

Behavioral strategies of American kestrels during mate replacement

Reed Bowman* and David M. Bird

Macdonald Raptor Research Centre, Macdonald College of McGill University, 21, 111 Lakeshore Rd., Ste-Anne-de-Bellevue, Québec, H9X 1C0, Canada

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Summary. To determine the influence of mate replacement on the behavior and reproductive success of wild American kestrels (*Falco sparverius*) we removed 4 female and 16 male members of breeding pairs during incubation in 1983 and 1984. Eight males and 1 female were replaced within a mean time of 43 h. Widowed females that received a replacement spent less time hunting, but incubated and performed aerial displays more frequently than females that did not receive a replacement. After replacement, widowed females continued to incubate the original clutch, yet copulated and performed other courtship behaviors with the incoming male. Overlapping of normal temporally separate behavioral cues may be a female strategy to gain assistance from a replacement mate. However, none of the original clutches was successfully hatched. Of 8 pairs with replacement males, 2 pairs abandoned their territory, two remained on territory but did not reneest, and 4 reneested within a mean interval of 18 days. The lone female replacement and her mate copulated and performed nest inspections but then abandoned the territory. Incubation behavior was similar between replacement and control pairs; however, replacement males fed more invertebrate prey to nestlings and made many more nest visits. All 3 replacement nests that hatched young failed within 8 days.

Introduction

The existence of surplus populations of nonbreeding birds and their capability of replacing lost members of the breeding population is well docu-

mented. Controlled removal experiments (Hensley and Cope 1951; Stewart and Aldrich 1951) have tested the effects of territorial behavior on population densities of several avian species (Tompa 1962; Watson and Jenkins 1968; Manuwal 1974; Village 1983) as well as the effects of mate loss on male singing performance (Krebs et al. 1981; Saether and Fonstad 1981; Johnson 1983), female reproductive success (Weatherhead 1979), and foraging rates (Powers 1975). In many of the above studies mate replacement was incidental to the primary objective, and little attention was paid to behavioral interactions between the replacement mate and the widowed bird.

Whether replacement birds occasionally behave altruistically remains unresolved (Emlen and Powers 1976; Konecni and Powers 1976). Several studies reporting seemingly altruistic behavior have explained it as “reproductive error” (Powers 1975; Weatherhead and Robertson 1980; Brown 1983), and to date only one study has convincingly eliminated reproductive error as an explanation for observed altruistic behavior (Pierotti 1980).

Newton (1979) provided several anecdotal reports of mate replacement and altruism in raptors, but the only controlled removal experiment involving falconiformes showed that replacements reneested with widowed birds in a non-altruistic fashion (Village 1983).

American kestrels (*Falco sparverius*) have been observed to replace lost mates and reneest (Mayr 1938; Enderson 1960). Moreover, adult kestrel mortality rates of 46–54% (Roest 1957; Henny 1972) indicate that mate loss during breeding may be relatively frequent in this species. Kestrels are relatively common and readily adapt to managed nest box programs (Hamerstrom et al. 1973), thus providing an opportunity to perform controlled removal experiments in a raptor. Hence, our objec-

* *Present address:* National Audubon Society, Ornithological Research Unit, 115 Indian Mound Trail, Tavernier, FL 33070, USA

tives were to determine the existence of surplus populations of non-breeding American kestrels and the frequency with which they replace lost mates. We compared the behavior of widowed birds that received a replacement with those that did not.

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 land interspersed with natural hedgerows and small areas of northern hardwoods.

To test whether surplus populations of non-breeding kestrels existed in the study area, we erected nest boxes late in the season, after the majority of kestrel territories were firmly established. During 1981 and 1982, breeding kestrels generally set up their territories by May 1st; hence experiments were started on that date. To ensure incoming birds were not excluded from experimental nests by existing kestrel pairs, we erected all late nest boxes at least 300 m from the nearest occupied box.

All mate removals were performed between 23 May and 19 June during 1983 and 1984. We chose experimental nests randomly from both established pairs and pairs from late nest box experiments. Four male and 4 female breeding adult kestrels were removed from separate territories in 1983. In 1984 12 additional males were removed to increase sample sizes for statistical comparisons. Logistical problems precluded the removal of additional females. We waited until 10–12 days of incubation to minimize disturbance and possible desertion and then trapped, color-banded, and released the non-removal bird from each pair. Removal birds were trapped after 16–24 days of incubation or as close as possible to 1 week after the trapping of its mate in order to minimize the influence from the initial trapping experience. The normal incubation period in kestrels is 27 days (Porter and Wiemeyer 1972); we avoided removing birds during late incubation to reduce the chance of a widowed bird successfully incubating the clutch unaided.

We trapped kestrels on territory using 1 of 3 methods. Females were trapped on the nest using a telescoping aluminum pole to block the nestbox entrance. Males were captured with a bow-net trap modified from Tordoff (1954) or with a mist-net using a live, trained great horned owl (*Bubo virginianus*) as a decoy. Removal birds were housed at the Macdonald Raptor Research Centre of McGill University and released after the experiments ended.

We conducted one-hour observation sessions once every 6 daylight hours for 4 days following a removal and once daily thereafter. Observation sessions were advanced by 3 h daily to avoid a diurnal bias. Where mate replacement occurred, pairs were observed until either the abandonment of the territory or the onset of laying a new clutch. After laying, 1 hour observations were made once every 4 days until hatch. Similar observation sessions were conducted on control nests throughout the study.

Using an alphanumeric notation (Walter 1983), we recorded behavioral data on individual birds. Behaviors were measured in duration or frequency for each individual. Behaviors were categorized into 5 groups; incubation, hunting, maintenance, perched and alert, and other. Hunting behavior included perched and hover hunting. Maintenance behavior was distinguished from perched and alert behavior by bouts of preening, scratching, and feeding. Other behaviors included court-

ship, flying time, and time when individuals were out of the observers' sight. Displays were mainly aerial flight displays. We compared behaviors between individuals within a group (e.g. replacement male vs. widowed female) and between groups (e.g. control vs. experimental pairs, females acquiring a replacement vs. those not). We transformed behaviors measured in duration into hundredth decimal notation for analysis. Distribution functions between groups were compared using a means and moments program and Mann-Whitney *U*-Tests performed on the means (Siegel 1956). All means are reported with standard errors.

We observed six control nests for 12 continuous hours during both 1983 and 1984 when the nestlings were 16–20 days of age. We classified all prey delivered to the nest as vertebrate or invertebrate. The sex of the parent was noted, and the total trips per 12-h period was recorded. Since replacement pairs did not fully rear any young, prey composition and frequency of delivery per 12-h period was estimated from 1 h daily observations conducted during the first 5 days following hatch.

At hatch, we individually color-marked nestlings from both control and replacement nests.

Results

Late nest experiments

Of a total of 12 late nest boxes erected, 5 of 6 were subsequently occupied in 1982, and 4 of 6 occupied in 1983. The interval between nest availability and laying ranged from 7 to 24 days ($\bar{x} = 17.1 \pm 5.25$, $n = 9$). The mean interval is slightly longer than 14.1 days reported by Village (1983) for a similar experiment in Eurasian kestrels (*Falco tinnunculus*) as well as the interval from first pairing to laying for captive American kestrels (Porter and Wiemeyer 1972, 13 days; Bird and Laguë 1982, 11 days).

Replacement frequency

Of 20 birds (4 females and 16 males) removed from their breeding territory in both years, a total of 9 (1 female and 8 males) were replaced. All but 1 of the birds not receiving a replacement mate abandoned their nesting attempt. None of these birds was subsequently observed in the study area. During 1983, when replacement did not occur, males tended to abandon their territories within 24 h, whereas females remained as long as 56 h. However, 1 female whose mate was removed after 24 days of incubation, remained on her territory and hatched and fledged 3 young unaided.

The interval between removal and replacement ranged from 18–144 h ($\bar{x} = 42.9 \pm 38.4$, $n = 9$), however most replacements occurred within 36 h. The number of female removals was too small to assess the frequency of female replacement accurately (1 of 4); however, in both years 50% of all males removed were replaced.

Post-removal behavior

All 3 males not receiving a replacement abandoned their territory within 24 h. Although they inspected the nest site several times after the female's removal, the males lost interest in the nest, commenced hunting, and soon afterward left the territory. The lone male receiving a replacement continued inspecting the nest site throughout the day of the removal and performed aerial flight displays, i.e. repetitive bouts of stooping associated with the klee vocalization (Balgooyen 1976).

We collected data on female behavior following mate loss for 77 h at 16 nests during 1983 and 1984. Since observations were continued only until replacement occurred, on average 42.0 ± 2.1 h, we used only observations made during the first 42 h following mate loss from females not acquiring a replacement for comparisons.

Females that eventually acquired a male replacement incubated their original clutches for significantly longer periods than females that did not (Table 1). The former also spent significantly less time hunting than the latter. Time spent in maintenance did not differ between the 2 groups, but females eventually acquiring a replacement spent significantly more time perched and alert. These females also performed aerial flight displays significantly more than females not receiving a replacement mate. Females have been observed performing "flutter-glide" aerial flight displays (Balgooyen 1976), but this display is markedly different from the aerial display, normally described for males (Balgooyen 1976), performed by the females in this study. Females often displayed when no potential replacement could be seen by the observer, but on several occasions we observed females stooping and kleeing to neighboring males.

Replacement pair-formation behavior

Our observation schedule only allowed a total of 4 h of observations on the only female replacement before the pair abandoned their territory. Besides several copulations and nest inspections by the male, the female entered the nest on 2 occasions, but remained in the box only a short time before leaving. The pair was not subsequently seen in the area.

Of the 8 females that received replacements, 2 pairs abandoned their territory within 3 days and disappeared. Two other pairs remained on their territories but did not reneest. These two pairs occupied the same territory, one in 1983 and the other in 1984. The remaining 4 pairs, all from 1984, re-

Table 1. Behavior of female American kestrels during interval between mate loss and mate replacement (mean duration in min per h \pm SE)

Behavior	Females receiving replacement (n=8)	Females not receiving replacement (n=8)	Tests of significance
Incubation	35:14 \pm 6:54	24:13 \pm 7:30	$U=7, P<0.005$
Hunting	2:14 \pm 2:00	20:15 \pm 7:14	$U=0, P<0.001$
Maintenance	9:27 \pm 5:31	10:18 \pm 2:45	$U=23, NS$
Perched (alert)	7:32 \pm 2:16	3:35 \pm 2:35	$U=3, P<0.001$
Flight display ^a	5.08 \pm 2.06	0.05 \pm 0.02	$U=0, P<0.001$

^a Measured in frequency per hour

mained on their territories and laid new clutches. The mean interval between replacement and reneesting was 18.25 ± 2.99 days. This is somewhat longer than the reported interval of 17 days between removal and laying for Eurasian kestrels (Village 1983), especially since Village's interval includes the time between removal and replacement.

The 8 nests with male replacements were observed for 112 h during pair formation. For pairs remaining on territory but not reneesting, only those observations falling within the 18 day interval between replacement to reneesting were used for analysis.

Males spent almost half their time hunting, significantly more so ($U=0, P<0.001$) than females. Time spent in maintenance and perching was similar for both males and females. Females spent more than 25% of their time incubating the original clutch. Although male kestrels normally incubate (Wilmers et al. 1985), we never observed replacement males to do so. The large variation in female incubation time ($26.4 \pm 23.0\%$) was due to variable time intervals before replacement. Where replacement times exceeded 36 h, females spent considerably less time incubating. Incubation of the original clutch declined with time, so that after 7–10 days, with the exception of the female hatching her eggs unaided, no female was seen incubating the original clutch. Approximately 20% of male and female time was spent in other activities, e.g. flight and courtship behavior. Both males and females performed aerial flight displays (Table 2), although less frequently than did females prior to replacement. Copulations occurred as often as 20 times a day and other behaviors associated with kestrel pair-formation, such as food-transfers, were common (Table 2). Males made almost twice the number of nest inspections as females (Table 2). On only 1 occasion was a replacement male ob-

Table 2. Courtship behavior of widowed American kestrels and their replacement mates during pair-formation. (Mean frequency per h \pm SE)

Behavior	Male (n=8)	Female (n=8)	Tests of significance
Flight display	1.41 \pm 0.85	2.42 \pm 1.47	NS
Copulation	1.28 \pm 0.52	1.28 \pm 0.52	NS
Food transfer	0.35 \pm 0.17	0.35 \pm 0.17	NS
Nest inspection	0.82 \pm 0.35	0.46 \pm 0.04	(U=16, P=0.052)

served to destroy the eggs from the original clutch. At other nests, we removed eggs once it was apparent normal incubation had ceased and we determined that the eggs were inviable. Replacement pairs laid an average of 27 days later than control pairs and in no instance did they incubate an original clutch to hatch after replacement.

Incubation behavior

We observed 10 nests, 4 replacement and 6 control, for 88 h during the incubation period. One replacement nest failed after 24 days of incubation when the adults abandoned the nest, probably due to pressure from juvenile European starlings (*Sturnus vulgaris*) using the nest tree as a roost. We found few differences between the 2 groups for incubation, hunting, and maintenance behaviors (Table 3). Replacement males tended to incubate more than control males and females receiving replacements hunted significantly more than control females (Table 3). Both control and replacement group females were frequently fed by the males.

Replacement nest success

Mean clutch size of the 4 replacement nests was 4.5 eggs. This is similar to the mean clutch size for control nests during 1982–1984 (4.7 \pm 0.48) and to other reports for wild kestrels (Balgooyen 1976, 4.0). Hatching success of fertile eggs was 66.7% in replacement nests, only slightly lower ($P > 0.05$) than in control nests (73.8 \pm 12.01%), but much lower than the 89.3% for kestrels laying second clutches (Bowman and Bird 1985). Weights of newly hatched chicks from replacement ($n=12$) and control ($n=38$) nests averaged 21.0 \pm 3.0 g and 20.8 \pm 5.2 g, respectively. Overall fledging success from control nests was 84%; Balgooyen (1976) reported fledging success of 87.5%. All replacement nests, however, had 100% nestling mortality by 8 days post-hatch. The absence of nestling remains in the nest and the finding of a banded tarsus be-

Table 3. Incubation behavior by replacement and control pairs of American kestrels (mean duration in min per h \pm SE)

Behavior	Replacements (n=4)	Controls (n=6)
Incubation		
Male	12:59 \pm 4:41	9:35 \pm 2:25*
Female	42:06 \pm 8:19	48:12 \pm 7:21 NS
Hunting		
Male	31:42 \pm 5:21	36:54 \pm 6:51 NS
Female	7:24 \pm 1:19	1:46 \pm 0:16**
Maintenance		
Male	13:31 \pm 3:16	11:26 \pm 2:41 NS
Female	9:28 \pm 2:03	7:46 \pm 1:36 NS

* U=21, P=0.062

** U=14, P<0.05

Table 4. Frequency and composition of prey delivery by nesting replacement^a and control^b American kestrels

Experimental group	Frequency of delivery (per 12 h)	Prey composition
Control (n=6) (72 h obs.)	7.00 \pm 2.33	78.61% Vertebrate 21.38% Invertebrate
Replacement (n=3) (15 h obs.)	21.60 \pm 3.84	8.89% Vertebrate 91.11% Invertebrate

^a Deliveries by replacement males only

^b Deliveries by control males and females

neath an adult feeding perch suggested cannibalism by the adults, though the young may have been eaten after death. After nest failure, replacement pairs remained on the territory for a mean period of 4.2 days, then left the study area.

Feeding rates

We observed control nests for 72 h and replacement nests for 15 h to determine frequency of prey delivery and prey composition. Both male and female control birds fed young, but only males fed young at replacement nests. This is likely due to the difference in the timing of observations; females spend most of their time brooding soon after hatching. Replacement males, however, made 3 times as many prey deliveries as male and female controls combined, and also delivered a higher proportion of invertebrate prey than did control pairs (Table 4). However by day 5, feeding rates at all replacement nests sharply decreased, and by day 6, 2 days before nest failure was discovered, all feeding of nestlings ceased.

Discussion

Surplus populations

Dramatic increases in local populations after the introduction of nest boxes (Hamerstrom et al. 1973) suggest some kestrel populations are limited by the number of available nest sites. Results of late nest box provisioning and removal of breeding birds in American kestrels indicate the presence of individuals that are capable of breeding but that do so only after a nest site becomes available. Kestrel replacements may have moved in from adjacent, sub-optimal habitat where they might have bred eventually. However, most kestrel pairs had laid eggs at the start of the experiments, and no shifting of breeding pairs was observed in the study area. Replacements probably did not move in after a failed nesting attempt elsewhere because kestrels that lay second clutches after initial failure usually do so on their original territory (Bowman and Bird 1985).

Smith (1978) described 2 strategies for surplus birds: forming hierarchical flocks in areas undefended by breeders or spending some time in defended territories. Although some promiscuity occurs early in the season and juvenile bands may form late in the season, we have never observed congregations of kestrels during the middle of the breeding season. Rather, individual nonbreeding kestrels appear to reside near breeding territories with high prey densities and large amounts of suitable, but undefended habitat adjacent to them (Bowman and Bird 1986), suggesting kestrels employ the second strategy.

Post-removal behavior

Although the strategies for finding available nests by surplus birds have been discussed (Smith 1978), there has been little mention of strategies to attract a replacement mate by widowed birds. Our results suggest that differences in behavior patterns by widowed birds may relate to their probability of finding a replacement.

Several studies have reported continuation of incubation by most but not all unaided females after mate loss (Pierotti 1980; Weatherhead and Robertson 1980). Longer incubation bouts by females acquiring a replacement may be an effort to maintain a viable clutch until replacement occurs. Replacement in common buzzards (*Buteo buteo*) depended not only on the existence, but also on the proximity of suitable recruits (Dare 1961). If widowed birds knew that surplus birds were

nearby they might modify their behavior to attract them, as suggested by the increased time spent perched and alert by females acquiring a replacement. Since all but 1 widowed kestrels were unable to rear young unaided, birds not expecting replacements should cut their losses quickly and commence hunting to recoup any energetic costs incurred by the failed nesting attempt. Alternatively, females perceiving nearby recruits may not have commenced hunting because males commonly provision females during courtship. Our results strongly support the latter idea.

Several studies on passerines have shown an increase in male song rate after female mate loss (Krebs et al. 1981; Saether and Fonstad 1981; Johnson 1983). Krebs et al. (1981) convincingly argued that besides territory defense, singing in great tit (*Parus major*) males serves to attract females. Picozzi (1984) reported that female hen harriers (*Circus cyaneus*) who lost their mates, remained on territory and displayed to passing males. Many open-country breeding birds perform aerial displays for territorial advertisement, attraction of a mate, and repulsion of rivals (Armstrong 1947), thus the increase in aerial display by widowed females may be analogous to increased song rates in passerines. The lone male acquiring a replacement also performed aerial displays after its mate was lost. Widowed birds, perhaps aware of nearby recruits, may modify their behavior to increase the probability of replacement.

Low rates of natural mate loss in purple martins (*Progne subis*) led Brown (1983) to believe that replacement behavior may have little selective importance. Although few or no data on natural mate loss in American kestrels exist, it may occur frequently. Male kestrels normally arrive on territory 1 to 2 weeks before females and perform aerial displays to attract mates (Willoughby and Cade 1964; Balgooyen 1976). Since the same behavior exists in the females' repertoire, the most likely scenario for this to occur is after loss of male mates.

Pair-formation behavior

Kestrels readily reneest upon loss of the first clutch (Morrison and Walton 1980; Bowman and Bird 1985) and even raise second broods (Stahlecker and Griese 1977; Toland 1985); thus the best strategy for male replacements may be to reneest with the widowed bird. On the other hand, a widowed female kestrel faces a high energetic cost by reneesting. Her best strategy should be to complete the initial nesting attempt, either unaided, or better

with the help of the replacement. When replacement occurs these conflicting strategies must be resolved with a cost to one of the pair.

Many removal studies on passerines report successful rearing of the young by unaided females (Powers 1975; Weatherhead and Robertson 1980). Females capable of rearing young unaided may not seek assistance, thereby easily winning the conflict in strategies by ignoring the replacement. When replacement male mountain bluebirds (*Sialia currucoides*) attempted copulation with courted females they were repulsed (Powers 1975).

In kestrels, most females seem unable to raise the original clutch unaided. Thus the male can win the conflict simply by withholding parental care. Females nevertheless try to raise the original clutch unaided, since the replacement clutch has little chance of success.

Powers (1975) attempted to explain altruism by suggesting that replacements in a certain hormonal condition, replacing at a nest at a corresponding nesting stage, may commit "reproductive error" and assume paternity. Some female kestrel behavior, such as copulating with the male during incubation, may be aimed at inducing the male to help. Normally these two behaviors occupy 2 distinct periods in the breeding cycle, copulations ceasing or greatly decreasing in frequency with the onset of incubation (Willoughby and Cade 1964). Males, faced with conflicting behavioral cues, may, on occasion, mistakenly assume paternity. If so, the behavior in kestrels was not successful, but since all replacement nests failed, the advantage imparted to a successful female may be enough to maintain the behavior. Thus, reproductive error may not be random as Powers infers, but may be induced by the behavior of widowed birds.

Indifference of replacements towards unrelated young may be an intermediate strategy due to constraints against infanticide. The larger female may successfully defend the nest from a male.

Replacement nest success

Once a replacement pair commences a nesting attempt the amount of parental investment should equal that of control pairs. Our results on clutch size, hatching success, and nestling weight support this contention. Both Balgooyen (1976) and Rudolph (1982) noted that late breeding kestrels fed on invertebrate prey more than early breeders. Longer incubation bouts by late nesting replacement males with respect to earlier nesting controls suggest a strategy designed to conserve energy in response to changing prey. Males provisioning in-

cubating females with invertebrates make many more nest trips than do males providing vertebrates. By incubating the eggs himself and allowing the female to hunt, the male lessens the cost incurred by frequent nest trips (Rudolph 1982).

Replacement males feeding over 90% invertebrates to their mate and newly hatched young made over 3 times the number of nest trips as did both male and female control birds feeding vertebrate prey to 18 day old young. Although the total biomass delivered to the nests was similar, the frequent nest trips likely incur a heavy cost to replacement males.

Cavé (1968) found that late breeding Eurasian kestrels produced smaller clutches and fledged young more likely to die during their first year than did early breeders. Village (1983) reported reneating by Eurasian kestrel replacement pairs, but did not compare reproductive success with early breeders.

If feeding invertebrates to kestrel nestlings entails a higher cost for the male, kestrels rearing young after this dietary shift should experience decreased reproductive success. Since replacement pairs obviously nest late in the season, this may explain the observed nest failure rate.

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