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Reproductive Success Increases with Age in American Kestrels (Falco sparverius), Especially in Breeding Males

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Abstract

Age-related differences in reproductive success have been well documented in many species of birds. The experience gained through successive breeding attempts can improve survival skills, foraging abilities, access to resources through social dominance, and familiarity with each stage of reproduction. In this study we examined 669 nesting attempts by American kestrels (*Falco sparverius*) from a population that bred in nest boxes in northwestern New Jersey, 1995 to 2018. We tested the hypothesis that older kestrels would have greater nesting success than those in their first reproductive attempt. Clutch size, hatching rate, and the number of chicks that survived to fledging varied significantly and positively with age for both male and female breeders. These trends were associated with the date of clutch initiation and amount of parental attentiveness. Older birds initiated clutches earlier than those in their first breeding attempt, and older birds of both sexes were more likely to be present in the vicinity of the nest site, especially during the incubation and nestling periods. The relationship between age and breeding success was much more pronounced in males than in females. This difference is consistent with the behavioral role that each sex has during a breeding attempt. After laying a clutch, the female performs most of the incubation and broods the young chicks. In contrast, the male provides food to the female prior to egg laying and throughout incubation, and to the entire family until the chicks no longer are brooded by the female. Pairs in which both adults were older had significantly greater nesting success than mixed or young pairs, and we never observed an older female paired with a male in his first reproductive attempt.

MONTCLAIR STATE UNIVERSITY

Reproductive Success Increases with Age in American Kestrels *(Falco sparverius)*.

Especially in Breeding Males

By

Emilie Rehm Luttman

A Master's Thesis Submitted to the Faculty of

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In Partial Fulfillment of the Requirements

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College of Science and Mathematics

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REPRODUCTIVE SUCCESS INCREASES WITH AGE IN AMERICAN KESTRELS

(*FALCO SPARVERIUS*), ESPECIALLY IN BREEDING MALES

A THESIS

Submitted in partial fulfillment of the requirements

For the degree of Master of Science

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EMILIE REHM LUTTMAN

Montclair State University

Montclair, NJ

2019

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Introduction

Age-related differences in breeding success have been well documented in many species of birds. Experimental evidence has suggested that these age-based variations are the result of natural differences in experience (Daunt et al. 1999). With increased experience through successive breeding attempts, individuals can gain improved survival skills, foraging abilities, access to resources through social dominance, and familiarity with each stage of reproduction (Nol and Smith 1987, Hamer and Furness 1991, Forslund and Pärt 1995). Increased age and reproductive experience may result in earlier laying dates, larger clutches, healthier fledglings, and more efficient coordination of parental roles (Newton et al. 1981, Perrins and McCleery 1983, Pyle et al. 1991, Fowler 1995, Badyaev and Hill 2002, Cichoñ 2003, Limmer and Becker 2009).

The American kestrel (*Falco sparverius*) is North America's smallest falcon. It typically occurs in open grasslands where it preys upon insects, rodents, and small birds (Roest 1957, Bird and Palmer 1988, Smallwood and Wargo 1997, Smallwood and Bird 2002). This species breeds in the late spring and early summer, although breeding has been occurring earlier with recent warmer winter temperatures in certain western populations (Smallwood and Bird 2002, Heath et al. 2012). In North American migratory populations, males arrive to the breeding areas first to become established in the more plentiful territories; females arrive shortly thereafter and select their mates in part based on the amount of courtship feeding the male provides her (Smallwood and Bird 2002). This species is an obligate secondary cavity nester, meaning that it requires a cavity that has already been excavated or a natural cavity. Females typically lay one egg every two days until a full clutch of four or five eggs is completed (Smallwood and Bird 2002).

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These eggs will hatch after 26-32 days of incubation (Smallwood and Bird 2002). Chicks fledge 26-31 days later (Smallwood and Bird 2002). These kestrels are then able to breed the following spring as second-year individuals (Smallwood and Bird 2002). The American kestrel is not considered a long-lived species, with an average lifespan of less than five years in the wild, although the oldest wild individual on record was 11 years 7 months (Clapp et al. 1982, Bird and Palmer 1988, Smallwood and Bird 2002).

American kestrels have been experiencing long-term population declines, especially in the Northeast (Smallwood and Bird 2002, Farmer et al. 2009, Smallwood et al. 2009, Hinnebusch et al. 2010). These declines have resulted in this species being classified as threatened across its range (IUCN 2018). Several recent studies have focused on the potential causes of these declines (Smallwood et al. 2009, McClure et al. 2017). However, much less is known about how parental age plays a role in kestrel breeding success. A number of studies have examined the relationship between age-related physical characteristics and potential breeding success in male kestrels (Wiehn 1997, Bostrom and Ritchison 2006). Another study conducted with a population of known-age adult kestrels in southwestern Idaho found that reproductive rates increased from the first to the second breeding attempt, and did not further increase significantly thereafter (Steenhof and Heath 2009). These researchers found that this rise in breeding success supported the selection hypothesis, which suggests that breeding success should increase due to the elimination of poor producers early in life (Curio 1983, Forslund and Pärt 1995, Brown and Roth 2009).

In the present study, we examined age-related differences in breeding success and parental attentiveness in American kestrels from a breeding population in northwestern

New Jersey from 1995 to 2018. Compiling breeding data from these years allowed us to

examine aspects of breeding such as early versus late nesting, overall fecundity, and

parental attentiveness of known-age adults in this population. We tested the hypothesis

that older kestrels would have greater rates of nesting success than those during their first

reproductive attempt.

Methods

Study Area:

A nest box program for kestrels was established in Sussex and Warren counties,

northwestern New Jersey, in 1995 (Smallwood 2016). The study area was southeast of

the Kittatinny Ridge and was composed largely of agricultural fields, residential lands,

and patches of woodland. Beginning in 1995, we erected wooden nest boxes in the area

by attaching them to roadside trees, utility poles, and barns within patches of suitable

open grassland habitats (Smallwood and Wargo 1997, Smallwood and Bird 2002). The

internal dimensions of the nest boxes were approximately 33-cm high with a 20- by 24-

cm floor covered with a 5-cm layer of wood shavings (Smallwood 2016). Over time, nest

boxes were lost, removed, or replaced so that approximately 100 nest boxes were

available for the kestrels in the study area each year (Smallwood 2016).

Monitoring:

The monitoring methods we used in this study were similar to those described in

Steenhof and Heath 2009 and Smallwood 2016. In our study area, kestrels lay their

clutches between March and June, but mostly during late April and early May. We visited

each nest box at 21- to 28-day intervals, which ensured that all attempts were discovered

during the laying or incubation stages. We determined that a breeding attempt had occurred with the presence of at least one egg in a nest box, and we considered an attempt to be successful if at least one chick fledged (survived to banding age). Our estimate of success rate was the maximum possible rate because an attempt that began and failed between monitoring visits might not be detected.

Once we discovered an attempt, we scheduled additional visits to determine the completed clutch size and to observe the chicks after hatching. During the visits after hatching, we assessed the age and overall condition of the hatchlings and used this information to schedule which day to return for banding. We banded the chicks between 20 and 22 days of age, or about 6 to 8 days before fledgling. We typically visited each nest box four to six times during a breeding attempt. As this species is prone to premature fledging, the nest boxes generally were not visited after the chicks were banded.

We also made efforts to capture the adults at nest boxes where the kestrels were breeding. We captured adults in the nest box by placing a net attached to a PVC pipe over the entrance hole. The principle investigator would then climb up to the nest box and gently pick up the incubating or brooding bird while also ensuring the safety of the eggs or chicks inside of the nest box. After we captured an adult or nestling kestrel, we banded it with a USGS aluminum leg band and marked it with a patagial wing tag made from military-grade fabric which was painted with a bright letter or number that could be read at long distances, allowing for individual identification in the field (Varland et al. 2007). All kestrels were handled in accordance with federal and state banding permits as well as Montclair State University IACUC permits. Birds were handled for approximately 10-15

minutes and were then released on site. We captured more female kestrels than males due to the incubation and breeding role of the females, i.e., females were more likely than males to be present in the nest box.

<u>Developing the Dataset:</u>

We obtained data from three separate data files for these analyses: (1) a set of summary data that contained the results of each nesting attempt during the study for any given year; (2) a banding data set that included the individual characteristics of each banded kestrel such as age, gender, and measurements of other physical features; and (3) a monitoring file comprising what was inside of a nest box during each visit, along with a description of adult behavior. We combined the files into one dataset in Microsoft Excel that compiled the data for each nesting attempt, including: clutch initiation date, clutch size, brood size, number of fledglings, information on the breeding adults, and how frequently each adult was in the vicinity or inside the nest box during monitoring visits.

We categorized breeding attempts as having been discovered during the laying or incubation stages. If it was unclear during which stage the nest was discovered because the attempt had already failed, then we classified the stage of discovery as unknown. Determining the date of clutch initiation was contingent upon whether the nest was discovered during the laying or incubation stages. If we discovered the attempt during the laying stage, then the most recent egg could have been laid earlier that day, one day before, or two days before (i.e., the next egg could be laid soon after our visit). We then counted back two days per egg to determine that 3-day window, and the middle date was considered the date of clutch initiation. If we found the attempt during the incubation stage, when the clutch was already completed, we determined a minimum and maximum

clutch initiation date. The minimum clutch initiation date would be the date of the last visit in which the nest box was empty. We determined the maximum clutch initiation date by counting back two days per egg from the day of discovery. If the range was smaller than 15 days, then the middle date was considered the date of clutch initiation. If the range was larger than 15 days, we classified the date of clutch initiation as unknown.

We assumed that hatching would occur approximately 30 days after the onset of incubation, so we scheduled the first visits with chicks in the nest boxes to be within a few days after hatching. The exact hatching date was determined by direct observation of the chicks. We could determine to within 0.5 days the age of the chicks during the first few days after hatching (J. A. Smallwood unpub. data).

We determined the completed clutch size by observing the number of eggs during multiple monitoring visits. Apparent clutch size could be less than the actual number of eggs laid if an egg was laid and then lost between visits. Brood size was the confirmed number of hatchlings in the nest box. Consistent with other field studies of raptors, we considered chicks that survived to banding age to be fledglings (e.g., Smallwood and Smallwood 1998). For each attempt, we calculated hatching rate by dividing brood size by clutch size, and we calculated chick survival rate by dividing the number of fledglings by brood size.

Adult kestrels were given an age classification, either SY for second-year individuals that were therefore in their first breeding attempt, or ASY (after second-year) for birds determined to be older than SY and to have possibly bred before. We assigned the designation of AHY to those adults for which exact age could not be determined. For

the purposes of the age-related statistical analyses, we used data only from individuals that were SY or ASY.

We used the data from the monitoring file to determine the number of times adults of either sex were in the vicinity of, or inside of, the nest box during the laying, incubation, and nestling stages. We used these counts to calculate the mean attendance of the adults, which was the mean proportion of monitoring visits during which the bird was observed either in the vicinity of or inside the nest box, during each stage of reproduction. We considered each visit to a nest box separately, even if they occurred on the same day. We did not include a monitoring visit if the sex of the only adult observed could not be determined. If two adults were seen during a visit and one or both of their sexes could not be determined, we considered both the male and the female as being present. For failed attempts, we did not include in the analysis visits occurring after the expected hatch date when no adults were present.

Statistical Analyses:

We tested the variables for normality using Shapiro-Wilk Tests. We found significant deviations in all of the variables, so nonparametric tests were used for the subsequent analyses. We used a Fisher's Exact Test to compare success rates between older and younger breeders of both sexes, and to compare the success rates of pairs in which the exact age of both members was determined. We used both univariate statistical treatments (Wilcoxon Signed Rank Tests, Spearman Correlation Coefficients) and multivariate techniques (Principle Component Analysis) to examine the breeding success and parental attentiveness variables.

Results

Of the 668 total breeding attempts occurring over 24 years, 488 (81%) of them were successful. We captured a total of 438 adults (350 females and 88 males). Of these adults, 112 females were determined to be ASY and 111 females were determined to be SY, while 25 males were determined to be ASY and 7 males were determined to be SY. Most completed clutches had four or five eggs and 61.5% of these eggs produced fledglings (Table 1). Breeding attempts in this population began around 01 May, with successful nesting attempts occurring an average of four days earlier than those that were unsuccessful (mean Julian date of clutch initiation; 120 ± 0.67 SE and 124.4 ± 1.55 SE, respectively; Wilcoxon $Z = 2.29$, $P = 0.011$). Correlation analyses indicated that the relationship between the date of clutch initiation and the other reproductive variables was significant (Table 1).

ASY females had significantly larger mean clutch sizes than SY females, while there was no significant difference in mean clutch sizes between ASY and SY males (Fig. 1). There was no significant difference in mean hatching rates between ASY and SY females, but ASY males had significantly higher mean hatching rates than SY males (Fig. 2). Mean brood size also was significantly higher in ASY females than in SY females, but there was no significant difference between ASY and SY males (Fig. 3). In both males and females, older breeders had significantly greater mean chick survival rates than SY breeders (Fig. 4). The mean number of fledglings produced also was higher in ASY birds of both sexes (Fig. 5). There was no significant difference between the success rates of ASY and SY females, but ASY males had higher success rates than SY males (Table 2).

Univariate analyses revealed that ASY females were more likely than SY females to be observed in the vicinity of the nest box during incubation (mean proportion of monitoring visits, 0.203 ± 0.026 SE and 0.110 ± 0.020 SE, respectively; Wilcoxon $Z = 2.73$, $P = 0.003$; Fig. 6). ASY males were more likely than SY males to be observed in the nest box during the nestling stage (mean proportion of visits, 0.0148 ± 0.006 SE, 0.005 ± 0.005 SE, respectively; Wilcoxon $Z = 1.88$, $P = 0.029$; Fig. 7), though at a lower frequency than females of either age category. No other attendance variables were significantly associated with parental age.

Principle component analysis of the 12 attendance variables describing the presence of adults either in the vicinity or inside of nest boxes generated a first principle component that accounted for 21.3% of the sample variability (eigenvalue = 2.6), and a second principle component that accounted for an additional 13.3% of the sample variability (eigenvalue = 1.6; Table 3). The first principle component was largely determined during the incubation period by the female not occurring in the nest box (eigenvector = -0.530), the female occurring in the vicinity of the nest box (eigenvector = 0.472), and the male occurring in the nest box (eigenvector = 0.338; Table 3). There was a significant difference in the first principle component between ASY and SY females (Wilcoxon $Z = 1.09$, $P = 0.021$), but not between ASY and SY males (Wilcoxon $Z = 0.58$, $P = 0.280$).

ASY females initiated clutches 5 days earlier than SY females (mean Julian date of clutch initiation 119 ± 1.28 SE, 125 ± 3.82 SE, respectively), while ASY males began nesting 11 days earlier than SY males (mean Julian date of clutch initiation 119 ± 2.776 SE, 130 ± 6.015 SE, respectively; Fig. 8). We were able to determine the age of both

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members of a pair in only 15 instances. All attempts by ASY-ASY pairs ($N = 9$) were successful, 66% of ASY male-SY female pairs ($N = 3$) were successful, and only 33% of SY-SY pairs ($N = 3$) were successful (Fisher's exact test, $P = 0.024$). We did not detect any ASY females breeding with an SY male.

Discussion

Overall, parental age did play a significant role in kestrel breeding success in this population. We found that older breeders produced larger clutches and larger broods, and had greater numbers of fledglings and higher overall rates of success. These results are consistent with those of other studies examining age and reproductive success in birds (Nol and Smith 1987, Burger et al. 1996, Badyaev and Hill 2002, Ruthrauff 2002, Steenhof and Heath 2009). Variation in breeding success between the age groups in our study can be attributed largely to age-based differences in parental attentiveness and in the date of clutch initiation. The first principle component was meaningful for our study, and it was largely determined during incubation by the female occurring in the vicinity of the nest box, rather than inside of it, and the male occurring in the nest box. We interpret these results as the male relieving the female during incubation. Higher attendance rates in older males than in younger males has been documented in species such as great skuas (*Catharacta skua*; Catry and Furness 1999), greater flamingos (*Phoenicopterus roseus*; Schmaltz et al. 2011), and house finches (*Carpodacus mexicanus*; Badyaev and Hill 2002). Higher provisioning rates in older males also have been demonstrated in studies of house finches (Badyaev and Hill 2002). In great skuas, less efficient pair coordination of breeding activities in younger birds has been demonstrated to influence their overall reproductive success (Catry and Furness 1999, Furness and Ratcliffe 1999).

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In regard to the date of clutch initiation, we found that successful attempts were initiated four days earlier than those that were unsuccessful, and that the relationship between this date and the other reproductive variables was significant. We found that for both sexes, older kestrels began their nesting attempts earlier than those in their first breeding attempt. Previous studies have demonstrated a significant relationship between the date of clutch initiation and nesting success in European kestrels (*Falco tinnuculus*; Dijkstra et al. 1990), house finches (Badyaev and Hill 2002), and blackbirds (*Turdus merula*; Jankowiak and Wysocki 2016). Clutch size, hatching success, and overall breeding success have been observed to decline over the course of the breeding season past an optimal reproductive window in song sparrows (*Melospiza melodia*; Nol and Smith 1987), roseate terns (*Sterna dougallii*; Burger et al. 1996), western sandpipers (*Caladris mauri*; Ruthrauff 2002), snow geese (*Chen caerulescens*; Bêty et al. 2003), and guillemots (*Uria aalge*; Wanless and Harris 2007). The amount of provisioning the male kestrel provides to his mate also has been shown to be a limiting factor for the female in her ability to produce eggs (Dawson and Bortolotti 2002); the more he feeds her prior to laying, the earlier she will initiate her clutch (Perrins 1990). Fledglings from these earlier breeding attempts have a higher probability of surviving and breeding the following year (Perrins 1990, Monrós et al. 2002). Chicks that fledge earlier have more time to gain necessary survival skills, as well as have the opportunity to take full advantage of seasonally abundant food resources while they are still available (Smallwood and Smallwood 1998, Smallwood and Bird 2002).

The age-based variations in breeding success we observed in our study were much more pronounced in males than in females. ASY males not only initiated clutches earlier,

but also had higher hatching rates and chick survival rates than younger males and females of both age categories. These findings are consistent with the sex specific roles of American kestrels during breeding (Roest 1957, Smallwood and Bird 2002). The female performs the majority of incubation and she broods the chicks for about the first two weeks after hatching. She also tears apart the prey brought to the nest site and feeds the chicks these morsels. In contrast, a primary roles of the male kestrel is to provision the female prior to laying and during incubation, which is important not only because of the date of clutch initiation, but especially because the number and weight of her eggs is influenced by how much the male provisions her (Perrins 1990, Wiebe and Bortolotti 1995, Daan et al. 2008). The male also must provide for the entire family from the time the chicks hatch until they are no longer brooded or need help in feeding. Males with less experience may not yet have attained the necessary skills to hunt and provide sufficiently for himself and up to six other members of a family.

Our analyses of known-age pairs revealed differences in success rates among older, mixed, and younger pairs. Although our sample size was small, there was a large enough difference in the success rates for the result to be significant. All attempts made by pairs where both parents were older were successful. Of mixed pairs where the male was older and the female was breeding for the first time, 66% were successful. Only 33% of pairs where both parents were first-time breeders were successful. Remarkably, we did not detect any instances in which an ASY female bred with an SY male.

Intersexual selection in favor of more experienced breeding partners has been demonstrated in species such as Eurasian sparrowhawks (*Accipiter nisus*; Newton et al. 1981), great tits (*Parus major*; Perrins and McCleery 1983), house finches (Badyaev and

Hill 2002), and greater flamingos (Cezilly et al. 2008). In kestrels, a female first ascertains the health of their potential partner using indicators such as the color intensity of a male's yellow cere and legs, as well as the brightness of his plumage (Wiehn 1997, Smallwood and Bird 2002, Bostrom and Ritchison 2006). She then directly assesses a male's quality as a provider through the amount of prey he gives to her during courtship (Smallwood and Bird 2002). The female may make a selective mate choice in favor of a more experienced male if his physical cues indicate that he is healthy (Wiehn 1997, Bostrom and Ritchison 2006), and if he provides her with more food during courtship rituals than a less experienced, first-time breeding male (Smallwood and Bird 2002). Ultimately, these results demonstrate that the probability of breeding success in kestrels can be predicted based upon male parental age, and that females, especially those with prior breeding experience, are able to recognize high quality males and select their mates accordingly.
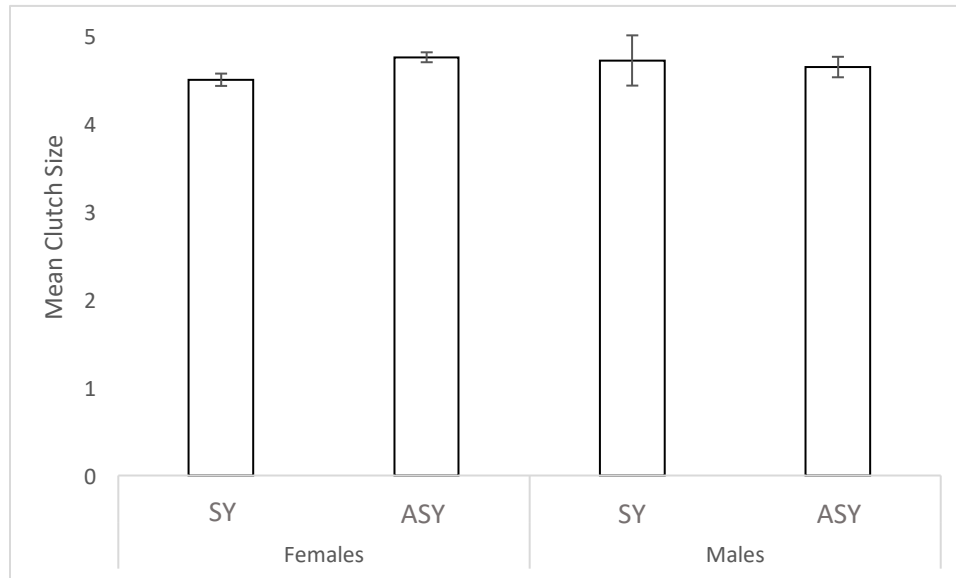
Figure 1: Mean clutch size increased with age in female kestrels ($Z = 3.14$, $P = 0.001$), but not in male kestrels ($Z = 0.00$, $P = 0.50$). *P*-values are from Wilcoxon signed-rank tests, and bars indicate standard error. Data from 255 breeding attempts, northwestern New Jersey, 1995-2018.
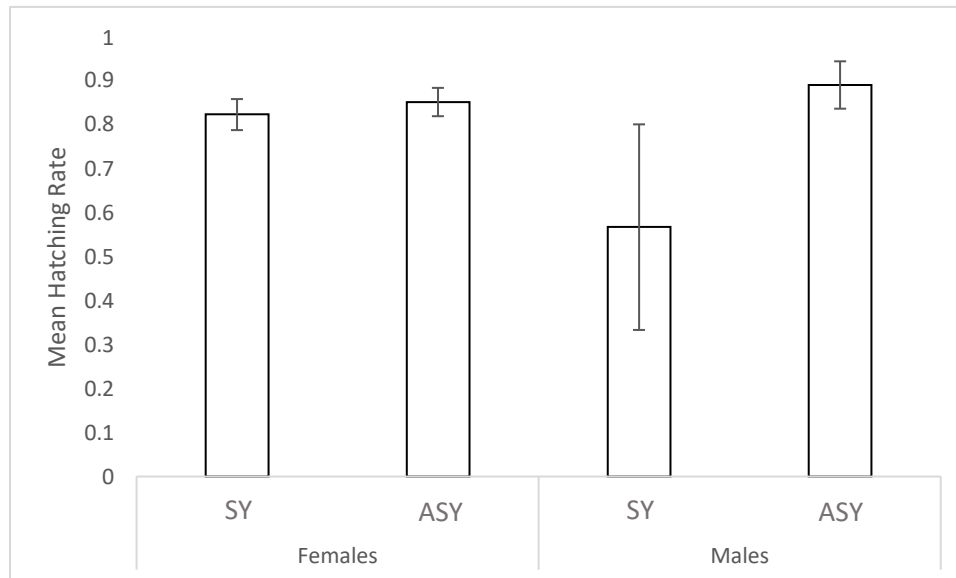
Figure 2: Mean hatching rates did not vary with age in female kestrels ($Z = 0.10$, $P = 0.459$), but it did increase with age in male kestrels ($Z = 1.80$, $P = 0.036$). *P*-values are from Wilcoxon signed-rank tests, and bars indicate standard error. Data from 214 breeding attempts, northwestern New Jersey, 1995-2018.

Figure 3: Mean brood size increased with age in female kestrels ($Z = 1.65$, $P = 0.049$), but not in male kestrels ($Z = 0.60$, $P = 0.28$). *P*-values are from Wilcoxon signed-rank tests, and bars indicate standard error. Data from 214 breeding attempts, northwestern New Jersey, 1995-2018.
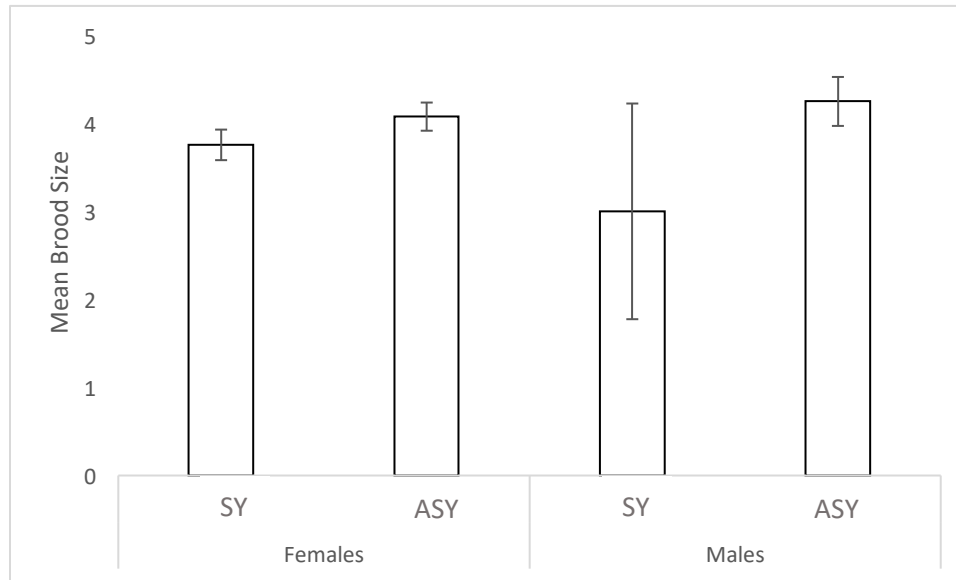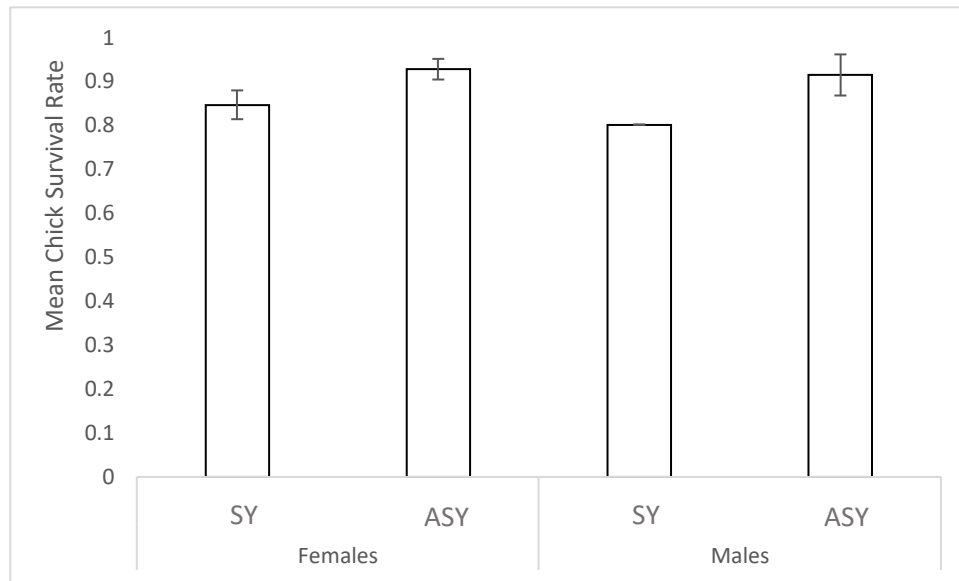
Figure 4: Mean chick survival rate increased with age in both female ($Z = 2.27$, $P = 0.012$) and male kestrels ($Z = 2.33$, $P = 0.01$). *P*-values are from Wilcoxon signed-rank tests, and bars indicate standard error. Standard error for SY males was 0. Data from 190 breeding attempts, northwestern New Jersey, 1995-2018.
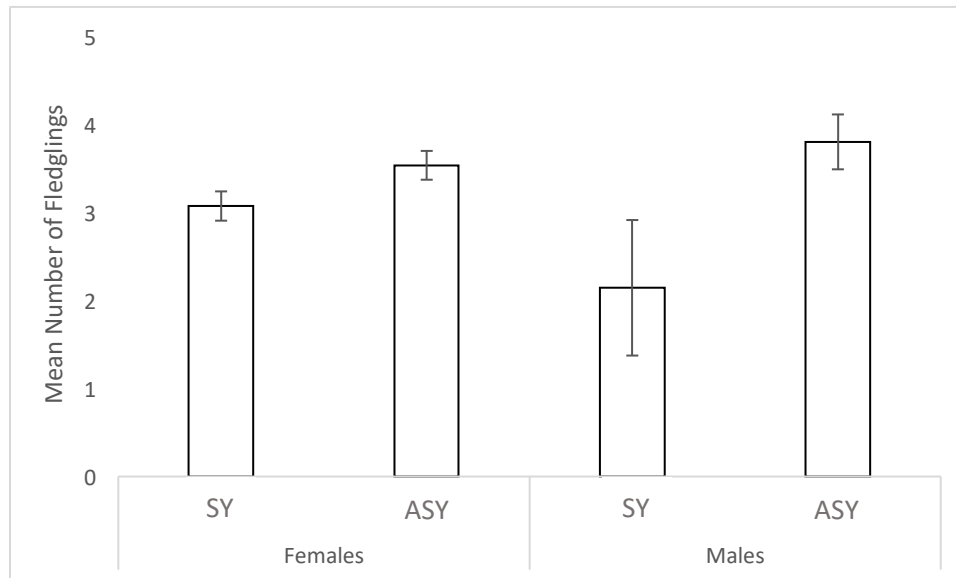
Figure 5: Mean number of fledglings increased with age in both female ($Z = 2.43$, $P = 0.008$) and male kestrels ($Z = 2.26$, $P = 0.012$). P-values are from Wilcoxon signed-rank tests, and bars indicate standard error. Data from 255 breeding attempts, northwestern New Jersey, 1995-2018.

Figure 6: Mean attendance (mean proportion of monitoring visits during which the bird was observed) by female kestrels during each stage of reproduction. ASY females were significantly more often observed in the vicinity of the nest box during incubation than were SY females (mean proportion of monitoring visits, 0.203 ± 0.026 SE and 0.110 ± 0.020 SE, respectively; Wilcoxon $Z = 2.73$, $P = 0.003$). None of the other five pairwise comparisons (In the vicinity during Laying, In the Nest Box during Laying, etc.) were significant. Data from 162 breeding attempts, northwestern New Jersey, 1995-2018.
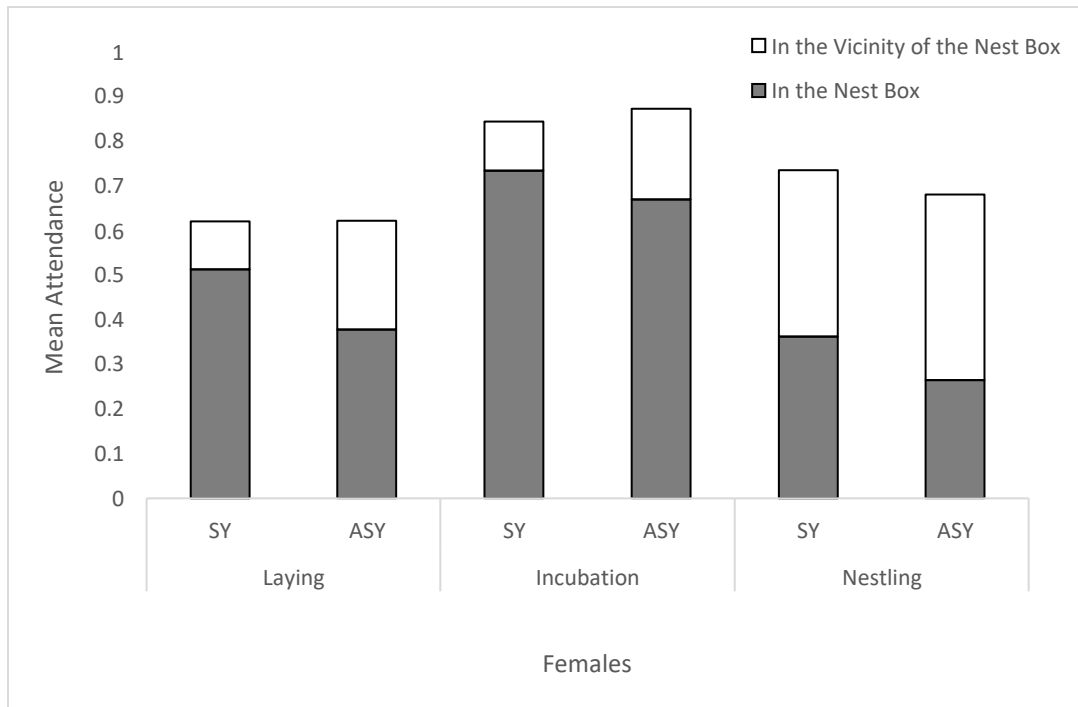
Figure 7: Mean attendance (mean proportion of monitoring visits during which the bird was observed) by male kestrels during each stage of reproduction. ASY males were significantly more often observed inside of the nest box during the nestling stage than were SY males (mean proportion of visits, 0.0148 ± 0.006 SE, 0.005 ± 0.005 SE, respectively; Wilcoxon $Z = 1.88$, $P = 0.029$). None of the other three pairwise comparisons (In the vicinity during Laying, In the Nest Box during Laying, etc.) were significant. Data from 32 breeding attempts, northwestern New Jersey, 1995-2018.
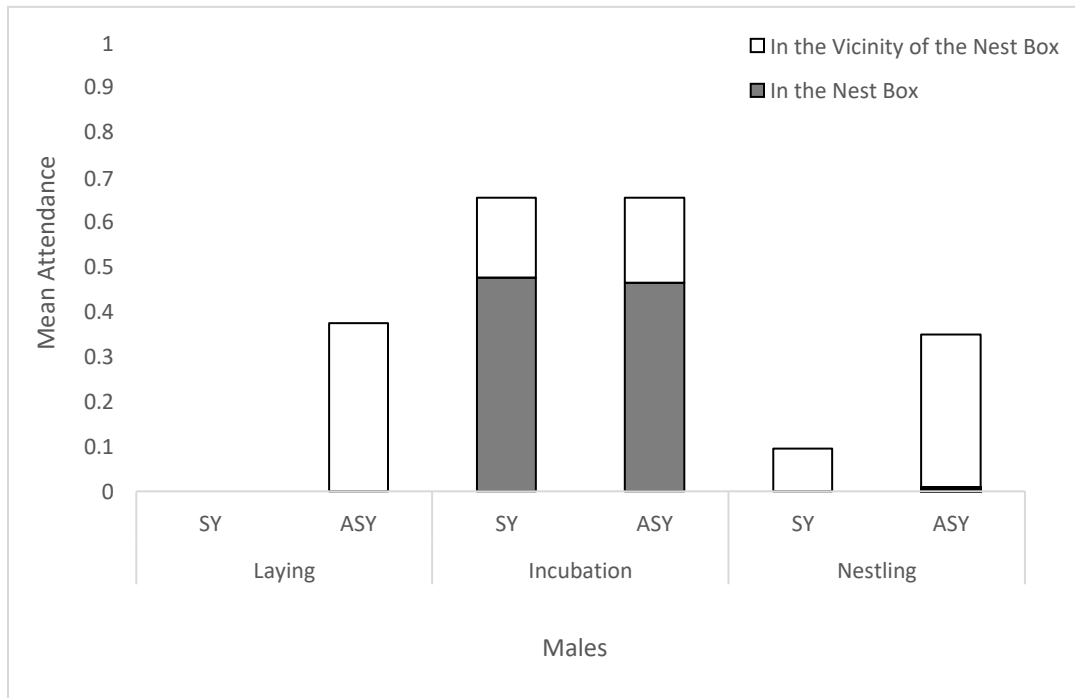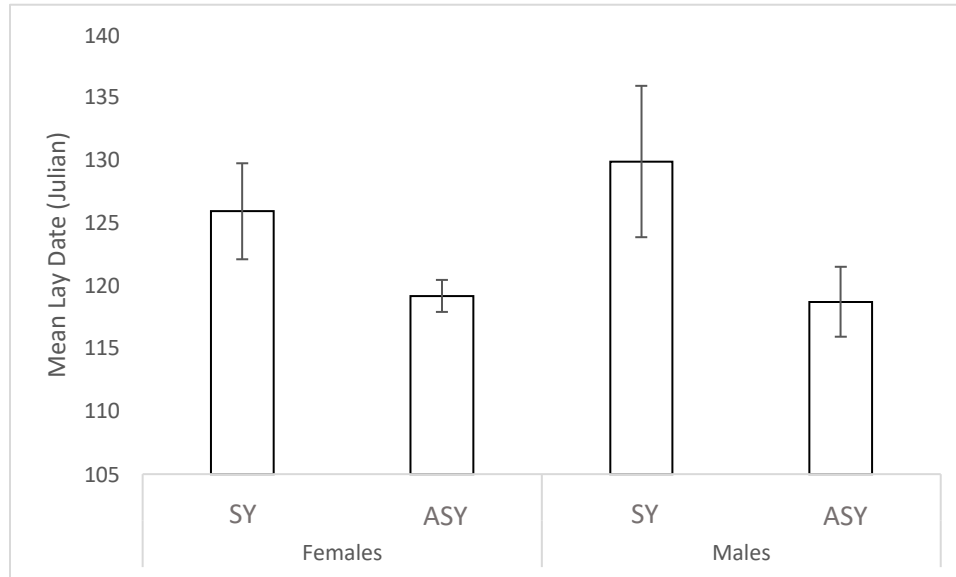
Figure 8: Mean Julian date of clutch initiation decreased with age, or occurred earlier, with age in both female ($Z = 1.83$, $P = 0.034$) and male kestrels ($Z = 1.80$, $P = 0.036$). P-values are from Wilcoxon signed-rank tests, and bars indicate standard error. Data from 246 breeding attempts, northwestern New Jersey, 1995-2018.

Tables

Table 1: Kestrel breeding performance was significantly correlated with the date of clutch initiation. Data from 669 breeding attempts, northwestern New Jersey, 1995-2018. Spearman correlation *P*-values were Bonferroni corrected for five non-independent comparisons.

Variable	N	Mean $\pm$ SD	Spearman Correlation	
			r_s	P
Clutch Size	640	4.67 $\pm$ 0.70	0.360	<0.005
Brood Size	549	3.35 $\pm$ 2.07	0.310	<0.005
Hatching Rate	526	0.73 $\pm$ 0.41	0.210	<0.005
Chick Survival Rate	411	0.89 $\pm$ 0.25	0.003	<0.005
Number of Fledglings	669	2.87 $\pm$ 1.99	0.238	<0.005
Success Rate (%)	488	81.1	2.290*	0.011*

*Wilcoxon Rank Sum Test

Table 2: ASY female kestrels did not have significantly higher success rates than SY females, but ASY males did have higher rates of success than SY males. Data from 562 breeding attempts, northwestern New Jersey, 1995-2018.

Breeding Attempt Outcome	Females			Males		
	SY	ASY	Total	SY	ASY	Total
Successful	91	96	187	4	23	27
Failed	20	16	36	3	2	5
% Success	82.0%	85.7%		57.1%	92.0%	
Fisher's Exact Test	$P=0.28$			$P= 0.057$		

Table 3: Principle component analysis for attendance variables used to describe the presence of adult American kestrels either in the vicinity or inside of nest boxes. Data from 110 breeding attempts, northwestern New Jersey, 1995-2018.

Variable	Eigenvectors	
	PC1	PC2
Female in Nest Box during Incubation Stage	-0.530	0.009
Female in Vicinity during Incubation Stage	0.472	0.020
Male in Nest Box during Incubation Stage	0.338	0.046
Female in Vicinity during Nestling Stage	0.303	-0.496
Female in Nest Box during Laying Stage	-0.295	-0.399
Female in Vicinity during Laying Stage	0.293	0.448
Female in Nest Box during Nestling Stage	-0.276	0.500
Male in Vicinity during Nestling Stage	0.129	-0.113
Male in Vicinity during Incubation Stage	0.109	0.047
Male in Vicinity during Laying Stage	0.078	0.305
Male in Nest Box during Laying Stage	0.069	0.143
Male in Nest Box during Nestling Stage	0.049	-0.116

Literature Cited

Badyaev, A. V., and G. E. Hill (2002). Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. Behavioral Ecology 13:591–597.

Bêty, J., G. Gauthier, and J. Giroux (2003). Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. The American Naturalist 162:110–121.

Bird, D. M., and R. S. Palmer (1988). American kestrel. *In* Handbook of North American Birds. Yale University Press, New Haven, CT U.S.A., pp. 253–290.

Bostrom, M. R., and G. Ritchison (2006). Possible relationships between morphology, territory quality, and skin color of American kestrels. Journal of Field Ornithology 77:392–398.

Brown, W. P., and R. R. Roth (2009). Age-specific reproduction and survival of individually marked wood thrushes, *Hylocichla mustelina*. Ecology 90:218–229.

Burger, J., I. C. T. Nisbet, C. Safina, and M. Gochfeld (1996). Temporal patterns in reproductive success in the endangered roseate tern (*Sterna dougallii*) nesting on Long Island, New York, and Bird Island, Massachusetts. The Auk 113:131–142.

Catry, P., and R. W. Furness (1999). The influence of adult age on territorial attendance by breeding great skuas *Catharacta skua*: an experimental study. Journal of Avian Biology 30:399–406.

Cezilly, F., V. Boy, C. J. Tourenq, and A. R. Johnson (2008). Age-assortative pairing in the greater flamingo *Phoenicopterus ruber roseus*. Ibis 139:331–336.

Cichoñ, M. (2003). Does prior breeding experience improve reproductive success in collared flycatcher females? Oecologia 134:78–81.

Clapp, R. B., M. K. Klimkiewicz, and J. H. Kennard (1982). Longevity records of North American birds: Gaviidae through Alcidae. Journal of Field Ornithology 53:55–73.

Curio, E. (1983). Why do young birds reproduce less well? Ibis 125:400–404.

Daan, S., M. Hall, and T. Meijer (2008). Family planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. Behaviour 114:117–136.

Daunt, F., M. P. Harris, and P. Monaghan (1999). Experimental evidence that age-specic reproductive success is independent of environmental effects. Proceedings of the Royal Society of London Series B-Biological Sciences 266:1489–1493.

Dawson, R. D., and G. R. Bortolotti (2002). Experimental evidence for food limitation and sex-specific strategies of American kestrels (*Falco sparverius*) provisioning offspring. Behavioral Ecology and Sociobiology 52:43–52.

Dijkstra, C., S. Daan, and J. B. Buker (1990). Adaptive seasonal variation in the sex ratio of kestrel broods. Functional Ecology 4:143–147.

Farmer, C. J., J. P. Smith, and C. H. J. F. Armer (2009). Migration monitoring indicates widespread declines of American kestrels (*Falco sparverius*) in North America. Journal of Raptor Research 43:263–273.

Forslund, P., and T. Pärt (1995). Age and reproduction in birds - hypotheses and tests. Trends in Ecology & Evolution 10:374–378.

Fowler, G. S. (1995). Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. American Zoology 35:318–328.

Furness, R. W., and N. Ratcliffe (1999). The effect of parental age and experimentally manipulated brood size on the foraging effort and breeding performance of great skuas (*Catharacta skua*). Journal of Zoology 249:195–201.

Hamer, K. C., and R. W. Furness (1991). Age-specific breeding performance and reproductive effort in great skuas (*Catharacta skua*). Journal of Animal Ecology 60:693–704.

Heath, J. A., K. Steenhof, and M. A. Foster (2012). Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American kestrels *Falco sparverius*. Journal of Avian Biology 43:376–384.

Hinnebusch, D. M., J.-F. Therrien, M.-A. Valiquette, B. Robertson, S. Robertson, and K. L. Bildstein (2010). Survival, site fidelity, and population trends of American kestrels wintering in southwestern Florida. The Wilson Journal of Ornithology 122:475–483.

IUCN (2018). The IUCN red list of threatened species. Version 2018-1. [Online.] Https://www.iucnredlist.org/. Last accessed 15 May 2019.

Jankowiak, L., and D. Wysocki (2016). Do individual breeding experience and parental

 effort affect breeding season length in blackbirds? Behavioral Ecology 27:829–834.

Limmer, B., and P. H. Becker (2009). Improvement in chick provisioning with parental

 experience in a seabird. Animal Behaviour 77:1095–1101.

McClure, C. J. W., S. E. Schulwitz, R. Buskirk, B. P. Pauli, and J. A. Heath (2017).

 Commentary: research reccomendations for understanding the decline of American

 kestrels (*Falco sparverius*) across much of North America. Journal of Raptor

 Research 51:455–464.

Monrós, J. S., E. J. Belda, and E. Barba (2002). Post-fledging survival of individual great

 tits: the effect of hatching date and fledging mass. Oikos 99:481–488.

Newton, I., M. Marquiss, and D. Moss (1981). Age and breeding in sparrowhawks.

 Journal of Animal Ecology 50:839–853.

Nol, E., and J. N. M. Smith (1987). Effects of age and breeding experience on seasonal

 reproductive success in the song sparrow. British Ecological Society 56:301–313.

Perrins, C. M. (1990). The timing of birds' breeding seasons. Ibis 112:242–255.

Perrins, C. M., and R. H. McCleery (1983). The effect of fledging mass on the lives of

 great tits *Parus major*. Ibis 127:306–315.

Pyle, P., L. B. Spear, W. J. Sydeman, and D. G. Ainley (1991). The effects of experiance

 and age on the breeding performance of western gulls. The Auk 108:25–33.

Roest, A. I. (1957). Notes on the American sparrow hawk. The Auk 74:1–19.

Ruthrauff, D. R. (2002). Seasonal and age-related trends in the reproductive output of western sandpipers (*Calidris mauri*) at Kanaryaraq, Alaska. M.S. thesis, Humboldt State University, Arcadia CA.

Schmaltz, L., F. Cézilly, and A. Béchet (2011). Using multistate recapture modelling to assess age-specific bottlenecks in breeding success: a case study in the greater flamingo (*Phoenicopterus roseus*). Journal of Avian Biology 42:178–186.

Smallwood, J. A. (2016). Effects of researcher-induced disturbance on American kestrels breeding in nest boxes in northwestern New Jersey. Journal of Raptor Research 50:54–59.

Smallwood, J. A., and D. M. Bird (2002). American kestrel (*Falco sparverius*). *In* The Birds of North America (A. F. Poole and F. B. Gill, Editors). 2nd edition. Cornell Lab of Ornithology, Ithaca, NY, USA.

Smallwood, J. A., M. F. Causey, D. H. Mossop, J. R. Klucsarits, B. Robertson, S. Robertson, J. Mason, M. J. Maurer, R. J. Melvin, R. D. Dawson, G. R. Bortolotti, J. W. Parrish, Jr., T. F. Breen, and K. Boyd (2009). Why are American kestrel (*Falco sparverius*) populations declining in North America? Evidence from nest-box programs. Journal of Raptor Research 43:274–282.

Smallwood, J. A., and P. J. Wargo (1997). Nest site habitat structure of American kestrels in northwestern New Jersey. Bulletin New Jersey Academy of Sciences 42:7–10.

Smallwood, P. D., and J. A. Smallwood (1998). Seasonal shifts in sex ratios of fledgling American kestrels (*Falco sparverius paulus*): the Early Bird Hypothesis. Evolutionary Ecology 12:839–853.

Steenhof, K., and J. A. Heath (2009). American kestrel reproduction: evidence for the

    selection hypothesis and the role of dispersal. Ibis 151:493–501.

Varland, D. E., J. A. Smallwood, L. S. Young, and M. N. Kochert (2007). Marking

    techniques. *In* Raptor Research Management Techniques (D. M. Bird and K. L.

    Bildstein, Editors). Hancock House Publishers, Surrey, B.C. Canada and Blaine,

    WA U.S.A, pp. 221–236.

Wanless, S., and M. P. Harris (2007). The importance of relative laying date on breeding

    success of the guillemot *Uria aalge*. Ornis Scandinavica 19:205.

Wiebe, K. L., and G. R. Bortolotti (1995). Egg size and clutch size in the reproductive

    investment of American kestrels. Journal of Zoology 237:285–301.

Wiehn, J. (1997). Plumage characteristics as an indicator of male parental quality in the

    American kestrel. Journal of Avian Biology 28:47.