we suggest that replacement strongly relates to the proximity of surplus nonbreeding birds foraging in the area.

The mean territory size for all nests (0.24 ± 0.04 km²) during the two years is considerably smaller than those previously reported for
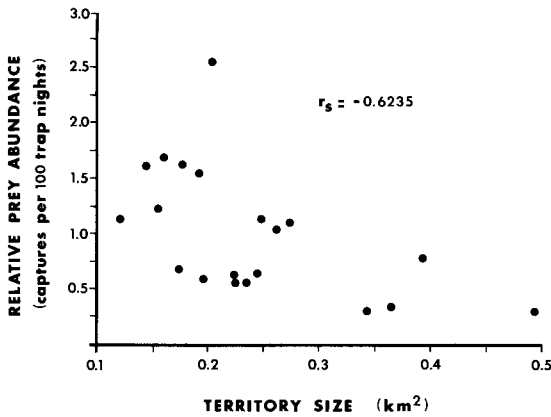
FIGURE 1. Relationship between relative prey abundance (captures per 100 trap nights) and size of breeding kestrel territories.
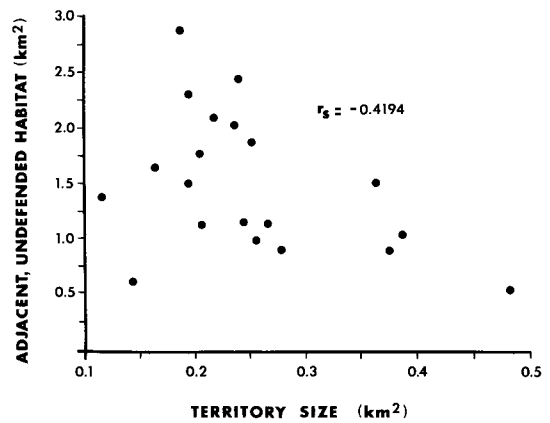

FIGURE 2. Relationship between kestrel breeding territory size and the amount of undefended, but suitable habitat adjacent to them.

American Kestrels. From 1982 to 1984, the mean breeding density of kestrels in our area was 1.7 pairs/km^2 (Bowman and Bird, unpubl.). Breeding densities may have a direct influence on territory size (Village 1982) and studies reporting large territories for kestrels (Craighead and Craighead 1956, Enderson 1960) also reported very low breeding densities. Smith et al. (1972) found breeding densities of 1.98 pairs/km^2 in Utah and reported a small mean home range size of 0.82 km^2. The negative correlation between territory size and relative prey abundance found in this study suggests that differences in territory sizes between studies may relate to regional differences in food availability.

Negative correlations between food supply and territory size have been demonstrated for raptors (Craighead and Craighead 1956, Village 1982) and other avian species (Stenger 1958, Gill and Wolf 1975). Moreover, territory size may be indirectly related to food supply by habitat type, competition from other individuals, and other proximate stimuli (Lack 1954, Myers et al. 1979). Territories where replacement occurred also had larger areas of suitable, undefended habitat adjacent to them. The negative correlation between territory size and the area of suitable adjacent but undefended habitat seems to support Village's (1982) contention that small territory size during good vole years was also due to increased persistence of incomers trying to settle nearby. Village also implied that large territories were due to clumping of nests in areas with suitable nest sites but poor foraging areas. In our study area, nest boxes were uniformly distributed in areas of suitable habitat. Hence, territories should be relatively smaller because kestrels can forage nearby. Where prey densities are low, kestrels must forage farther afield and defend a larger home range. Surplus birds may

be more likely to reside near small territories with high prey densities, but with large areas of suitable undefended habitat nearby. Blue Grouse (*Dendragapus obscurus*) replaced mates more frequently at persistent territorial sites which tend to be better foraging areas than transient, or seasonal territories (Lewis and Zwickel 1980). Mate replacement of kestrels appears to be more frequent when surplus birds are nearby, utilizing abundant prey in suitable undefended areas.

Why kestrels do not appear to have developed a strategy to monitor territories for replacement potential is beyond the scope of this paper, but it may relate to the ability of replacement pairs to renest successfully. Kestrels readily renest following the loss of a clutch early in the incubation period (Bowman and Bird 1985). Though they are known to raise second broods (Toland 1985), there is good evidence that the later in the season a breeding attempt occurs the less likely it will be successful (Cavé 1968). This suggests that replacements attempting renesting later in the season relative to first breeding attempts, should fail more frequently. Of four replacement pairs that laid eggs in this study, none successfully fledged young (Bowman and Bird, in press). Year-long resident species such as the Rufous-collared Sparrow (*Zonotrichia capensis*) studied by Smith (1978) breed year-round and do not experience a sharp seasonal decline in productivity. Thus, they may evolve specific strategies to ensure replacement with the highest potential for reproductive success since they have a high probability of renesting successfully. The benefits to a migratory species such as the kestrel, where breeding is limited by a seasonal availability of resources, may be too low since most late breeding attempts experience high failure rates.

Replacements did not occur more frequently with removals performed earlier in the season, yet only replacements occurring early attempted to lay a new clutch. This supports the idea that the optimal strategy of surplus kestrels may be to optimize survivability for a future chance at breeding, but if the opportunity arises to replace a lost mate, i.e., one is lost at a nearby territory, the experience gained may be sufficient benefit to attempt replacement. Once replacement occurs, however, factors influencing future reproductive success, such as the time of renesting, may influence the replacement's breeding strategy. Widowed birds may cue in on the proximity of surplus birds and modify their behavior accordingly (Bowman and Bird, in press) to increase the probability of successful replacement.

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