REPRODUCTIVE PATTERNS IN CAPTIVE AMERICAN KESTRELS (SPARROW HAWKS)

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A colony of captive American Kestrels (*Falco sparverius*) was established in outdoor pens at Patuxent Wildlife Research Center, Laurel, Maryland, in 1964 to investigate effects of pesticides on raptor reproduction. We have reported on the breeding success, clutch size, and management of the colony (Porter and Wiemeyer 1970), on effects of DDT and dieldrin on reproduction (Porter and Wiemeyer 1969), and on effects of DDE on eggshells (Wiemeyer and Porter 1970). In this paper we report on the chronology of egg laying, incubation behavior, duration of incubation and nestling periods, and nestling sex ratios of captive kestrels untreated with pesticides.

There are relatively few published accounts on the breeding biology of either captive or wild American Kestrels. Basic reproductive behavior of kestrels housed in indoor pens was investigated by Willoughby and Cade (1964). Heintzelman and Nagy (1968) reported on clutch sizes, success of hatch, and nestling sex ratios of wild kestrels nesting in artificial nest boxes in Pennsylvania. Koehler (1968) gave similar data for captive kestrels of two species (*F. s. sparverius* and *F. tinnunculus*) in Germany. Sherman (1913) published detailed observations of the nest life of an Iowa pair. Nesting chronology was reported by Enderson (1960) for Illinois, by Craighead and Craighead (1956) for Michigan and Wyoming, by Roest (1957) for the Pacific Northwest, and by Cade (1955) for southern California. Clutch size, success of hatch, and fledging success also were reported in the Michigan-Wyoming study (Craighead and Craighead 1956). More generalized reproductive data have been summarized by Bent (1938) for the species in the United States and Canada.

SOURCE, AGE GROUPS, AND PAIRING OF HAWKS

Our original colony included 93 kestrels acquired in the wild as nestlings from Massachusetts, New Hampshire, New York, Pennsylvania, and Ohio in 1964; the remainder were trapped in Maryland in the fall of the same year. An additional male and 17 females, all of unknown age, were trapped in Florida during the winter of 1965–66. They probably were wintering birds of the large northern race, *sparverius*, rather than resident birds of the small Florida race, *paulus*, since their average weight (138.2 g; range, 130–142 g; $n = 5$) did not differ significantly ($P > 0.05$, t-test) from that of our northeastern females ($\bar{x}$, 142.2 g; range, 125–159 g; $n = 13$). These weights were from the birds whose laying dates for 1966 are shown in figure 1, and all were weighed in November 1966 except a northeastern female that weighed 129 g in December 1964. Willoughby and Cade (1964) trapped representatives of both races in the vicinity of Gainesville, Florida, in late January and early February 1962. They observed that some females of the race, *paulus*, were one-third smaller than the largest males of the race, *sparverius*; although normally the males weigh less than the females (see Willoughby and Cade 1964, and Porter and Wiemeyer 1970).

The females that were wintering in Florida were paired with yearling offspring of northeastern hawks. In June 1969 an additional 22 male and 27 female nestlings from Massachusetts were added to the colony.

RESULTS

INITIATION OF CLUTCH

The earliest date of first egg laying in our northeastern falcons was 24 March in 1966 and 1967, 22 March in 1968, and 18 March in 1969. For the yearling birds, the earliest dates were 25 March in 1968 and 8 March in 1969. The egg laying dates of our captive kestrels from the Northeast coincided more closely with Bent's (1938) earliest record of 30 March–6 April ($n = 53$) for a wild population in Florida than with his earliest records of 9–23 April for wild populations in New York, New Jersey, Pennsylvania, Ohio, Illinois, and the New England states ($n = 155$). Heintzelman and Nagy (1968) give 15 April as the earliest nesting date for wild populations in Pennsylvania, and Stewart and Robbins (1958) give 31 March as the earliest laying date for Maryland and the District of Columbia. The earliest date of first eggs laid by our Florida-wintering birds was 19 May in 1966, 5 May in 1967, 23 April in 1968, and 26 April in 1969. These dates were comparable to those of the aforementioned populations in northeastern United States and to Bent's (1938) earliest record of 22 May for southeastern Canada.

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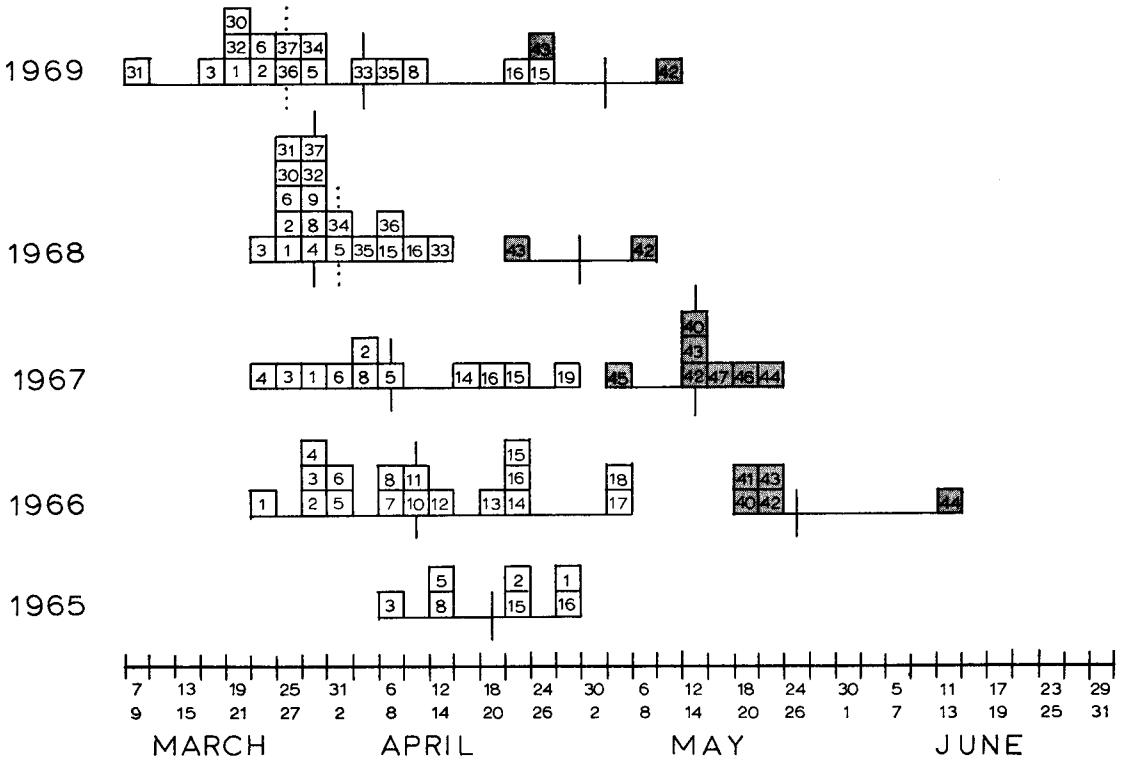

FIGURE 1. Initiation of clutches by captive American Kestrels, by 3-day periods. Each square represents the first egg of a clutch; the number in each square represents the female that laid the clutch; numbers 1–19 represent females obtained from the northeastern states; 40–47, in shaded squares, females obtained in Florida and paired with 1965 offspring of northeastern females; 30–36, 1967 offspring of females from the Northeast; 37, a 1967 offspring of a female from the Florida-wintering population. Females placed on pesticide treatment just prior to the 1968 season (number 40, 41, 44, 45, and 47) are not included for the years 1968 and 1969. Solid vertical lines represent the mean laying dates for northeastern females and Florida-wintering females; dotted vertical lines, the mean laying dates for 1967 offspring of northeastern females and Florida-wintering females.

In 1966 through 1968, the dates of the first eggs laid by the Florida-wintering females did not overlap with those of females from the northeast (fig. 1), even when females of the two groups were housed in adjacent pens. In 1967, for example, our only Florida-wintering female housed among northeastern birds laid a month later than did the latest nesting northeastern bird, and two northeastern females housed among Florida-wintering females laid their first egg 28 and 4 days earlier than did the earliest nesting female from Florida. In 1969 one of two Florida-wintering females laid her first egg on the same date as did one of eight northeastern females; however, this represented a shift to the right (later nesting) by two northeastern females rather than a shift to the left (earlier nesting) by the females from Florida (fig. 1). Although the shift each year from 1966 through 1969 in the average laying dates of the two groups of females was similar in direction (fig. 1), there was a tendency for the laying dates of the two groups of birds to come closer together. This represented greater shifts (to the left, earlier nesting) by the Florida-wintering females than by the northeastern females in 1967 and 1968. The number of days between the average laying dates of the two groups decreased from 44 days in 1966 to 36 days in 1967, 33 days in 1968, and 31 days in 1969 (fig. 1). Management methods had been the same for both groups of birds during each of the four years (Porter and Wiemeyer 1970).

Although the normal breeding range of the Florida-wintering birds is not known, they probably nested in captivity at Patuxent farther south of their normal breeding range than did those obtained from the Northeast. Their late laying dates probably were a response to their need for a long day such as occurs in Canada, since photoperiodism was found by Willoughby and Cade (1964) to be an important factor in the stimulation of egg laying in captive kestrels. A northern origin also is suggested by banding recoveries and by similarities in size (weight) between birds from

Florida and those from the Northeast. Roest (1957), for example, suggests that kestrels from more northern populations tend to winter farther south than do those from populations in more temperate areas, and Henny (in press) found that kestrels in the northern parts of their breeding ranges tend to be more migratory than do those in the southern segments of their population. In support of his suggestion, Roest (1957) cited a record of a kestrel from Nova Scotia that was recovered in Florida. An examination of 87 kestrel banding recoveries through 5 August 1969 from outside of the 16 eastern states where the kestrels were banded, tends to substantiate Roest's contention. Only two the the 87 were recovered in Florida, but since both of them were banded during fall migration, we do not know their original breeding population. Only six kestrels banded in Florida during the winter were recovered outside of Florida, and they were recovered either before or after nesting season in North Carolina (April), New York (August), New Hampshire (April and October), and Quebec (November).

The Florida-wintering birds were acquired between December 1965 and March 1966 and were paired with 1965 offspring of the northeastern birds on 7 March 1966. The effects of the late dates of capture and of pairing on their dates of egg laying are not known.

These data pose a number of interesting problems regarding initiation of egg laying in the kestrel. For example, although it is known that egg laying in the kestrel is triggered by the presence of a nest hole, in response to a required photoperiod (Willoughby and Cade 1964), we do not know how the egg laying date is established. We do not know whether it is fixed in the genes of the species or whether it is imprinted into the behavioral pattern at date of hatching or at some other point in the life cycle. These problems need to be investigated experimentally.

Answers to these problems in the kestrel also may be applicable to the Peregrine Falcon (*Falco peregrinus*). Since, like those of the kestrel, northern populations of the peregrine are more migratory than are those of its more southern populations (White 1968), initiation of egg laying may be established and triggered in the same way in both species. This is further suggested by the general failure of arctic peregrines (*F. p. tundrius*) to lay eggs in captivity at latitudes lower than those of their normal breeding range.

The apparent tendency for our captive kestrels to lay progressively earlier in successive years as shown by the average dates for the laying of the first egg (fig. 1), is supported by statistical analyses only in the following three instances: (1) the same northeastern females laid eggs earlier in 1968 than they did in 1967 ($P < 0.01$); (2) the same Florida-wintering females laid eggs earlier in 1967 than they did in 1966 ($P < 0.05$); and (3) the same northeastern females laid eggs earlier in 1966 than they did in 1965 ($P < 0.05$, paired t-tests).

We have no definitive explanation for this progressively earlier nesting, nor for the earlier nesting of our northeastern kestrels than that of their wild counterparts in Maryland, but confinement may have been involved since it provided a ready availability of food, nesting sites, and mates. In addition, large numbers of our captive birds were confined to a relatively small area (Porter and Wiemeyer 1970), thus placing them close to adjacent nesting pairs where they were constantly exposed to possible visual and vocal reproductive stimuli during nesting season. Contagion, which has been shown by Emlen and Lorenz (1942) to stimulate mating behavior in the California Quail (*Lophortyx californicus*), however, appears not to stimulate mating behavior in kestrels since it played little part in stimulating our aforementioned female kestrels from Florida that were housed among northeastern birds. Its effects on the other northeastern birds in speeding up their laying dates is more difficult to evaluate, and needs further study. The males seem to have little to do with date of egg laying. This is illustrated by the fact that although males of northeastern origin were paired with both the northeastern females and the Florida-wintering females, the Florida females nested much later than did the northeastern females.

Willoughby and Cade (1964) found that the absence of a nest hole either delayed or interfered with normal courtship behavior, but gave no instance of egg laying by female kestrels in absence of a nest hole. One of our yearling females housed in a pen containing 10 other females, no males, and no nest boxes laid an egg on 15 May 1969 which broke on the floor of the pen.

Between 11 and 30 April 1969, after the nesting season was well under way, 16 kestrels of each sex previously segregated as to sex and without nest boxes, were paired, and each pair was placed in a separate pen containing a nest box with a hole entrance. A mean of 13.2 days elapsed between pairing and deposition of the first egg by these females (table 1). Success of hatch was not determined for four

TABLE 1. Time intervals between pairing and first egg laid (first clutches), and between removal of unsuccessful first-clutch eggs and initiation of second clutches (renesting) in captive American Kestrels.

Group and year	Date paired or $\bar{x}$ date of egg removal	No. of clutches	Days[a] to 1st egg	
			$\bar{x} \pm$ SE	Range
First clutches[b]				
1969, yearling ♀ ♀	11–25 April	10	13.6 ± 0.46	11–15
1969, 2-yr-old ♀ ♀	21–30 April	6	12.5 ± 1.48	8–17
Totals	—	16	13.2 ± 0.60	8–17
Renesting (1st clutches failed)[c]				
1970, yearling ♀ ♀	20 May	15	12.5 ± 0.38	11–16
1970, 2-yr-old ♀ ♀	13 May	2	13.5	12–15
1970, 3-yr-old ♀ ♀[d]	19 May	4	13.5 ± 0.60	12–15
1968, 4-yr-old ♀ ♀	20 May	1	—	13
Totals	—	22	12.8 ± 0.31	11–16

[a] Number of days may vary + 1 day from the actual value, since we did not always know whether an egg was laid in late evening or early morning.
[b] Males and females of this group were housed in separate pens prior to pairing.
[c] Eggs of first clutches were removed approximately 1 week after expected hatching date.
[d] In 1970, one 3-yr-old female laid no other eggs in her second clutch, but one after 40 days, nor did she incubate, which suggests that her renesting period was abnormally long. If the 40-day value were included, the mean and SE values would be 18.8 ± 5.3 with a range of 12–40 for the 3-yr-olds, and 14.0 ± 1.22 with a range of 11–40 for the combined renesting data.

of these pairs, since they were sacrificed prior to laying their second egg; success for the remaining pairs was 47 per cent. More complete data on fertility are unavailable. Willoughby and Cade (1964) tell of a kestrel that laid the first egg of her clutch 9 days after the nest hole had been unblocked for a second time. However, since the hole had been opened 34 days earlier for an 8-day period, they were uncertain of the significance of the 9-day period. The eggs of this female were infertile.

The average period of time between removal of first-clutch eggs that failed to hatch and the initiation of second clutches (renesting) for 22 pairs of kestrels in 1968 and 1970 was 12.8 days, with the omission of a possible anomaly of 40 days (table 1). We know of no renesting data for wild kestrels, but according to Green (1916), wild Peregrine Falcons (*Falco peregrinus pealei*) that have lost their first clutch eggs in an advanced stage of incubation have laid second clutches in about three weeks. Herbert and Herbert (1965) recorded the laying of two eggs and the initiation of their incubation only 12 days after desertion of the first clutch by a female peregrine in New York. Since three days were required for the laying of the two eggs, the time period between first and second clutches was only nine days, which is comparable with that of our kestrels. They observed a similar pattern between the laying of both the second and third and the third and fourth clutches of this same female; however, there is some question regarding the exact dates of desertion for the first, second, and third clutches.

In 1968 three pairs of kestrels began their second clutches 11, 12, and 14 days, respectively, after the young of their first clutches had fledged. Two of these clutches were begun one day after the fledged young were removed from the pens, and a third was begun two days after the young were removed. In 1967 two pairs of kestrels began second clutches 16 and 21 days after young from first clutches had fledged, and 13 days after removal of the young from the pens.

Laying of second-clutch eggs may take place prior to fledging of first-clutch young. For example, one female began her second clutch one day before fledging of the single young of her first clutch, and two other females began their second clutches on the first and fourth days following fledging of their first-clutch young, four and seven days before removal of the young from the pens.

We recorded unusually short periods between removal of a clutch and initiation of the subsequent clutch in our only two unpaired females in 1967. They were induced to lay additional clutches by removing the eggs either on the day the fifth egg was laid, or a day or two later. One female laid two clutches of five eggs each, plus an additional clutch of two eggs, all during a 38-day period. The other female laid four clutches of five eggs each, plus an additional clutch of three eggs, during a 61-day period. The intervals between all eggs laid by this female averaged 2.7 days, which is within the two- to three-day inter-egg, intra-clutch interval reported by Sherman (1913), Willoughby and Cade (1964), and

Heintzelman and Nagy (1968). However, this included an interval of seven days between the laying of the 21st and 22nd egg; the average interval for eggs laid between eggs 1–21 was 2.4 days. These data suggest that the American Kestrel may be an indeterminate layer.

The Peregrine Falcon (*F. p. pealei*), which has an incubation period and inter-egg interval equivalent to those of the American Kestrel (Herbert and Herbert 1965), has been reported by Green (1916) to lay more than one set of eggs in the wild. He found that the Peregrine Falcon began second sets of eggs in about 10 days if the eggs of the first sets were taken fresh, which is the approximate period of time required for the initiation of second clutches in the kestrel, after failure of the first clutch eggs. Bond (1946) tells of a pair of peregrines that laid four successive clutches in one season, each after the removal of the previous clutch. Herbert and Herbert (1965) cite an example in New York where four successive clutches were laid by a peregrine following desertion of earlier clutches.

Female kestrels usually became quite broody just prior to the initiation of egg laying, although the degree of broodiness was variable. At these times they appear rather lethargic and sometimes will not flush from their nest boxes, even though they have no eggs. The presence of a female in her nest box for two or three days in succession usually was an indication that she was about to lay. Of 20 females, whose 1970 nest boxes were checked once each day for 8 days preceding deposition of the first egg of their first clutch, one was recorded in her nest box six times, two were recorded four times each, two three times each, three two times each, five only once each, and seven were never found in their nest boxes. Ten of these females were not recorded in their nest box on the day immediately preceding the day of egg laying; three were recorded in their nest box only the day before egg laying; five females were in their nest box for the two successive days before egg laying and one female was in her nest box for six successive days before egg laying. One female was in her nest box on day, 7, 6, 5, and 1 prior to egg laying and was absent from her nest box on the intervening days.

EGG-LAYING INTERVALS AND TIMES

The intervals between deposition of consecutive eggs in clutches with four or five eggs are shown in table 2; they averaged 2.4 days. An interval of three days was not unusual in our study, particularly between the laying of the first two and last two eggs of a clutch (table 2). Similarly, in domestic hens, the intervals between the laying of the first two and last two eggs of an egg sequence are greater than those between intervening eggs (Sturkie 1954). The average interval between the laying of the first and last egg for seven five-egg clutches was 9.1 days, and for one four-egg clutch, 7 days.

TABLE 2. Laying intervals for consecutive eggs in American Kestrel clutches of four or five.

Consecutive eggs	1st clutches Days between eggs:			2nd clutches Days between eggs:	
	2	3	4	2	3
1 and 2	5	4	0	2	0
2 and 3	6	1	1	1	1
3 and 4	7	1	0	1	2
4 and 5	4	4	0	–	–

Although new additions to clutches usually were present at our early morning visits (08:00–10:00), diurnal egg deposition was a rather common phenomenon among our captive kestrels. In 1970, 13 of 42 females were known to have laid at least one egg during the daylight hours. Four of these 13 females were unpaired. Ten of the 19 diurnally laid eggs for which we have the approximate hour of laying were deposited between 10:00 and 15:00. The first, second, and third eggs of the laying sequence were most frequently laid during daylight (first eggs, 21 per cent; second, 26; third, 32; fourth, 11; sixth and seventh eggs, both laid by unpaired females, each 5 per cent). Diurnal egg laying has been reported for a wild kestrel by Sherman (1913), who tells of the deposition of the second egg of a clutch between 09:30 and 16:00.

OVA AND EGG SIZE

All but one of 24 female kestrels that were sacrificed and autopsied in 1969 after laying their first egg, contained a second egg in the oviduct. The mean diameters (mm) $\pm$ SE of the first, second, and third largest ovarian follicles of these birds were 16.5 ± 0.23, 11.8 ± 0.39, and 6.4 ± 0.38 ($n = 22$ for the smallest group; one follicle ruptured). The four largest follicles of a female whose second egg had not yet been released were: 19, 16, 11, and 6 mm in diameter.

Weights and dimensions of the first egg laid in each nest in 1968 and 1969 are given in table 3. Eggs laid by first-generation yearlings in 1969 (paired on 25 April) weighed significantly less ($P < 0.01$; t-test) than those laid by second-generation yearlings in 1969 (paired on

TABLE 3. Comparison of size of first egg laid in nests of captive American Kestrels.

Group and year laid	n	Weight (g) $\bar{x} \pm$ SE	Weight (g) Range	Length (mm) $\bar{x} \pm$ SE	Length (mm) Range	Diameter (mm) $\bar{x} \pm$ SE	Diameter (mm) Range
Parent							
1968 (4-yr-old)	8	15.55 ± 0.42	14.16–17.13	35.3 ± 0.51	33.9–37.1	28.5 ± 0.21	27.8–29.4
1969 (5-yr-old)	8	15.73 ± 0.46	14.09–16.97	34.0 ± 0.56	32.7–37.0	28.4 ± 0.26	27.5–29.6
1st generation (hatched 1967)							
1968 (1-yr-old)	6	15.60 ± 0.38	14.06–16.66	36.0 ± 0.72	34.2–38.5	28.3 ± 0.26	27.2–29.1
1969 (2-yr-old)	6	16.09 ± 0.24	15.16–16.55	36.1 ± 0.47	34.6–37.6	28.6 ± 0.12	28.2–28.9
1st generation (hatched 1968)							
1969 (1-yr-old)	4	14.02 ± 0.36	12.96–14.51	33.7 ± 0.68	32.0–35.2	27.7 ± 0.28	27.1–28.3
2nd generation (hatched 1968)							
1969 (1-yr-old)	4	15.80 ± 0.41	15.06–16.87	36.0 ± 0.35	35.1–36.7	28.4 ± 0.27	28.0–29.2

11 April) and than those laid by first-generation yearlings in 1968 (paired 28 February 1968). We have no explanation for this phenomenon.

There was no apparent shift in size of eggs with increased age of female kestrels (table 3), nor was there a difference in size of eggs between the parent generation and their yearling first-generation offspring in 1968 or their yearling second-generation offspring in 1969. There was no direct correlation ($P > 0.05$) between weights of females and the size of their eggs.

INCUBATION

Females did most of the incubating. In 1967, 8 of 16 males were recorded on the eggs at least once during incubation of first clutches as were 5 of 10 parent males and 5 of 9 yearling males in 1968 (56 per cent) and 22 of 35 males in 1970 (63 per cent). Observations were made once each day in 1970 and one or more times each day in 1967 and 1968. Distribution of the number of times individual males were recorded on the eggs in 1970 is as follows: one time, 12 males; two times, four males; three times, three males; five, seven, and eight times, one male each. The extent to which the male incubates the eggs appears to be an individual characteristic, both in captivity and in the wild. In the kestrel colony maintained by Willoughby and Cade (1964), males were seldom seen on the eggs. Sherman (1913) observed a male kestrel incubating the eggs only once during the complete incubation period at a nest in Iowa. In Oregon, Roest (1957) observed a male that regularly incubated at night while his mate perched in an adjacent tree. Nocturnal incubation by the male also was the usual occurrence at a nest observed in southern California (Willoughby and Cade 1964).

Females usually begged food from the males during the incubation period. Males were very attentive to the females' needs at this time. One male, however, appeared oblivious to the utterances of his mate, but this did not adversely affect the hatching success of the eggs or the fledging success of the young.

Incubation of clutches containing five eggs usually began with the laying of the fourth egg, and less frequently with the third egg (table 4); the first two or three eggs usually were left unattended and were cold to the touch. We observed female kestrels sitting on incomplete clutches containing two, three, and four cold eggs, indicating that incubation had not yet begun despite the female's presence on the eggs. For two pairs whose complete clutches contained four eggs, incubation began following the laying of the second egg. For two pairs whose complete clutches contained six eggs, incubation began with the laying of the fifth egg, while in a third six-egg clutch, incubation began the day after the fourth egg was laid.

The time between laying and hatching of the last egg in a clutch best represents the incubation period (Moreau and Moreau 1940; Nice 1954; Davis 1955). For three complete first clutches of five eggs and one complete first clutch of four eggs in which all eggs hatched, the incubation period (last egg laid

TABLE 4. Initiation of incubation by American Kestrel pairs with clutches eventually containing five eggs ($n = 20$).

Incubation began on:	3rd egg n	3rd egg %	4th egg n	4th egg %	5th egg n	5th egg %
Day laid	2	10	12	60	1	5
One day later	1	5	2	10	0	0
Two days later	1	5	0	0	1	5

TABLE 5. Time interval between laying and hatching of given eggs for American Kestrels with clutches containing five eggs.

Eggs[a]	Days between laying and hatching		
	n	$\bar{x} \pm$ SE	Range
1st laid to 1st hatched	6	33.7 ± 0.33	33–35
2nd laid to 2nd hatched	3	31.7 ± 0.88	30–33
3rd laid to 3rd hatched	6	29.7 ± 0.33	29–31
4th laid to 4th hatched[b]	5	28.8 ± 0.25	28–29
5th laid to 5th hatched	3	27.0 ± 0.58	26–28
1st laid to 5th hatched	4	36.0 ± 0.41	35–37

[a] Eggs were not individually marked.
[b] One nest containing only four eggs (not included here) hatched the fourth egg on the 27th day, for an egg-laying and incubation period of 34 days.

to last egg hatched) averaged 27 days (26–28 days) (table 5). This is somewhat shorter than the average incubation period of 28.4 days (27–33 days) recorded by Willoughby and Cade (1964).

Two days elapsed between hatching of the first and fifth eggs in each of the four first clutches containing five eggs for which we have complete data. On the first day of hatch, the first egg hatched in one of these nests, and the first three eggs hatched in three of the nests. A day later, one egg hatched in three of the nests, and three eggs hatched in one of the nests; on the following day, the final egg in each nest hatched. In two kestrel nests containing four eggs, the first two eggs in each nest hatched on the first day of hatch and one egg in each nest hatched on each of the two subsequent days. This suggests that incubation may have begun in the two four-egg clutches with the laying of the second egg. Heintzelman and Nagy (1968:309) reported that the first three eggs in a nest of wild kestrels in Pennsylvania all hatched on the same day, and inferred that incubation probably began with the laying of the third egg.

NESTLING PERIOD

In 1967, the nestling period of first clutches, covering the time from the first egg hatched to the first young fledged, averaged 27.4 days (26–30 days) at 10 nests of northeastern parents, and 29.3 days (27–32 days) at six nests of Florida-wintering females. In 1968, first clutch nestling periods averaged 28.4 days (26–32 days) at five nests of northeastern parents, and 29.1 days (27–31 days) at eight nests of first-generation yearlings. The average first clutch nestling period for both years and all groups combined was 28.4 days (26–32 days). Craighead and Craighead (1956) reported nestling periods of 29 and 31 days for wild kestrels in Michigan and Wyoming.

NESTLING SEX RATIOS

True secondary sex ratios (at hatching) can be obtained only by examining nestlings when full complements of eggs hatch (McIlhenny 1940). Our eight pairs of kestrels that successfully reared complete clutches in 1967 fledged 19 young of each sex, confirming the expected 1:1 secondary ratio. Nineteen pairs in 1967 fledged 37 males and 34 females, for a tertiary ratio of 1.1:1, which was not significantly different from 1:1 ($P > 0.70$). Thus, neither incubation nor post-hatching mortality appeared to favor either sex. This agrees with the 1:1 tertiary ratio (nestlings) observed by Heintzelman and Nagy (1968) over a period of several years in a wild population in Pennsylvania. Secondary and tertiary sex ratios were unavailable in 1968 because sex determinations were not possible for the eggs removed from each clutch.

SUMMARY

Female kestrels acquired in Florida in winter as full-grown birds began laying eggs a month later than did those acquired as nestlings from northeastern United States. Egg laying dates of the two groups did not overlap in 1966 through 1968. The later nesting Florida-wintering females may have nested in captivity at a latitude farther south of their normal breeding range than did those from the Northeast. There was an apparent trend of earlier laying in successive years between 1965 and 1968 in our captive birds.

Time intervals between pairing of previously unpaired kestrels and initiation of their first clutches ranged from 8 to 17 days; time intervals between removal of first-clutch eggs and initiation of second clutches for kestrels whose first clutches failed to hatch ranged from 11 to 16 days, with the exception of an apparent anomaly of 40 days. Some females laid second clutches prior to fledging of first-clutch young. The egg laying interval averaged 2.4 days, and appeared to be greater between the first two and last two eggs of the clutch than between intervening eggs. Egg sizes differed only slightly between age groups, and no statistical correlation was evident between weights of female kestrels and the size of their eggs.

Although both sexes incubated the eggs, the female assumed a much greater role than the male. Incubation of clutches of five eggs usually began with the laying of the fourth egg. The incubation period (last egg laid to last

egg hatched) averaged 27 days. The average interval between hatching of the first and last eggs of clutches containing five eggs was two days.

The average nestling period for the first young hatched in 29 nests was 28.4 days. An exact 1:1 secondary sex ratio was recorded in 1967 for complete clutches in which all young fledged.

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