

DETERMINATION OF CLUTCH SIZE AND THE BREEDING BIOLOGY OF THE SPUR-WINGED PLOVER (*VANELLUS SPINOSUS*) IN ISRAEL

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ABSTRACT.—The breeding biology of the Spur-winged Plover (*Vanellus spinosus*) was studied in an agricultural area in central Israel from 1989 through 1993. The breeding season extended from March to September. The average clutch size was 3.4 eggs and modal clutch size was four eggs. Clutch size declined slightly during the season. Eggs were laid at about two-day intervals. The average incubation period was 28 days, but it declined during the season in correlation with increased ambient temperatures and laying order. In four-egg clutches the last egg was incubated 3.4 days less than the first. Hatching of a four-egg clutch was asynchronous and lasted 1.9 days. Field hatchability was 86.4% of all eggs laid. In the laboratory, the highest hatching success (97.7%) occurred at an incubation temperature of 37.5°C. Field experiments showed that in four-egg clutches incubation temperature was significantly higher, incubation periods tended to be shorter (but not significantly so), and hatching success was higher (but not significantly so) in comparison with artificially enlarged five-egg clutches. This lends some, but not unequivocal, support to the hypothesis that clutch size may be limited by incubation ability. However, females whose clutches were removed upon completion were capable of laying continuously without altering either clutch or egg size, suggesting that clutch size is not limited by egg-formation abilities. Received 5 December 1994, accepted 25 April 1995.

THE CLUTCH SIZE of most bird species is variable, but in several groups intraspecific variation is very small. Among Temperate Zone members of the Charadrii, four-egg clutches are the norm (Winkler and Walters 1983). This constancy raises the question: is there a limiting factor preventing larger clutch sizes? Three main hypotheses have been suggested to explain this phenomenon: (1) the incubation-ability hypothesis proposes that parents are limited by their ability to cover eggs and incubate them effectively (Perrins and Birkhead 1983, Szekely et al. 1994); (2) the egg-formation hypothesis proposes that the ability of a female to produce eggs may be limited (Perrins and Birkhead 1983); and (3) the parental-care hypothesis claims that clutch size is limited by the parental ability to protect eggs and hatchlings (Perrins and Birkhead 1983, Safriel 1975, Szekely et al. 1994). However, only a few attempts have been made to test the above hypotheses in shorebirds (Safriel 1975, Walters 1982, Shipley 1984, Lank et al. 1985, Kalas and Lofaldi 1987, Szekely et al. 1994).

The Spur-winged Plover (*Vanellus spinosus*) is the most common charadriid species resident in Israel. During the last three decades, it has spread from river banks and other natural water bodies

in the north of the country to fish ponds, water reservoirs, road banks, airports, and agricultural areas in northern and central Israel (Paz 1987). The meager information published on its breeding biology has been summarized by Cramp and Simmons (1983). Like most other species in the Charadriiformes, this species typically has four-egg clutches.

We studied the breeding biology of Spur-winged Plovers to determine if clutch size is limited to four eggs by an inability to produce more eggs and/or an inability to incubate a larger clutch. The data also enabled us to determine the effect of incubation temperature on hatching success in this species.

MATERIALS AND METHODS

Our study was conducted in an agricultural area of about 0.6 km² in Kibbutz Giv'at Hayyim (32°23'N, 34°55'E) during the breeding seasons (March–September) of 1989 through 1992 (Yogev 1993). The study site was located in the Mediterranean coastal plain 20 to 30 m above sea level; it has a mild climate with about 600 mm rainfall and mean annual temperatures ranging between 9° and 17°C in January, and between 21° and 31°C in August.

Birds were trapped using metal-wire traps set on their nests. Each individual was tagged with a unique

TABLE 1. Morphological data ($\bar{x} \pm SD$) for 78 male and 78 female Spur-winged Plovers. Left and right wings and spurs of the same individuals are not significantly different.

Variable	Males	Females	<i>t</i> -values
Body mass (g)	191.5 \pm 9.4	183.8 \pm 10.2	4.90***
Bill length (mm)	27.2 \pm 1.3	26.7 \pm 1.3	2.45**
Wing length (mm)	203.0 \pm 5.0	200.7 \pm 4.9	2.91**
Spur length (mm)	10.0 \pm 1.8	7.5 \pm 2.0	8.17***

P* < 0.01; *P* < 0.001.

combination of a numbered metal and three plastic color bands, using two bands on each tibia. The length of both wings, spurs, and beak (exposed culmen) were measured with metal calipers to 1-mm accuracy, and body mass determined to within 1 g using a Pesola spring balance. Observations were made with binoculars and telescope from blinds. All nests found were marked and visited at least once daily, and each egg was individually marked with a felt pen, weighed with a Pesola spring balance to 0.1-g accuracy, and measured for length and breadth with metal calipers to 0.1-mm accuracy.

In order to evaluate the incubation-ability hypothesis, we measured temperatures of incubated eggs in four- and five-egg clutches by implanting copper-constantan thermocouples in dummy eggs made from original egg shells filled with polyacrilamid and ammonium sulfate gel. We changed the filling to plaster of Paris after numerous eggs were damaged by the incubating birds. Heat conductance of plaster (Weast 1986) is very similar to that of real eggs (Henderson 1963). All four eggs in a nest were replaced with dummy eggs, and one additional dummy egg was hung about 5 cm above the ground in a shady place near the nest in order to determine air temperature. Another dummy egg was one-half buried in the ground in order to determine ground-surface temperature. All thermocouples were connected to a Campbell Micrologger 21X, where values were recorded every 30 s and averaged for 10 consecutive measurements. Temperatures were recorded in each nest for two days, and each measurement period lasted 6 h. The data presented in the Results section are for continuous incubation sessions, which occur in this species between 0900 and 1500 during the day and 2100 and 0300 during the night. Temperatures were recorded for gel-filled eggs in four clutches during 1990, and for plaster eggs in eight clutches during 1991. In total, we had 16 6-h measuring periods with four-egg clutches during the day and 16 similar periods during the night. The same procedure was repeated for five-egg clutches.

Egg volume (*V*) was calculated using the equation

$$V = 0.5LB^2, \quad (1)$$

where *L* is egg length and *B* is breadth (in millimeters; Hoyt 1979). Only eggs whose mass was determined on the day of laying were included.

In 1991, eggs were incubated in Victoria incubators in which temperatures and humidities were controlled so that the daily mass loss of an egg was 0.5% of its initial mass per day (calculated total of 15% mass loss throughout incubation as expected in normal incubation; Ar and Rahn 1980). Eggs were incubated at five temperatures: 32.5°, 33.5°, 35.0°, 37.5°, and 38.5°C. At each of the above temperatures, 44 eggs from at least 11 nests were incubated. Whole clutches were taken for incubation on the day of laying of the last egg.

In order to test the female egg-formation hypothesis, during the breeding season of 1991 we removed all the eggs from nine nesting females on the day of laying of the fourth egg, and repeated this procedure for a mean of 99 days. The rationale for this procedure was that, if the laying potential of the female is limited, the frequent removal of a clutch would cause the female to reduce either clutch size or egg size.

Permission to use eggs and manipulate nests was obtained from the Israel Nature Reserve Authority. Conventional linear statistics were used throughout. All mean values are accompanied by $\pm SD$.

RESULTS

Morphological data, breeding season, and clutch size.—We banded 202 adult birds during three years. For the 101 pairs we could identify 78 males and 78 females by their behavior. Morphological data on the sex-identified birds are given in Table 1. On the average, males have significantly longer (by 32%) spurs, beaks (1.8%), and wings (1.1%) than females, and are significantly heavier (by 4%) than females. There was a significant positive correlation between female mass and the mean volume of her eggs ($r = 0.40$, $P < 0.001$).

In each year of the study, laying started in mid-February and ended in September. Since there were no significant differences in clutch size among years (ANOVA, $F_{2, 545} = 0.34$, $P = 0.71$), the data are pooled. Mean clutch size was 3.4 ± 0.84 eggs ($n = 632$). In our sample, 60% of the clutches had four eggs, 30% contained three eggs, and the remainder had one or two

eggs. In most of the nests with less than four eggs, we found that eggs disappeared without leaving traces during laying or incubation periods; thus, the actual mean clutch size is probably closer to four. Clutch size declined during the breeding season from an average of 3.75 between mid-February until the end of May to 3.24 eggs during June (one-way ANOVA with Duncan's multiple range test, $F_{9,544} = 6.34$, $r = 0.857$, $P < 0.001$). On average, it took a female 5.48 ± 0.62 days ($n = 120$) to lay a four-egg clutch, or 3.75 ± 0.43 days ($n = 57$) to lay a three-egg clutch. The mean time interval between the laying of the first and second eggs was 1.98 days ± 0.08 ($n = 177$), between the second and third eggs 1.77 ± 0.42 days ($n = 177$), and between the third and fourth eggs 1.72 ± 0.47 days ($n = 120$).

Egg dimensions.—The mean length and breadth of the eggs were 39.9 ± 1.6 mm ($n = 2,110$) and 28.6 ± 0.8 mm ($n = 2,110$), respectively. There was a significant linear relationship between the calculated fresh egg volume (V in cm^3) and its mass (M in grams):

$$M = 0.93 + 0.99V, \quad (2)$$

($r = 0.964$, $P < 0.001$, $n = 736$). Egg volume did not vary among years (ANOVA, $F_{2,2109} = 2.09$, $P = 0.124$), but mean egg volume varied during the breeding season (one-way ANOVA with Duncan's multiple-range test, $F_{10,2109} = 3.98$, $P < 0.001$). The difference between the minimum and maximum two-week average was only 3.9%. There were significant, though small, differences in egg volumes in relation to laying order (ANOVA with repeated measures, $F_{3,1030} = 12.18$, $P < 0.001$; only four-egg clutches included). The difference between the third (biggest) and fourth laid (smallest) eggs was only 2%. No differences in either color or marking in relation to clutch sequence were noticed.

Duration of incubation and hatching success.—The incubation period (time from egg laying until hatching) did not vary among years (ANCOVA with repeated measures, $F_{2,45} = 2.81$, $P = 0.07$); thus, data were pooled across years. The mean incubation period of individual eggs in four-egg clutches was 28.15 ± 1.78 days ($n = 39$), and declined significantly during the season (Fig. 1; ANCOVA with repeated measures, $F_{1,45} = 14.57$, $P < 0.001$), probably due to increasing ambient temperature. There was an interaction between incubation period of the eggs in relation to their laying order with the time

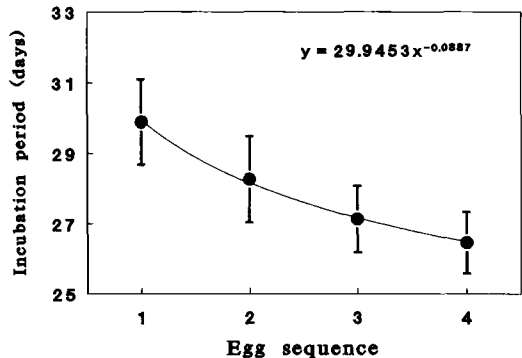


Fig. 1. Incubation period ($\bar{x} \pm \text{SD}$) of single eggs in four-egg clutches in relation to their order of laying ($n = 49$ clutches).

in season (ANCOVA with repeated measures, $F_{1,137} = 11.53$, $P < 0.001$), which declined from the first to last laid egg (Fig. 2). The incubation period shortened in relation to order of laying (ANCOVA with repeated measures, $F_{3,137} = 6.69$, $P < 0.001$), with a 3.44 days difference in incubation period between the first and last eggs. The interaction effect indicates that hatching asynchrony became more pronounced as the season progressed because first-laid eggs developed even more rapidly than the fourth laid eggs, probably due to higher ambient temperatures causing embryo development without parental incubation.

Hatching was asynchronous, with an average hatching time between the first and last egg of 1.90 ± 0.99 days ($n = 100$). Eggs typically hatched in the order they were laid with a time interval of 0.44 ± 0.57 days, 0.63 ± 0.71 days, and 0.83 ± 0.75 days between the first and second, second and third, and third and fourth eggs, respectively.

There was no significant difference in hatching success (percent eggs hatched) among the years (ANCOVA with repeated measures, $F_{2,228} = 2.38$, $P = 0.09$), or during the breeding season (ANOVA, $F_{4,228} = 1.09$, $P = 0.36$). Hence, all results were pooled. Hatching success of three- and four-egg clutches (which comprised 30 and 60% of all clutches, respectively) was $86.4\% \pm 21.1$ ($n = 229$), and there was no significant difference between four- and three-egg clutches. There was no significant difference between the years in the percentage of nests in which eggs hatched ($X_2^2 = 2.87$), and 51.26% of the 539 clutches found during this study produced

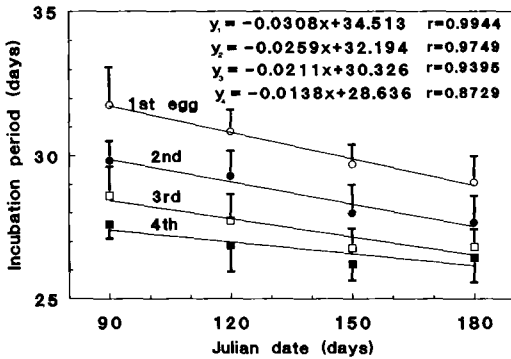


Fig. 2. Relationship between incubation period ($\bar{x} \pm SD$) in the field and Julian date of first, second, third and fourth egg in a clutch. Regression equations for each egg and their correlation coefficients are presented. Equation for y_1 refers to first egg, y_2 to second egg, etc.

hatchlings. The eggs in the other nests were either predated, mainly by Hooded Crows (*Corvus corone*) or Egyptian Mongooses (*Herpestes ichneumon*), or disappeared.

Incubation temperature.—During 1990 and 1991 we used gel-filled and plaster eggs respectively, but there was no significant difference in average egg temperatures between years (ANCOVA with repeated measures, $F_{1,12} = 0.14, P = 0.72$). Hence, results from the two years were pooled (Table 2). Egg temperatures during the day were significantly higher than those measured at night by an average of 1.6° and 1.9°C in four- and five-egg clutches, respectively (ANCOVA with repeated measures, $F_{1,14} = 22.34, P < 0.001$), and in-nest egg temperatures in four-egg clutches were significantly higher than in five-egg clutches by 0.3° and 0.6°C during day and night, respectively (ANCOVA with repeated measures, $F_{1,12} = 7.46, P = 0.018$). The incubation period tended to be shorter in four-egg than in five-egg clutches (four-egg clutches

TABLE 2. In-nest temperatures (°C; $\bar{x} \pm SD$) of dummy eggs in the field. All temperature values (°C) are significantly different from each other ($P < 0.02$).

	Mean in-nest temperature		Ambient temperature	
	Four-egg clutch	Five-egg clutch	Air	Soil
<i>n</i>	12	12	—	—
Day	37.1° ± 0.80°	36.8° ± 0.99°	35.2°	46.6°
Night	35.5° ± 0.78°	34.9° ± 1.00°	21.5°	23.3°

TABLE 3. Effect of incubator temperature on incubation periods ($\bar{x} \pm SD$) and hatching success of artificially incubated eggs.

Temperature (°C)	Incubation		Hatching success	
	Period (days)	<i>n</i> (eggs)	Percent	<i>n</i> (eggs)
32.5	—	1	2.2	46
33.5	31.31 ± 0.67	16	70.6	51
35.0	27.61 ± 1.03	36	93.2	44
37.5	27.00 ± 0.84	40	97.7	44
38.5	25.78 ± 0.65	36	90.9	44

27.94 ± 1.69 days, $n = 39$; five-egg clutches, 28.56 ± 0.83 days, $n = 17$), and hatching success was higher (four-egg clutches, 86.91% ± 21.47, $n = 149$; five-egg clutches, 83.48% ± 17.74, $n = 23$). However, these results were not statistically significant ($P > 0.05$).

The effect of incubation temperature on incubation period and hatching success was tested in the laboratory by incubating four-egg clutches at five temperatures ranging between 32.5° and 38.5°C. Only 1 of the 46 eggs incubated at 32.5°C hatched; hence, this temperature was not included in further analysis. There was a significant negative correlation between incubation temperature and incubation period (Table 3; ANOVA with repeated measures, $F_{3,28} = 68.34, P < 0.001$). Incubation period was shortened with respect to laying order (ANOVA with repeated measures, $F_{3,84} = 86.51, P < 0.001$), and there was an interaction between the period of incubation in relation to laying order and incubation temperatures (ANOVA with repeated measures, $F_{9,84} = 4.84, P < 0.001$). The incubation temperature affected hatching success (Table 3; $X^2 = 19.219, P < 0.001$); success was highest at 37.5°C.

Repetitive clutch removal.—Most re-layings took place in new sites, and we did not notice any adverse effect of the experimental treatment on the females. The results of repetitive whole clutch removals are presented in Table 4 and show that females were able to lay another clutch within an average of 12 days of clutch removal; over a average period of 99 days, females laid an average of 6.6 clutches. There was no significant difference in clutch size and time taken to lay a clutch of the females used in the experiment and the population average. Mean egg volume did not change during the experiment (regression coefficients of egg volume against

TABLE 4. Values for females from experiment in which clutch was repetitively removed from nine nesting females on day of laying of fourth egg.

Variable	$\bar{x} \pm SD$
Female mass (g)	183 \pm 9
Period (days) ^a	99 \pm 19
No. clutches laid	6.56 \pm 0.73
Clutch size	3.56 \pm 0.22
Total no. eggs	23.4 \pm 2.96
Total egg mass (g)	403.0 \pm 54.8
Mean egg mass (g)	17.30 \pm 1.09
Time between clutches (days) ^b	12.25 \pm 3.09
Laying period (days)	4.80 \pm 0.33

^a Duration of experiment.

^b Days from removal of clutch until laying of first egg of next clutch.

date for nine experimental females ranged from -0.0093 to 0.0114).

DISCUSSION

Clutch size and egg size of the Spur-winged Plover were remarkably stable during the breeding season, but incubation periods declined significantly during the season and in relation to laying order. The first effect was probably due to the increase of ambient temperatures as the season progressed. The second was due to the incubation behavior of the parents whose nest attentiveness increased in relation to laying order, as indicated in the progressive decrease in both regression coefficients in Figure 2. Calculated incubation periods were 34.51 and 28.64 days, and incubation shortened by 0.031 and 0.014 days for each day for the first and fourth eggs, respectively.

Several hypotheses have been put forward to explain the fact that most Temperate Zone members of Charadrii lay four-egg clutches, and two of these were tested in our study. The incubation-ability hypothesis proposes that a parent is limited by its inability to incubate more than four eggs effectively, and the egg-formation hypothesis proposes that a female is not able to lay more than four eggs per clutch.

Based on our field and laboratory experiments, experimentally enlarged clutches are incubated less effectively than normal ones, but the differences in all parameters (incubation temperature, incubation period, and hatching success) are judged to be small. Szekely et al. (1994) reported for the Kentish Plover (*Charadrius alexandrinus*) that experimentally enlarged clutches took longer to hatch (by average of 3.2

days), and during incubation they lost mass more slowly, indicating cooler egg temperatures and, thus, less effective incubation. They concluded that their results were most consistent with the incubation-ability hypothesis, and our results also give some support to this hypothesis. Kalas and Lofaldi (1987) found that the condition of incubated Dotterel (*C. morinellus*) eggs deteriorated more rapidly in three-egg clutches after these were experimentally enlarged, suggesting that the incubating birds could not incubate enlarged clutches effectively. However, this might be due to uniparental care during incubation in this species.

The results of the clutch-removal experiment showed that females were able to lay renest clutches that did not differ from the population average in clutch size, egg volume or laying interval, thus refuting the egg-formation hypothesis. This is consistent with the conclusion by Szekely et al. (1994) that egg formation in the Kentish Plover is not constrained by food availability. Similar results were reported by Arnold (1992) for the American Coot (*Fulica americana*). We conclude that the incubation-ability hypothesis is most consistent with our results, and that the egg-formation hypothesis is not supported.

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