

# COVARIATION OF CLUTCH SIZE, LAYING DATE, AND INCUBATION TENDENCY IN THE AMERICAN KESTREL

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**Abstract.** Seasonal decline in clutch size is common in birds, but the proximate mechanisms for this phenomenon have not been elucidated. The most credible model to date posits that late-laying females lay fewer eggs due to a seasonal increase in the tendency to incubate during laying, which inhibits egg production. We tested this model with free-living and laboratory American Kestrels (*Falco sparverius*) by quantifying changes in clutch size and incubation tendency during laying over the course of the breeding phase. Consistent with the model, clutch size in free-living kestrels decreased while incubation increased with progress of the 74-day breeding phase. Inconsistent with the model, variation in incubation tendency during laying was not associated with clutch size in either the field or the laboratory. In the laboratory, incubation increased but clutch size did not decrease over the course of the 77-day breeding phase. In the laboratory, females that nested early in one breeding phase re-nested more quickly and nested in a second breeding phase more quickly than females nesting late in the first breeding phase. This indicates that timing of laying is, in part, a property of individual females, independent of environmental factors. Together, our findings suggest that both clutch size and timing of laying are inherent, correlated properties of particular females. Although incubation tendency may influence clutch size, other factors appear to override its influence.

**Key words:** *Falco sparverius*, incubation behavior, proximate control, reproductive effort, reproductive optimization, seasonal breeding.

## Covariación del Tamaño de la Nidada, la Fecha de Postura y la Tendencia de Incubación en *Falco sparverius*

**Resumen.** Aunque la disminución estacional en el tamaño de la nidada es común entre las aves, los mecanismos proximales para este fenómeno no han sido elucidados. El modelo de mayor credibilidad propuesto hasta el momento sugiere que las hembras que ovipositan tarde ponen menos huevos debido a un aumento estacional en la tendencia a incubar durante la postura que inhibe la producción de huevos. Pusimos a prueba este modelo con individuos de *Falco sparverius* en condiciones naturales y en cautiverio, cuantificando los cambios en el tamaño de la nidada y la tendencia a incubar durante la postura a lo largo de la época reproductiva. Tal como el modelo plantea, el tamaño de la nidada en individuos silvestres de *F. sparverius* disminuyó mientras que la incubación aumentó a medida que transcurrían los 74 días de la época de reproducción. Mientras tanto, en contraste con el modelo, la variación en la tendencia a incubar durante la postura no estuvo asociada con el tamaño de la nidada ni en el campo ni en el laboratorio. En el laboratorio, la incubación aumentó pero el tamaño de la nidada no disminuyó en el transcurso de la época reproductiva (77 días). En condiciones de laboratorio, las hembras que anidaron temprano en una fase reproductiva volvieron a anidar más rápidamente en una segunda fase que las hembras que anidaron tarde en la primera. Esto indica que el tiempo en que se hace la postura es en parte una propiedad de cada hembra y es independiente de factores ambientales. En conjunto, nuestros hallazgos sugieren que tanto el tamaño de la nidada como el momento de la postura son propiedades correlacionadas de cada hembra en particular. Aunque la tendencia a incubar podría influenciar el tamaño de la nidada, otros factores parecen anular su influencia.

## INTRODUCTION

Clutch size declines seasonally in many bird species (Klomp 1970). The proximate causation

of this phenomenon is not well understood (Klomp 1970, Perrins 1979), but, to date, Meijer et al. (1990) have posited the most credible model for a regulatory mechanism. They proposed that a seasonal increase in incubation tendency during laying gives rise to the seasonal decline in clutch size. They expand on earlier ideas that the seasonal decline in clutch size relates to a seasonal change in hormone levels

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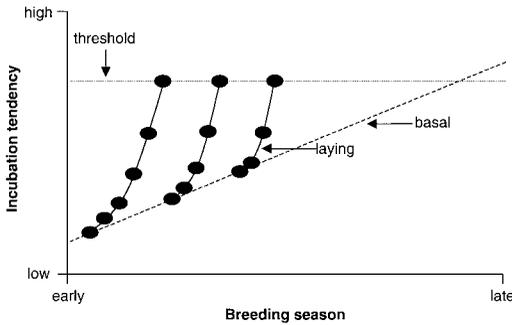


FIGURE 1. Model for the seasonal decline in clutch size as regulated by incubation tendency. A seasonal (basal) rise in incubation tendency is augmented by a quick rise during laying. When incubation tendency reaches a threshold, ovulation or follicular development ceases. Ovals indicate each follicle or egg of a 6, 5, and 4-egg clutch (modified from Meijer et al. 1990 with permission).

(Haftorn 1985), and that laying or ovulation is terminated by a rise in prolactin (Eisner 1960, Mead and Morton 1985), a hormone believed to promote incubation behavior in most species (El Halawani et al. 1986, Sharp et al. 1988, Sockman et al. 2000).

Meijer and coworkers base their model on studies of the European Kestrel (*Falco tinnunculus*). We have divided this model into several integrated components (Fig. 1). (1) Incubation tendency increases seasonally (Haftorn 1981). Two phenomena suggest the increase is based on an "endogenous seasonal program" (Meijer et al. 1990). First, the onset of a photoinduced breeding phase entrains the increase. Second, it occurs even in the absence of a naturally changing photoperiod probably because a seasonal increase in prolactin occurs in the absence of a naturally changing photoperiod (Meijer 1988, Dawson and Sharp 1998, Maney et al. 1999, Sockman et al., in press). (2) Early in laying, a positive feedback loop between egg-brood patch contact and incubation tendency forms, causing a steep rise in incubation tendency (Lea et al. 1981, Meijer 1995). This rise superimposes over the seasonally increasing basal level of incubation tendency, resulting in a seasonal elevation of incubation tendency at any point during laying. (3) When incubation reaches a threshold, it inhibits follicular development, recruitment, or ovulation (Haftorn 1985), thus restricting the number of ova. (4) Females breeding late in the season when basal incubation tendency is high

reach this threshold sooner during laying than those breeding early in the season; thus late-laying females lay smaller clutches than early-laying females.

Meijer and coworkers did not clearly define incubation tendency, but they based their quantification of it on the time a female bird spends on the nest during the laying period. Using a thermistor placed in the nest and a temperature recorder to quantify changes in nest temperature (as would be induced by the presence of an attending female), they were able to determine whether a female was present (Beukeboom et al. 1988). In most species, full incubation does not commence at the onset of laying, and a female spending time on the nest does not necessarily warm eggs sufficiently to induce and maintain embryonic growth. An increase in the time the female spends on eggs from one day to the next characterizes a transition from laying to incubation behavior (Lea et al. 1981). In some species such as the White-crowned Sparrow (*Zonotrichia leucophrys*), the rise in nest attendance is very rapid (Mead and Morton 1985), whereas in others such as the American Kestrel (*Falco sparverius*), the rise is gradual (Sockman et al. 2000). Near the end of laying, this incubation tendency has usually developed into full, stereotyped incubation behavior that includes warming the eggs sufficiently to induce embryonic development.

Several predictions emerge from the Meijer and coworkers' model. Females laying at similar times in the photoinduced breeding phase and having equal access to resources should produce similarly sized clutches. Females laying late in the photoinduced breeding phase should have greater incubation tendency and smaller clutch sizes than females laying early. Incubation tendency during the laying cycle should be greater in females laying small than in females laying large clutches.

Physiological constraints may limit the ability of organisms to adapt to their environments (Jacobs and Wingfield 2000). For the seasonal change in clutch size to evolve, the mechanistic basis of clutch size regulation must also evolve. If the Meijer and coworkers' model is correct, the evolution of seasonal change in clutch size would give rise to a potential cascade of fitness consequences associated with incubation behavior and laying date. Thus, understanding the evolution of seasonal change in clutch size re-

lies, in part, on understanding the proximate mechanisms responsible for clutch size regulation. To determine whether this model for regulation of the seasonal decline in clutch size applies to a species closely related to the European Kestrel, we investigated the relationships among laying date, clutch size, and incubation tendency in free-living and laboratory American Kestrels.

## METHODS

### FIELD STUDY

We hung nest boxes (inside width  $\times$  depth  $\times$  height: 17.4  $\times$  16.3  $\times$  33.8 cm) at approximately 0.5-km intervals along roadsides within a 35-km radius of the Washington State University campus (Pullman, Washington; 46°44'N, 117°10'W). Originally a temperate steppe ecoregion (Bailey 1998), this area has undergone widespread conversion mainly to wheat, barley, and pea farming. We hung boxes 2–3 m high on trees or posts and provided pine shavings in each to protect eggs from the hard floor and to conceal thermistors (see below).

During spring of 1997, 1998, and 1999, we checked boxes every 3–4 days for signs of occupancy. We estimated date of clutch initiation using the modal laying interval of 2 days and the number of eggs in the nest when we first observed laying in a box. Laying intervals of 1 and 3 days sometimes occur, and due to this variation, we may have erred by 1 or 2 days in estimating date of clutch initiation in some nests (checking boxes too frequently causes pairs to abandon them). During laying, we checked boxes every 1–3 days and numbered new eggs with a permanent marker. We captured adults in nest boxes or with a bal-chatri trap (Berger and Mueller 1959) and affixed to them U.S. Fish and Wildlife Service bands as well as color bands.

After laying had begun, we taped a thermistor to the nest floor and connected it through a small hole in the floor to a temperature logger (Onset Computer Corp., Pocasset, Massachusetts) positioned on a shelf 3 cm below this false bottom. We placed a second logger on the shelf to record temperature of the nest's immediate surroundings (ambient temperature). Due to the proximity of the nest thermistor to the ambient temperature logger (3–10 cm) and their similar environments (they were in the same partially enclosed box but separated by the false bottom), ambient conditions affected both temperature re-

corders virtually equally. Only the presence of a warm object (i.e., an incubating bird) immediately adjacent to the nest thermistor would cause a divergence in the two temperature readings. These divergences were rapid, transient, and could occur at any time of the day, suggesting the nest thermistor and ambient temperature logger were not differentially exposed to environmental factors such as solar radiation (see Fig. 1 in Sockman and Schwabl 1998). Loggers recorded temperatures at intervals of approximately 3–5 min. We defined incubation as any time the nest was more than 5 Celsius degrees above ambient temperature, which reflected minimum temperature differences after clutch completion under all ambient temperatures. As indicated in the Introduction, this definition does not necessarily subsume periods when the behavior is sufficient to induce embryonic development. We calculated the percent of the day (beginning and ending at 06:00) spent incubating for each day to quantify female incubation tendency. Males sometimes incubate (Bortolotti and Wiebe 1993). However, in our population, incubation temperatures during laying were strongly associated with the presence of a female in the box and are a reliable measure of female behavior (Sockman et al. 2000). The days during laying for which we recorded incubation tendency varied among nests and depended on how early in laying we discovered nests (i.e., on the 1st versus 3rd egg) and how early we removed our limited number of temperature loggers for use in newly initiated nests.

### LABORATORY STUDY

On 10 December 1997, we obtained American Kestrels (all 3.5 years old) from researchers at McGill University (Quebec, Canada) where they had been held in outdoor aviaries on a naturally changing photoperiod. These birds were born and raised in captivity as were several generations of their progenitors. We randomly formed 18 pairs in individual pens, all in one room with a photoperiod of 8-hr light and 16-hr dark (8L 16D). We provided pairs with water and fed them 2–4 frozen-then-thawed one-day-old cockerel chicks per day. We equipped pens (approximately 0.7 m wide by 2.3 m high by 2.0 m deep) with perches and a nesting box (as in the field). We quantified incubation tendency as in the field study, with the exception that a single logger recorded room temperature, which we

compared to nest temperature to detect incubation. During laying, our laboratory males rarely entered nest boxes, so temperature records reflect changes in female behavior.

On 24 January 1998 we changed the photoperiod to 10L 14D, on 31 January to 12L 12D, and on 7 February to 14L 10D (similar to late April at the latitude of the field study). We checked nest boxes twice daily and marked new eggs. We removed eggs after clutch completion to induce renesting. The mean time between clutch completion and egg removal was 14 days (range 6–39 days), always at a time well into incubation. To induce a second breeding period, we changed the photoperiod to 8L 16D on 4 June 1998, and then on 9 October 1998, we changed the photoperiod to 10L 14D, stepped it by 2-hr intervals per week to 14L 10D, and recorded the days on which females initiated clutches.

#### STATISTICAL ANALYSES

We used linear regressions to examine the relationships between (1) clutch size and progress of the breeding phase (days after 1 April) in the field, (2) incubation tendency and progress of the breeding phase in the field, (3) time to renest and day of clutch initiation in the laboratory, and (4) day of clutch initiation in the second breeding phase and day of clutch initiation in the first breeding phase in the laboratory. In the laboratory study, we used analysis of covariance for repeated measures with progress of the photo-induced breeding phase (days after onset of 14L 10D) as a covariate to determine the effects of progress of the breeding phase and nest number on clutch size. We used a contingency table to determine whether clutch size in renests was independent of clutch size in first nests. Finally, we used analysis of variance with two hierarchical levels of repeated measures to determine the relationship between clutch size and incubation tendency in first and renests (first level) and among days after onset of laying (second level). After removing the nonsignificant factor clutch size, we used this model to examine the change in incubation tendency between first and renests. For statistical analysis, we used SuperAnova (Abacus Concepts 1991) and StatView (SAS Institute 1998), each for the Macintosh.

#### RESULTS

In the field study, we obtained both clutch initiation dates and incubation data for 56 nests (although the days during laying for which we have incubation data vary among nests), both clutch initiation dates and clutch sizes for 47 nests, and both clutch sizes and incubation data for 46 nests. Clutches were initiated from 8 April–25 June (11 April–23 June in nests with known clutch sizes), and clutch size ranged from 2–6 eggs over this 74-day period of clutch initiation. It is possible that some nests were renests rather than first nests of the season. However, this possibility should not influence the interpretation of our findings because the Meijer and coworkers' model should apply to renests as well.

In the laboratory study, of 16 females that laid in the first breeding period, there were 15 from which we collected incubation data and which completed clutches (for their first nests). We have incubation data for nine of 10 females that renested. All 16 laid in the second breeding period. Clutches were initiated from 26–102 (26–68 excluding renests) days after onset of 14L 10D. Clutch size ranged from 4–6 eggs over the 77-day period of clutch initiation in the laboratory. The modal clutch size for both the laboratory and field was five eggs, and variation in clutch size did not differ between the laboratory and field studies (Levene's test:  $F_{1,61} = 1.0$ ,  $P > 0.2$ ).

#### CLUTCH SIZE AND PROGRESS OF THE BREEDING PHASE

In the field, clutch size declined with progress of the breeding phase ( $F_{1,45} = 37.5$ ,  $P < 0.001$ ,  $r^2 = 0.45$ ), with the vast majority of clutch sizes being four ( $n = 15$ ) or five ( $n = 24$ ) eggs (Fig. 2a). The mean clutch-initiation date of small (<5-egg) clutches was 21.0 days after the mean clutch-initiation date of large (5 and 6-egg) clutches.

In the laboratory (Fig. 2b), clutch size did not vary with progress of the breeding phase ( $F_{1,15} = 0.1$ ,  $P > 0.2$ ) or from first to renests ( $F_{1,7} < 0.1$ ,  $P > 0.2$ ). When we considered only first nests, there was still no relationship between clutch size and progress of the breeding phase ( $F_{1,14} = 1.9$ ,  $P = 0.19$ ). Of 10 laboratory females that renested in response to egg removal, nine laid clutches equivalent in size to their first nests. Clutch size of first nests significantly predicted that of renests (Table 1;  $\chi^2_4 = 15.3$ ,  $P <$

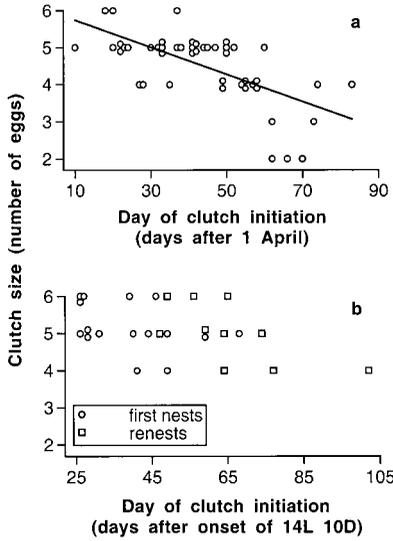


FIGURE 2. Change in clutch size with progress of the breeding phase in (a) free-living and (b) laboratory American Kestrels.

0.01). The mean clutch-initiation date of renests was 26.5 days after the mean clutch-initiation date of first nests.

CLUTCH SIZE AND INCUBATION TENDENCY

Because of the rarity of 2, 3, and 6-egg clutches in the field, we analyzed the relationship between clutch size and incubation tendency only for 4 and 5-egg clutches. We did not collect incubation data for one 5-egg clutch. We found no main effect of clutch size on incubation tendency (Fig. 3a;  $F_{1,36} = 0.6, P > 0.2$ ). However, the interaction between clutch size and day after onset of laying was significant ( $F_{5,140} = 2.3, P < 0.05$ ). Post-hoc linear contrasts indicated that the difference in incubation tendency between 4 and 5-egg clutches was significant ( $P < 0.05$ ) at 6 days after onset of laying but not at other days. We had very few temperature records for the first day of laying and therefore did not include this day in statistical analyses (for the field study). Beyond 6 days after onset of laying, most females producing clutch sizes of four eggs had finished laying, whereas females producing 5-egg or larger clutches were still laying. We were interested only in incubation tendency during the laying period. Therefore, we limited statistical analyses to incubation data for 1–6 days after onset of laying.

In the laboratory, we analyzed incubation data

TABLE 1. Frequency of clutch sizes of first nests and renests in laboratory American Kestrels. Clutch size of first nests significantly predicted that of renests ( $\chi^2_4 = 15.3, P < 0.01$ ).

Clutch size of renests	Clutch size of first nests		
	4 eggs	5 eggs	6 eggs
4 eggs	2	1	0
5 eggs	0	4	0
6 eggs	0	0	3

for each of days 0–6 after onset of laying. We did not have incubation data for one 5-egg female. Using first nests only, we found no relationship between clutch size and incubation tendency (Fig. 3b) when we included all clutch sizes ( $F_{2,12} = 1.4, P > 0.2$ ). Incubation tendency in 4-egg females seemed unusually low during this portion of laying. When we excluded them from the analysis, we still found no relationship between clutch size and incubation ( $F_{1,11} = 0.3, P > 0.2$ ). Interactions between clutch size and days after onset of laying were also not significant. We also analyzed the relationship between clutch size and incubation with both first and

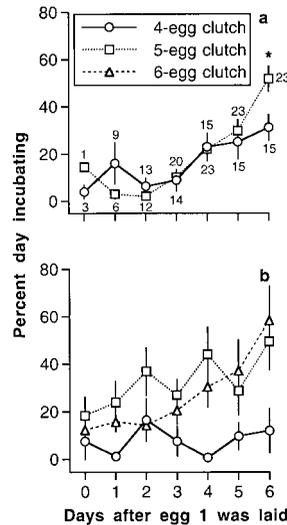


FIGURE 3. Relationship between incubation tendency (mean  $\pm$  SE) during laying and clutch size in (a) free-living and (b) laboratory American Kestrels. We indicate next to the points the number of free-living females used in each estimation of incubation. In the laboratory, sample sizes are 2 for 4-egg clutches, 8 for 5-egg clutches, and 5 for 6-egg clutches. The asterisk indicates a significant ( $P < 0.05$ ) difference between clutch sizes based on post-hoc linear contrasts.

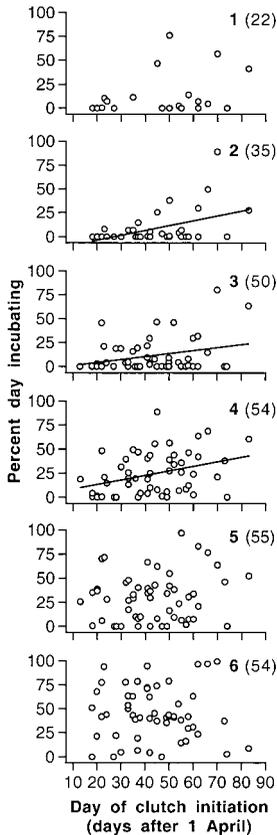


FIGURE 4. Change in incubation tendency with respect to progress of the breeding phase in free-living American Kestrels at 1, 2, 3, 4, 5, and 6 days after females laid egg 1 of the clutch. In parentheses we indicate the number of females in each plot.

renests included in the model, excluding the one female whose clutch size changed between first and renests. We again found no relationship between clutch size and incubation tendency ( $F_{2,11} = 0.2$ ,  $P > 0.2$ ).

#### INCUBATION TENDENCY AND PROGRESS OF THE BREEDING PHASE

To examine change in incubation tendency with progress of the breeding phase in the field, we regressed incubation tendency on date of clutch initiation for each of days 1–6 after onset of laying (Fig. 4). We found a significant, seasonal rise in incubation tendency on days 2 ( $F_{1,33} = 8.4$ ,  $P < 0.01$ ,  $r^2 = 0.20$ ), 3 ( $F_{1,48} = 4.3$ ,  $P < 0.05$ ,  $r^2 = 0.08$ ), and 4 ( $F_{1,52} = 6.9$ ,  $P < 0.02$ ,  $r^2 = 0.12$ ) but not on days 1 ( $F_{1,20} = 2.3$ ,  $P = 0.15$ ), 5 ( $F_{1,53}$

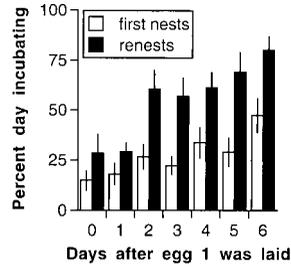


FIGURE 5. Incubation tendency (mean  $\pm$  SE) during the laying period for first ( $n = 15$ ) and renests ( $n = 9$ ) of laboratory American Kestrels.

= 1.2,  $P > 0.2$ ), or 6 ( $F_{1,52} < 0.1$ ,  $P > 0.2$ ) after onset of laying.

In the laboratory, the period during which females laid first clutches was quite short compared to the laying period in the field. Therefore, to examine change in incubation tendency with progress of the breeding phase in the laboratory, we compared incubation tendency between first and renests (Fig. 5). We found that incubation tendency in renests was significantly greater than that in first nests ( $F_{1,8} = 27.9$ ,  $P < 0.001$ ). The mean daily incubation tendency over days 0–6 after onset of laying in renests was 55%, greater than twice that in first nests (27%). The interaction between nest and day was not significant, indicating that there was a general rise in incubation with respect to nest number, irrespective of the day on which we measured incubation.

#### WITHIN-FEMALE PREDICTABILITY IN TIME TO LAYING

Time from onset of photostimulation to onset of laying (first breeding period) positively correlated with time from egg removal to renesting ( $F_{1,8} = 7.4$ ,  $P < 0.03$ ,  $r^2 = 0.48$ ), even when we controlled for time from clutch completion to egg removal by adding it to the model ( $F_{1,7} = 7.3$ ,  $P < 0.04$ ,  $r^2 = 0.55$ ). This indicates that females that lay early in the breeding phase tend to respond quickly to egg removal by renesting (Fig. 6a). Renesting intervals may depend on the time from clutch completion to egg removal. A relationship between time from clutch completion to egg removal and either variable in Figure 6a might render the correlation in Figure 6a spurious. But time from clutch completion to egg removal was not related to either the independent (linear regression:  $F_{1,8} < 0.1$ ,  $P > 0.2$ ) or

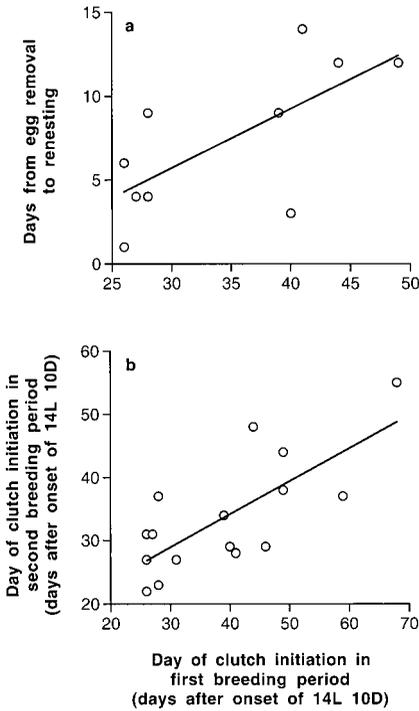


FIGURE 6. Relationship (a) between time from photostimulation to clutch initiation and time from egg removal to renesting in the first breeding period and (b) between time from photostimulation to clutch initiation in the first and second breeding periods in American Kestrels.

dependent ( $F_{1,8} = 0.7, P > 0.2$ ) variables, indicating that our methods did not bias our results. Time to onset of laying in the first breeding period was positively correlated with that in the second breeding period ( $F_{1,14} = 16.9, P < 0.01, r^2 = 0.55$ ), indicating that females that lay early in one breeding phase tend to lay early in a subsequent breeding phase (Fig. 6b).

DISCUSSION

In free-living American Kestrels, clutch size declined and incubation tendency increased over the course of the breeding phase. In the laboratory, clutch size varied as much as in the field, but did not decrease over the course of the breeding phase. However, incubation increased with progress of the breeding phase in the laboratory, just as it did in free-living birds. In neither the laboratory nor the field was incubation tendency during laying associated with clutch size. Thus, in the laboratory, where environmental conditions were homogeneous, the relation-

ship between clutch size and incubation was uncoupled; clutch size varied independently of incubation, and incubation varied independently of clutch size.

Our results are consistent with components 1 and 2 (see Introduction) of the Meijer and co-workers model for proximate regulation of the seasonal decline in clutch size. We observed a clear rise in incubation tendency with respect to the breeding phase in free-living (Fig. 4) and also in laboratory kestrels, as indicated by their enhanced levels of incubation during laying of renests over first nests (Fig. 5). Because we maintained laboratory kestrels on a constant photoperiod, these results are consistent with the idea that the seasonal rise in incubation is endogenously programmed (Meijer et al. 1990). Further, as in many species, there is a steep rise in incubation tendency over the course of laying. Of note is that the seasonal rise in incubation in the field did not occur for all of the 6 days after onset of laying. Incubation tendency may be too low during early laying (day 1) and too high during late laying (days 5 and 6) to show any seasonal change.

In Great Tits (*Parus major*; Haftorn 1981), European Starlings (*Sturnus vulgaris*; Meijer 1990), and possibly American Kestrels in northern Canada (Bortolotti and Wiebe 1993), the rate at which incubation tendency increases during laying is negatively associated with clutch size. In both Great Tits and starlings, clutch size declines seasonally as it did in our field study. The relationship between clutch size and incubation may be the result of independent seasonal changes in clutch size and incubation rather than a reflection of a causal relationship. Our study indicates that the negative association between incubation and clutch size found in some studies may be due to a seasonal increase in incubation and an independent seasonal decrease in clutch size.

Inconsistent with components 3 and 4 of the model by Meijer and co-workers, our results suggest that clutch size may vary independently of season and environmental conditions and that incubation tendency may not regulate seasonal change in clutch size. First, we observed as much variation in clutch size in laboratory females held under very similar environmental conditions as we observed in the field, where environmental conditions are likely to promote variation in clutch size. Clutch size was equally

variable among laboratory and free-living kestrels, notwithstanding a much shorter population-wide laying period in laboratory than in free-living females. In other words, variation in clutch size in the laboratory was independent of time to laying (Fig. 2b). Our findings are similar to those from European Kestrels in which clutch size and laying date become dissociated when feeding conditions are manipulated (Aparicio 1994). However, of particular importance is the fact that, in our study, variation in clutch size occurred under homogeneous environmental conditions. Further, we cannot attribute our failure to observe a relationship between clutch size and incubation tendency or between clutch size and progress of the breeding phase to a lack of variation in clutch size in the laboratory. In fact, clutch-size variation in the laboratory was not significantly different from that in the field.

Second, even though more time elapsed between the mean clutch-initiation dates of first and renests in the laboratory than between the mean clutch-initiation dates of large and small clutches in the field, in the laboratory clutch size did not decline over that period (Table 1, Fig. 2b). This is despite a profound rise in incubation tendency between first and renests (Fig. 5). The lack of change in clutch size between first and renests contrasts with another study on captive American Kestrels (Bird and Laguë 1982) in which forced reneesting caused a decline in clutch size. In that study, the reneesting interval (time between first and reneest) was substantially less, on average, than that for our study, and kestrels were exposed to natural photoperiods, possibly causing the disparity with our results. In fact, the mechanistic basis for the seasonal decline in clutch size may be related to seasonally changing photoperiod or other factors such as seasonally changing light intensity. However, these possibilities do not implicate a regulatory role for incubation tendency, which we found increased substantially from first to renests under constant environmental conditions (Fig. 5).

Third, clutch size and incubation tendency were not inversely related in the field or laboratory (Fig. 3). In fact, if anything there was some suggestion of a positive relationship, as evidenced by the relatively low incubation tendency in 4-egg laboratory clutches and the enhanced incubation in 5-egg compared to 4-egg field clutches at 6 days after clutch initiation. In the laboratory, the lack of relationship between

incubation and clutch size may have been because clutch size varied irrespective of progress of the reproductive phase.

As mentioned previously, several lines of evidence implicate a role for the hormone prolactin in the development of incubation behavior during laying. This role has now been confirmed for the American Kestrel (Sockman et al. 2000). However, that study suggests that prolactin may not be involved in the regulation of clutch size, further supporting the notion that clutch size and incubation tendency may be proximately regulated by different mechanisms. Taken together, our results do not support the hypothesis that a seasonal increase in incubation tendency induces a seasonal decline in clutch size in the American Kestrel.

Manipulations of factors such as food availability indicate that phenotypic plasticity clearly accounts for some variation in clutch size and laying date (Meijer et al. 1988, Aparicio 1994, Kelly and Van Horne 1997, Korpimäki and Wiehn 1998). However, both clutch size and laying date may have genetic components, as well. Some females are genetically predisposed to lay large or small clutches (Gwinner et al. 1995). Similarly, some are genetically predisposed to lay early in the season and others late (Lambrechts et al. 1997). Our laboratory females that laid early not only reneested quickly after egg removal but also laid early in a second breeding period (Fig. 6). Similarly, under homogeneous environmental conditions, these females tended to lay identical clutch sizes early and late in the reproductive phase (Table 1). Thus, inter- as opposed to intra-individual differences seem to give rise to a large component of the variation in both clutch size and laying date. We propose that both clutch size and laying date during a particular breeding season are, in part, inherent, correlated properties of a particular female, unregulated by her tendency to incubate.

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partment of Zoology, Washington State University). HS was supported by NIMH grant number MH 49877. We adhered to standards of the Washington State University Institutional Animal Care and Use Committee (in accordance with the National Institutes of Health) for the humane treatment of our subjects.

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