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Egg viability as a constraint on hatching synchrony at high ambient temperatures

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Summary

1. We tested experimentally the effects of exposure to high ambient temperatures, for periods of 1–9 days, on the viability of eggs of the green-rumped parrotlet.
2. The hatchability of 534 newly laid parrotlet eggs declined after exposure of 3 or more days.
3. The probability of hatching was not significantly affected by the duration or proportion of time exposed to temperatures below physiological zero or above normal incubation range.
4. Incubation periods were negatively correlated with exposure time, suggesting some embryo development occurred prior to incubation.
5. Results presented here corroborate similar studies of temperate zone birds, and suggest that the decline in egg viability may be particularly extreme in hot climates, such as tropical lowlands.
6. We suggest that the relationship between ambient temperature and egg viability could contribute to both seasonal and latitudinal trends in clutch size, hatching success and hatching asynchrony.

Key-words: clutch size, embryo development, *Forpus passerinus*, hatching asynchrony, parrot, temperature, viability.

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Introduction

Many birds initiate incubation before their clutch is complete, which causes eggs to develop and hatch asynchronously (Clark & Wilson 1981; Stoleson & Beissinger 1995) and often results in the mortality of the smallest chicks. Most studies of hatching asynchrony have focused on identifying an adaptive function for the nestling size disparities that result from asynchronous hatching (Amundsen & Slagsvold 1991; Nilsson 1995; Stoleson & Beissinger 1995). The possible functional significance of the early onset of incubation has received scant attention, despite the fact that early incubation is the proximate cause of hatching asynchrony. Potential benefits include protection of eggs from brood parasitism (Wiley & Wiley 1980; Lombardo *et al.* 1989; Romagnano, Hoffenberg & Power 1990), predators (Amundsen & Stokland 1988; Bollinger, Bollinger & Malecki 1990), or intra- or interspecific competitors looking for nest sites (Beissinger & Waltman 1991; Beissinger 1996; Beissinger, Tygielski & Elderd 1998). Initiating incubation before the clutch is completed could also serve to maintain the viability of early laid eggs (Hussell 1985; Arnold, Rohwer & Armstrong 1987; Veiga 1992). This last hypothesis in particular, the 'egg viability hypothesis', may be broadly applicable among birds.

The egg viability hypothesis proposes that avian parents may maximize the hatchability of eggs by initiating incubation before their clutch is completed because the viability of unincubated eggs declines over time (Arnold *et al.* 1987; Ewert 1992). Temperature is the most critical condition affecting hatchability of unincubated eggs, although humidity, gaseous environment, egg orientation and egg turning are also important (Wilson 1991; Deeming 1992; Fasenko *et al.* 1992; Meijerhof 1992). Embryos

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are especially susceptible to death from overheating, are less affected by exposure to cool temperatures, and are susceptible to developmental failure under moderate temperature conditions (Webb 1987).

Hatching failure may often occur because development can begin below normal incubation temperatures. For almost all birds, optimal temperatures for normal embryonic development fall within a narrow range between about 36 and 38 °C, although incubation temperatures recorded in the field can often be a few degrees lower (Drent 1975; Webb 1987; Rahn 1991). Avian embryos do not develop below 24–27 °C (Rol'nik 1970; White & Kinney 1974; Wilson 1991), and this threshold is known as physiological zero (Drent 1973; O'Connor 1984; Webb 1987). When birds in temperate springtime climates delay incubation until the last egg, cold torpor suspends development of earlier eggs, which allows development and hatching to be synchronous (Drent 1975; Ewert 1992). The viability of unincubated eggs maintained in cold torpor declines slowly (Decuypere & Michels 1992; Ewert 1992). However, if ambient temperatures fall between physiological zero and normal incubation temperatures, some, but not all, embryonic tissues begin to develop in the absence of incubation. Prolonged exposure to temperatures above physiological zero yet below normal incubation levels results in unsynchronized growth, abnormal development and embryo mortality (Romanoff & Romanoff 1972; Wilson 1991; Deeming & Ferguson 1992). Development of neurological and brain tissues in very young embryos seems to be particularly sensitive to prolonged exposures to temperatures in this range (Webb 1987). Thus, once development begins, parent birds might be obliged to begin incubation early to maintain the viability of early laid eggs.

A decline in the viability of eggs resulting from prolonged exposure to ambient temperatures has been long known in synchronously hatching domestic fowl but was only recently demonstrated under field conditions in waterfowl (Drent 1973, 1975; Arnold *et al.* 1987; and references therein). Eggs showed a marked decline in hatchability when exposed to ambient temperatures for 5–10 days in a high latitude temperate site (Arnold *et al.* 1987; Arnold 1993). A similar effect was demonstrated more recently in an altricial bird, the house sparrow (*Passer domesticus* Linnaeus) in a Mediterranean climate. Eggs left unincubated for 3 or more days had lower hatching success than those unincubated for shorter periods, and hatching asynchrony increased later in the breeding season when ambient temperatures exceeded physiological zero (Veiga 1992; Veiga & Viñuela 1993). The effects of maintaining unincubated embryos in environments where ambient temperatures are regularly above physiological zero yet below incubation temperatures, such as tropical lowlands, are poorly known (Grant 1982). Presumably, egg viability should decline more rapidly in such environments.

In this paper we present the results of experiments designed to test the egg viability hypothesis in the green-rumped parrotlet (*Forpus passerinus* Linnaeus), a small Neotropical parrot. This species lays very large clutches for a tropical bird, which hatch extremely asynchronously (Beissinger & Waltman 1991). It inhabits hot, humid, tropical savannahs where the potential negative effects of ambient temperatures on unincubated eggs are likely to be especially pronounced. Our previous studies found no significant benefit to parents or offspring from asynchronous hatching in an extensive examination of the fitness consequences and costs of reproduction, but found clear costs in the form of reduced survival of penultimately and last-hatched young compared to synchronously hatched chicks (Stoleson & Beissinger 1997).

We tested the effects of high ambient temperatures on unincubated parrotlet eggs by experimentally subjecting newly laid eggs to varying lengths of exposure to ambient conditions and then returning them to active nests to be incubated normally by parrotlet parents. Unlike prior studies (Arnold *et al.* 1987; Veiga 1992), we assigned each experimental egg a control to account for differences in parental behaviour and nest microhabitat. We also monitored thermal conditions in holding boxes. The hatching success of experimental eggs was compared to unmanipulated control eggs to test the predictions that: (i) exposure of newly laid eggs to ambient temperatures above physiological zero should induce some embryological development even in the absence of incubation (because of this preincubation development, exposed eggs should require less incubation time to hatch than nonexposed eggs subject to similar incubation patterns); (ii) exposure to ambient temperatures should reduce the hatchability of eggs, and the reduction in hatchability should be proportional to the length of exposure; (iii) a greater proportion of embryo mortality in exposed eggs should occur after moderate to advanced development, rather than early development, because prolonged exposure to temperatures above physiological zero but below normal incubation temperatures should result in more embryos experiencing abnormal development; and (iv) the probability of hatching should be related to temperature extremes, duration of exposure to temperatures from 27 to 34 °C, or both.

Methods

STUDY SITE AND SPECIES

Field studies were conducted from May to November 1992–95, at Hato Masaguaral, a working

cattle ranch in the llanos of Gurco, Venezuela. The habitat is lowland, seasonally flooded savanna with patches of woodland (Troth 1979; Beissinger, Thomas & Strahl 1988). We studied a box-nesting population of green-rumped parrotlets, a small parrot that lays large clutches (x = 7·0 eggs, range = 4–10). Because parrotlets begin incubating on the first egg, and the interval between laying of successive eggs varies from 1 to 3 days (x = 1·5 days) hatching averages 10 days for a 7-egg clutch (Beissinger & Waltman 1991; Stoleson & Beissinger 1997).

EXPERIMENTAL PROCEDURES

To simulate delayed incubation, we removed newly laid eggs from nest boxes and sequestered them in secure, vacant nest boxes identical to those used by breeding birds. Parrotlets normally lay their eggs in the morning between 06.00 h and 09.00 h (Waltman & Beissinger 1992). Nests were checked daily for newly laid eggs immediately after 09.00 h during the laying period. All new eggs were individually marked. Freshness was judged by the degree of translucence of the eggshell. No eggs were removed after 11.00 h to avoid using eggs that may have been incubated enough to induce embryo development. Eggs were placed into one of five holding nest boxes (hereafter 'holding box') that were exact replicas of nest boxes in use. They were located on fence posts between active nest boxes in areas ranging from full sun to full shade, representing the range of thermal conditions of active nest boxes. No more than 10 eggs (the maximum clutch size in this species) occupied a holding box at one time. Thermistors attached to data loggers (Omega OM-160, Omega Engineering, Inc., Stamford, Connecticut, USA) simultaneously recorded temperatures every 0·5 s inside holding boxes (T_b) and ambient temperatures (T_a) in shade adjacent to holding boxes (after Evans 1989; Weathers & Sullivan 1989). Thermistors inside holding boxes rested on the upper surfaces of eggs.

After various lengths of exposure to ambient temperatures in holding boxes (see below), experimental eggs were placed in recipient nests (usually not their natal nest) and were incubated by females for up to 25 days. Parrotlet eggs are unmarked, and females readily accept and incubate eggs not their own (Beissinger & Stoleson 1991; Curlee & Beissinger 1995; Stoleson & Beissinger 1997). For each experimental egg, an egg newly laid in the recipient nest was assigned as a control. Because seventh and later eggs may have lower hatching success (Beissinger & Waltman 1991), experimental eggs were placed only in nests with five or fewer eggs. Most recipient nests received more than one experimental egg. Recipient nests were checked daily for hatching of experimental and control eggs.

Eggs that failed to hatch were examined visually under a dissecting microscope or reversed 10 × binoculars, and compared to photographs of embryos of domestic fowl to determine the degree of development. Eggs were assigned to one of three levels of development: (1) little or no visible development, corresponding to days 1–3 in the fowl (Freeman & Vince 1974, pp. 278–280); (2) intermediate development, corresponding to days 4–10 (Freeman & Vince 1974, pp. 281–287); and (3) advanced development, corresponding to days 11 and beyond (Freeman & Vince 1974, pp. 287–288). We could not distinguish between infertile eggs and very early embryonic development. The rapid putrefaction of dead eggs caused by long exposure to high ambient temperatures precluded classifying many unhatched eggs.

Two separate experiments were conducted. In the first experiment, experimental eggs were isolated in holding boxes for up to 9 days to determine gross patterns of viability loss. Based on results from the first experiment, we initiated a second set of treatments to examine more closely the effects on hatchability of 5 or fewer days of exposure.

Long exposure experiment

From May to November of 1992 and May to August of 1993, we removed 262 newly laid parrotlet eggs from 106 nests. Eggs were randomly assigned to one of three treatments of exposure to ambient temperatures: 1 day, equivalent to initiating incubation on the second egg in this species; 5 days, equivalent to initiating incubation after three eggs in this species; or 9 days, equivalent to beginning incubation on the penultimate of seven eggs, which would correspond to an incubation pattern typical of temperate passerines (Clark & Wilson 1981; Stoleson & Beissinger 1995). Eggs were not turned systematically while in the holding box because birds normally do not turn their eggs actively until incubation is initiated (Deeming 1992). However, incidental turning occurred while placing and removing eggs, so that each egg was probably turned at least once daily.

Short exposure experiment

From September to November of 1993 and June to November of 1994, we removed 272 newly laid eggs from 136 nests. Eggs were randomly assigned in the field to exposure treatments of 0, 1, 2, 3, 4 or 5 days. Eggs assigned to 0 days exposure were moved from their natal nest directly to a recipient nest to serve as controls for the effects of manipulation. Eggs assigned to 1–5 days exposure were sequestered in holding boxes and subjected to ambient temperatures as described above. Because results from the

first experiment suggested development occurred without incubation, eggs in holding boxes were turned systematically twice daily, in addition to any incidental movement, to isolate the effects of exposure from potential effects of development without turning. Afterwards, eggs were returned to nests, assigned a control egg, and incubated to term by females as described above.

Data analyses

In cases where both an experimental egg and its control egg failed to hatch, the fate of other eggs in the clutch was examined for evidence of failures resulting from ineffective incubation, intraspecific harassment or fertility problems. We excluded from analyses any nest in which more than two nonexperimental eggs failed to hatch, or in which no eggs hatched that were laid after the experimental egg was placed in the nest. The remaining proportion of double failures was compared to the expected proportion calculated from the hatching success rates of experimental and control eggs. Also excluded were eggs destroyed as a result of predation or infanticide (identified by triangular bite marks characteristic of parrotlets).

To determine whether preincubation development reduced the incubation time of experimental eggs, incubation periods were calculated as the number of days from placement in the recipient nest to hatching (inclusive) for experimental eggs, and the number of days from laying to hatching for control eggs. To control for differences in parental incubation behaviour and the thermal characteristics of nest boxes, differences in incubation periods were tested between experimental and control eggs on a pairwise basis. Wilcoxon signed rank tests (Sokol & Rohlf 1981) were used because these data could not be normalized by transformations. To test whether embryo mortality was more likely to occur later in experimental eggs than in control eggs, the number of control and experimental eggs that failed after little, intermediate and advanced development was compared using χ^2 tests. In these analyses, 0 day exposed eggs were pooled with control eggs because no differences in developmental stage at death were found.

The numbers of experimental and control eggs that hatched or failed to hatch were compared using 2×2 χ^2 tests for each exposure time. Because of frequent equipment failures, temperature data for the complete holding period was obtained for only 129 experimental eggs. For this subset of eggs, the following temperature variables were calculated for the period that each was in a holding box: (i) T_{max}, absolute maximum temperature; (ii) T_{min}, absolute minimum temperature; (iii) T_{mean}, mean temperature; (iv) Pt27, proportion of time spent below 27 °C; (v) Ptmid, proportion of time spent between 27 and 34 °C; and (vi) Pt34, proportion of time spent above 34 °C. Logistic regression (Trexler & Travis 1993) using the SAS CATMOD procedure (SAS Institute 1988) tested for the effects on egg hatching of exposure time, holding box, T_{max}, T_{min}, T_{mean}, Pt27, Ptmid and Pt34. Holding box was treated as a categorical variable; all other variables were treated as continuous. Logistic models employed a forward stepwise methodology using likelihood-ratio tests and a critical value of 0·05 to enter variables.

We estimated the relationship between the probability of hatching (H_E) and exposure time (E) for experimental eggs by modifying the logistic regression model of Arnold *et al.* (1987) $\{H_E = 0{\cdot}89/[1 + a(E)^b]\}$ using nonlinear regression in SYSTAT (Wilkinson 1990). The average daily decline in viability was calculated by fitting a linear regression of hatchability on exposure time and constraining the Y intercept to be 0·89, the hatching success of control eggs.

QUANTIFYING THERMAL ENVIRONMENTS AT THE STUDY SITE

Ambient temperatures recorded at holding boxes were used to characterize the ambient temperature regime at the study site. Data loggers sampled temperatures every 0·5 s during 30 separate sessions lasting from 5 to 10 days from June to November of 1992–95. From these data we obtained 5039 hourly temperature averages that were used for analyses.

The preceding experiments were based on the assumption that nest boxes provided a thermal environment similar to natural nest sites. To test this assumption, temperatures were monitored simultaneously in empty nest boxes (T_b), adjacent natural or seminatural cavities (T_c), and ambient shade temperatures (T_a) at 10 different sites. All natural cavities monitored had been used at least once by nesting parrotlets. Most recording sessions ran for approximately 72 h. To account for differing recording periods and to reduce problems of nonindependence of multiple observations at a single site, analyses were based on hourly averages of ambient, box and cavity temperatures (T_a, T_b, T_c) for each session. Hourly average temperatures were compared using a three-way ANOVA with hour of the day, site and box as factors.

Results

EFFECTS OF EXPOSURE ON EGG HATCHABILITY

Long exposure experiment

Of 262 eggs exposed to ambient air temperatures, 122 eggs were destroyed due to predation, infanti-

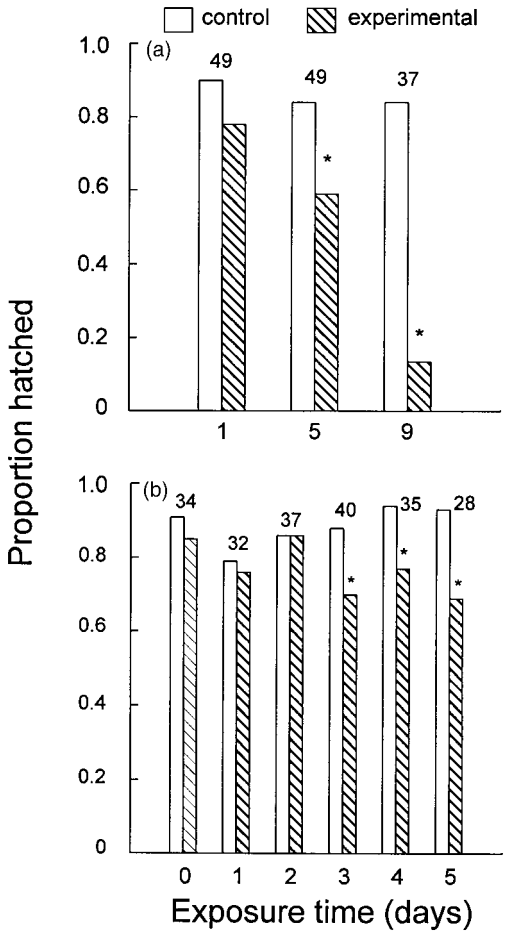

Fig. 1. Hatching success of experimental eggs subject to (a) 1, 5 and 9 days of preincubation exposure to ambient temperatures without systematic turning, and (b) 0, 1, 2, 3, 4 and 5 days of preincubation exposure to ambient temperatures with systematic turning, compared to unmanipulated control eggs. Sample sizes indicate the number of matched pairs of control and experimental eggs, and asterisks indicate differences between experimental and controls were significant at $P < 0{\cdot}05$.

cide, breakage by parents, or mortality of a parent, and were excluded from further analyses. Five pairs of eggs in which neither experimental nor control eggs hatched were excluded because low hatching success in the recipient nest suggested the eggs were poorly incubated. The number of remaining pairs ($n = 8$) in which both control and experimental eggs failed did not differ significantly ($\chi^2_1 = 2{\cdot}1$, $P = 0{\cdot}15$) from the expected number of double failures based on the average probabilities of hatching, and were included in all analyses. Of the remaining 135 experimental eggs, 72 hatched.

Hatching success declined with prolonged exposure (Fig. 1a). In this experiment, 86% of control eggs hatched. Compared to control eggs, hatchability was significantly reduced to 59% after 5 days ($\chi^2_1 = 7{\cdot}2$, $P = 0{\cdot}007$) and to 14% after 9 days ($\chi^2_1 = 36{\cdot}6$, $P < 0{\cdot}001$) of exposure. Eggs exposed for 1 day tended to be less likely to hatch than their controls, but this difference was not significant ($\chi^2_1 = 2{\cdot}7$, $P = 0{\cdot}10$).

Short exposure experiment

Of 272 eggs exposed to ambient air temperatures, 66 eggs were excluded from further analysis for reasons stated above. Fewer eggs were lost in this experiment because rates of predation by snakes were much lower. Six cases in which both experimental and control eggs failed were included in the analyses, as this number of double failures did not differ significantly ($\chi^2_1 = 1{\cdot}0$, $P = 0{\cdot}31$) from the frequency expected by chance. Of the remaining 206 eggs, 161 hatched.

Hatching success declined with exposure time after a few days (Fig. 1b). Compared to control eggs, hatchability was significantly reduced to 70% after 3 days ($\chi^2_1 = 3{\cdot}7$, $P = 0{\cdot}05$), to 77% after 4 days ($\chi^2_1 = 4{\cdot}2$, $P = 0{\cdot}04$), and to 69% after 5 days ($\chi^2_1 = 5{\cdot}5$, $P = 0{\cdot}02$) of exposure to ambient temperatures. Exposure times of 1 and 2 days produced no significant reduction in hatchability (both $\chi^2_1 > 0{\cdot}1$, both $P > 0{\cdot}75$). Eggs that were only moved between nests (0-day exposure) were about as likely to hatch as their controls ($\chi^2_1 = 0{\cdot}57$, $P = 0{\cdot}45$), suggesting that swapping eggs between nests had no detrimental effect on hatchability.

For further analyses experimental eggs from both experiments were pooled to boost sample sizes.

Exposure versus other factors affecting viability

Duration of exposure was the only factor found to have a significant effect on hatching success of eggs in a logistic regression (Table 1). The probability of hatching was not significantly affected by temperature extremes, the proportion of time spent within particular temperature ranges, or by holding box (Table 1).

Table 1. Logistic regression of parameters potentially affecting hatchability of experimental parrotlet eggs on hatching

Parameter†	d.f.	χ^2	P
Intercept	1	23·5	< 0·01
Exposure time	1	7·49	< 0·01
Holding box	4	7·44	0·12
T_{max}	1	0·15	0·70
T_{min}	1	0·03	0·87
T_{mean}	1	1·00	0·32
Pt27	1	0·20	0·65
Ptmid	1	0·28	0·59
Pt34	1	0·03	0·87
Likelihood ratio	4	4·97	0·29

†All nonsignificant parameters were added one at a time with exposure time to logistic regression.

Decline in viability in tropical parrotlets versus temperate species

The decline in egg viability (H) as a function of exposure (E) was fit well by a nonlinear regression (Fig. 2a), which accounted for 90·5% of the variance in average hatching success as a function of exposure time ($P < 0{\cdot}001$). A linear regression model ($H_E = 0{\cdot}89–0{\cdot}068E$) indicated that hatchability declined an average of 6·8% daily but did not yield as good a fit ($R^2 = 0{\cdot}83$, $P = 0{\cdot}004$). The logistic decline in viability of parrotlet eggs was much more extreme than that for pond ducks, and slightly more exaggerated than in house sparrows and late-breeding American coots (*Fulica americana* Gmelin) (Fig. 2b).

EVIDENCE FOR PREINCUBATION DEVELOPMENT

Experimental eggs generally required less time to hatch than their controls (all pairs combined: one-tailed paired Wilcoxon test, $z = 2{\cdot}85$, $P = 0{\cdot}008$, $n = 192$ pairs), but this relationship varied with the length of exposure (Table 2). Incubation periods were significantly shortened by one-half day for eggs exposed for 3 or 5 days, and were nearly significantly shorter for eggs exposed for 2 days. Eggs exposed for 4 days tended to have shorter incubation times than their controls, but the trend was not significant (Table 2). Mean incubation time was significantly correlated with duration of exposure for experimental eggs ($r = –0{\cdot}81$, $P = 0{\cdot}026$), but not for control eggs ($r = –0{\cdot}38$, $P = 0{\cdot}39$). Thus, relative to untreated eggs, the incubation period of experimental eggs generally decreased with increasing exposure times.

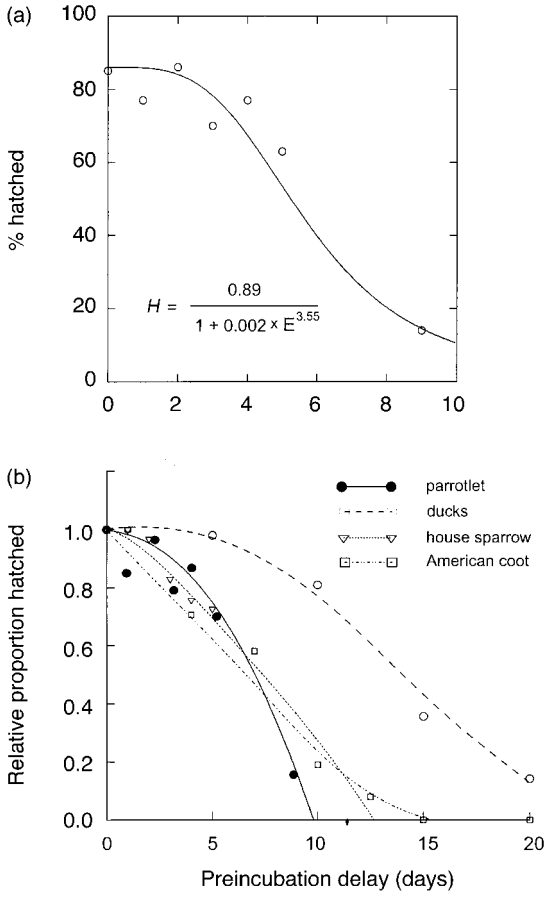

Fig. 2. (a) Average hatching success of experimental eggs (H_E) as a function of the length of preincubation exposure to ambient temperatures (E). The curve was plotted from the equation $H_E = 0{\cdot}89/(1 + 0{\cdot}002E^{3{\cdot}55})$. (b) Relative hatching success (% hatched experimental eggs/% hatched control eggs) as a function of the length of preincubation exposure to ambient temperatures for green-rumped parrotlets, ducks, house sparrows and American coots. Lines for house sparrows represent extrapolations beyond 7 days of preincubation delay. Data are from Arnold *et al.* (1987), Arnold (1990), Veiga (1992), and this study.

Table 2. Incubation times for parrotlet eggs as a function of exposure time

Exposure	N†	Incubation time in days			P‡
		Difference	Experimental	Control	
0	27	–0·09	19·70 ± 0·91	19·44 ± 0·84	0·63
1	62	–0·11	19·66 ± 0·87	19·54 ± 0·76	0·60
2	32	0·23	19·09 ± 0·53	19·31 ± 0·62	0·06
3	26	0·61	19·15 ± 0·88	19·70 ± 0·88	0·01
4	25	0·30	19·40 ± 0·82	19·65 ± 0·78	0·21
5	43	0·54	19·37 ± 1·00	19·82 ± 1·17	0·04
9	3	0·50	18·67 ± 0·58	19·00 ± 0·00	–

†Number of pairs of experimental and control eggs. Totals do not include 15 eggs for which exact incubation times were uncertain.

‡Wilcoxon signed rank tests.

TIMING OF EMBRYO MORTALITY

A total of 42 control and 0-day exposure eggs failed to hatch, excluding losses resulting from predation or egg damage, of which the stage of development could be assessed in 33 eggs. Control egg embryos mostly died after little or no development (88%), the remainder died after almost complete development, and none showed an intermediate level of development (Fig. 3). Of 99 experimental eggs (excluding 0-day exposure eggs) that failed to hatch, the stage of development at death was determined for 68 eggs. Of unhatched eggs exposed for 1 and 2 days, 67% showed little or no development, 11% showed an intermediate development, and slightly more (22%) showed advanced development (Fig. 3). This distribution of embryonic development was nearly significantly different from the pattern of control eggs ($\chi^2_2 = 5{\cdot}1$, $P = 0{\cdot}08$). Failed eggs that were exposed for 3 or more days mostly showed little or no development, 8% had intermediate development, and 10% died after advanced development (Fig. 3) but did not differ significantly from control eggs ($\chi^2_2 = 2{\cdot}8$, $P = 0{\cdot}36$). However, the distribution of development for all experimental eggs combined differed significantly from controls ($\chi^2_2 = 6{\cdot}5$, $P = 0{\cdot}04$).

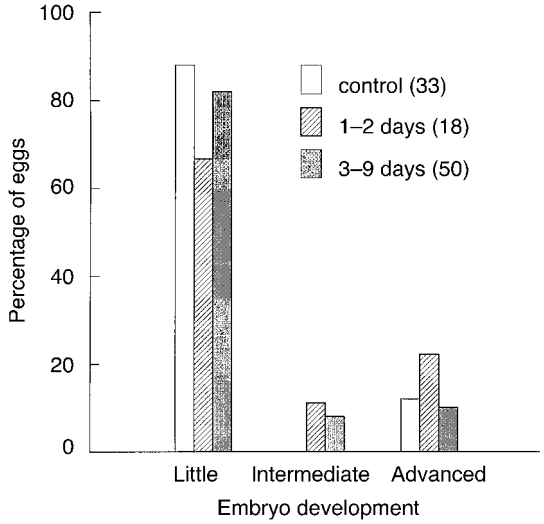

Fig. 3. Distribution of embryo mortality in relation to stage of embryo development and length of preincubation delay. Control eggs include eggs of 0-day exposure. Eggs exposed for 1 and 2 days have been pooled, and eggs exposed for 3 or more days have been pooled. Sample sizes are included in parentheses. See text for definitions of developmental levels.

THERMAL ENVIRONMENT OF THE STUDY SITE, NEST BOXES AND CAVITIES

Ambient temperatures at the study site were regularly warm enough to induce embryonic development, ranging from 19·9 to 44·6 °C ($x = 26{\cdot}2 \pm 4{\cdot}2$ °C). Daytime ambient temperatures (Fig. 4) exceeded physiological zero on 60·4% of recorded hourly means, infrequently reached 34 °C (15·3% of hourly means), and rarely exceeded 41 °C (1·8%). A large proportion (46·8%) of daylight temperatures fell in the range that induces abnormal development in avian embryos (27–34 °C). Most night-time ambient temperatures were below physiological zero (99·2%), none exceeded 34 °C and only a small fraction (0·8%) exceeded physiological zero.

Nest boxes and cavities had similar temperature profiles but there were some differences (Fig. 4). Temperatures in boxes and cavities varied significantly through the course of the day, and this hourly variation differed among sites as shown by a significant interaction term (Table 3). In shaded sites, cavities tended to be warmer than boxes, while in sites with full sun there was no difference between them (Stoleson 1996). Differences between boxes and cavities were nearly significant, but were smaller than hourly and site to site variation (Table 3). Compared to natural cavities, nest boxes tended to exaggerate slightly the extremes of ambient temperature.

Discussion

FACTORS AFFECTING EGG VIABILITY

As predicted by the egg viability hypothesis, hatchability of parrotlet eggs was strongly affected by the duration of exposure to ambient conditions prior to incubation (Fig. 1). If parrotlets were to delay incubation for 5 days until after laying the third egg, the probability of hatching would be reduced to about 64% for the first egg and 78% for the second egg. Delaying incubation for 9 days until the sixth (penultimate) egg, a common pattern among tempe-

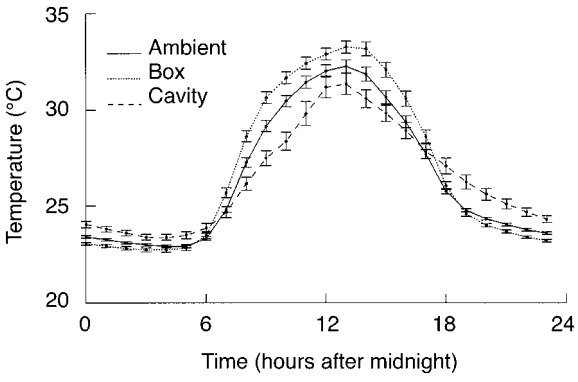

Fig. 4. Mean hourly temperatures (± 1 SE) at Hato Masaguaral, Venezuela, for ambient (shaded) air, nest boxes, and natural cavities, based on means for approximately 72 h sessions at 30 different sites.

Table 3. ANOVA of the effects of hour of the day, site and treatment (nest box vs. cavity) on temperatures at 10 nest sites in Venezuela

Source of variance	SS	d.f.	MS	*F*	*P*
Site	206·0	9	22·9	1·4	0·18
Hour	249·0	1	249·0	15·4	< 0·01
Treatment	59·2	1	59·2	3·7	0·06
Hour × treatment	18·2	1	18·2	1·1	0·29
Site × treatment	36·3	9	4·0	0·3	0·99
Hour × site	296·1	9	32·9	2·0	0·04
Hour × site × treatment	19·3	9	2·2	0·1	0·99
Error	7131	440	16·2		

rate passerines, would result in a probability of hatching of about 15% for first-laid eggs, 22% for second-laid eggs, and 35% for third-laid eggs (Fig. 2). Thus, an early onset of incubation appears to be important for maintaining the viability of early laid eggs in this species.

The decline in egg viability found in these experiments was almost certainly a result of exposure, and not because of damage resulting from handling and movement of eggs. Eggs that were moved among boxes (0-day exposure) did not hatch significantly less frequently than their controls (Fig. 1b). Eggs moved among nests in previous experiments (Stoleson & Beissinger 1997) using an identical protocol showed no difference in hatchability (90·9%, $n = 192$) from eggs that were not moved (85·2%, $n = 272$; $\chi^2_1 = 2{\cdot}37$, $P = 0{\cdot}12$). Avian eggshells are remarkably strong, and, even if fractured, embryos remain protected by a strong but flexible inner membrane (Deeming 1992). Thus, it seems highly unlikely that our experimental manipulations would have induced more than a small portion of the observed loss in viability.

The relationship between hatching success and exposure time for parrotlets was not linear (Fig. 2). A significant decline in hatchability did not occur until after 3 days of exposure. Hatchability of house sparrow eggs declined after 3 days of exposure (Veiga 1992), viability of poultry eggs can begin to decline after 2 or 3 days of preincubation storage (Meijerhof 1992), and hatching success of American Coot eggs declined significantly after 4 days (Arnold 1990). A loss of viability in waterfowl eggs occurred after 5–10 days of exposure at a high latitude (50·1°N), where springtime temperatures remained well below physiological zero (Arnold *et al.* 1987; Arnold 1993) and declines in viability should be slight. Studies of different taxa are needed to determine whether 3 days represents a threshold for the viability of unincubated eggs exposed to temperatures above physiological zero. Early egg failures may often be mistakenly attributed to infertility instead of loss of viability (Birkhead, Veiga & Fletcher 1995).

Other than length of exposure, we found no significant predictors of hatching success. The probability of hatching was not significantly influenced by maximum or minimum temperatures experienced by eggs prior to incubation, or by duration of exposure to temperatures below physiological zero, between physiological zero and 34 °C, or above 34 °C (Table 1). That hatchability did not relate to temperature may have resulted from the relatively uniform thermal environments experienced by parrotlet eggs. Temperatures were mostly just above or below physiological zero, minimum temperatures were well above levels that threaten embryos, and maximum temperatures rarely reached lethal levels (Fig. 4). In contrast, Arnold (1993) found significant effects of minimum, maximum and mean temperature on the hatchability of prairie duck eggs, with highest hatchability during periods of low temperatures. The temperatures we used to delineate ranges of importance to embryological development were based on values for domestic poultry (White & Kinney 1974; Webb 1987; Wilson 1991; Deeming & Ferguson 1992). Unfortunately, little is known about the effects of temperature on embryonic development and survival in wild birds (Webb 1987). Even for poultry there is some controversy over the exact value of physiological zero (Proudfoot & Hulan 1983). Although we used 27 °C as physiological zero, some development may have occurred below this temperature. It is also possible that exposure to temperatures outside of the normal incubation range may not have a simple cumulative effect on hatching success, as was tested for here. Rather the duration of single periods of exposure in particular temperature ranges or the number or sequence of changes in temperature may have affected hatching success. Hatchability of poultry eggs in artificial incubators is increased by periodically cooling them below normal incubation temperatures for brief periods (Batt & Cornwell 1979; Decuypere & Michels 1992). The exact mechanisms

of embryo mortality are poorly known, and further research is needed.

Relative humidity can affect hatching success but is unlikely to have been a factor in our experiments. Maximum egg hatchability is achieved when poultry eggs are maintained at relative humidity levels of 80–90% (Proudfoot & Hulan 1983; Meijerhof 1992). Ambient relative humidity at our study site was generally between 80 and 95%, and thus was unlikely to impair hatching success.

Exposure to ambient temperatures did appear to induce some development prior to incubation. Incubation times were shorter for experimental eggs than for controls (Table 2). Differences were small relative to overall incubation periods, in part because experimental eggs spent little time at normal incubation temperatures and development is retarded at lower temperatures (Rol'nik 1970; Romanoff & Romanoff 1972). In contrast, prior studies have noted protracted incubation times for eggs exposed to ambient temperatures (Crittenden & Bohren 1961; Arnold 1993; Viñuela 1997). However, those experiments were conducted in cool or Mediterranean climates (Viñuela 1997), in which little or no preincubation development should occur. In contrast, parrotlet eggs were exposed to optimal incubation temperatures for a portion of each day.

Embryo mortality in parrotlet eggs not exposed to ambient temperatures occurred mostly very early and, to a lesser extent, very late in development (Fig. 3). This bimodal pattern is typical of unmanipulated avian eggs, partly because mortality rates include infertile eggs as well as developmental failures (Romanoff 1949; Ancel, Liess & Girard 1995). In contrast, failed experimental eggs frequently showed an intermediate level of development (Fig. 3). Such mortality often results from gross anomalies in development that are commonly associated with abnormal temperatures early in the incubation period (Romanoff & Romanoff 1972).

Although our experiments were conducted using nest boxes, it is likely that the results closely reflected natural thermal conditions. Temperature differences between nest boxes and adjacent natural cavities were small relative to differences based on time of day and variation among sites (Table 3). Nest boxes tended to warm more quickly in the mornings and lose heat more rapidly in the late afternoons (Fig. 4). This difference suggests the possibility that viability effects may have been slightly exaggerated in nest boxes. However, we found no significant variation in hatchability as a result of storage in a holding box (Table 1), although holding boxes varied considerably in temperature and shade conditions (Stoleson 1996). Thus, it seems unlikely that the use of nest boxes as holding sites had a major adverse effect on the viability of parrotlet eggs.

VIABILITY AS A CAUSE OR CONSEQUENCE OF HATCHING ASYNCHRONY

It has been argued that the decline in the viability of unincubated eggs is a consequence of early incubation rather than its cause (Ankney, Afton & Alisauskas 1991). If complete asynchrony evolved in the parrotlet for some reason other than the maintenance of egg viability, unincubated eggs may no longer be subject to selection for high hatchability and could have lost that ability.

Although this possibility is not easily assessed (Arnold *et al.* 1987), comparative evidence suggests it is unlikely. First, artificial selection experiments indicate that egg hatchability is a conservative character that can not be increased without adverse pleiotropic effects (Crittenden & Bohren 1961; Nordskag & Hassan 1971). Variation in egg viability occurs among the few species where it has been characterized (Fig. 2b) and should because studies differed in thermal environments, methods, and goals. Second, if the ability of unincubated eggs to remain viable was lost after first-egg incubation evolved, then the viability of parrotlet eggs should have declined after just 1 day without incubation. However, we found no significant decline until 3 days. Third, viability might be expected to decay more slowly in taxa that delay incubation and hatch their eggs more synchronously. This does not appear to be the case, although egg viability has been examined for very few species under field conditions (Fig. 2b). Domestic hens have been artificially selected for the number and hatchability of eggs, yet their eggs still exhibit a loss of viability after 2–3 days of preincubation storage (Decuypere & Michels 1992; Meijerhof 1992). A similar loss of viability after 3 days of exposure was reported for house sparrows, which begin incubation on the third or fourth egg of a five egg clutch (Veiga 1992). It may not be a coincidence that a 3-day threshold is shared by asynchronous parrotlets, semi-asynchronous house sparrows and synchronous domestic fowl.

EGG VIABILITY AND LATITUDINAL AND SEASONAL TRENDS IN CLUTCH SIZE AND HATCHING ASYNCHRONY

Maintaining egg viability may be an important function of the early onset of incubation in birds. Our results corroborate studies of birds in temperate climates (Arnold *et al.* 1987; Veiga 1992; Arnold 1993; Veiga & Viñuela 1993), and suggest the loss of viability may be more extreme in warm environments. If a decline in the viability of incubated eggs proves to be a general phenomenon in birds, then egg viability may act as a constraint on avian reproductive patterns (Arnold 1993; Stoleson & Beissinger 1995). As ambient temperature increases, such as with latitudi-

nal or seasonal gradients, average clutch size may decline, hatchability of eggs may decrease, or prevalence and degree of hatching asynchrony may increase (Arnold 1993). These predictions are speculative, but they suggest potentially productive avenues for future research that we outline below.

A latitudinal decline in clutch size is well documented in birds (Lack 1968; Klomp 1970; Skutch 1985). If viability of unincubated eggs declines especially rapidly in warm climates, then benefits derived by delaying incubation for 3 days to gather food to lay additional eggs may start to be offset by a rapid decline in hatchability of early laid eggs. Clutch size in most lowland tropical species rarely exceeds three eggs (Cody 1966; Skutch 1985). Ambient temperatures in excess of physiological zero are typical of lowland tropical sites, and mean monthly maximums can be expected to exceed physiological zero for most tropical areas below 700–900 m during breeding seasons (Coen 1983). High ambient temperatures are not restricted to the tropics, but can occur in warm microhabitats in otherwise cool temperate areas (Arnold 1990).

There is conflicting evidence as to whether hatching asynchrony increases toward the equator (Clark & Wilson 1981; Slagsvold 1986). Recent work suggests preincubation delays increase with latitude (Viñuela & Carrascal, 1999), but not all tropical birds initiate incubation on the first egg (Clark & Wilson 1981). Tropical species that delayed incubation and exposed their eggs to the negative effects of high ambient temperatures should have lower hatching success than temperate species. Support for this prediction comes from a comparative analysis by Koenig (1982), which found a positive correlation between hatchability and latitude.

Finally, many temperate birds exhibit seasonal declines in clutch size (e.g. Stutchbury & Robertson 1988; Perrins & McCleery 1989; Kennedy & White 1991) or seasonal increases in hatching asynchrony (Clark & Wilson 1981; Veiga & Viñuela 1993; Murphy 1994). These patterns have been explained as a response to seasonal declines in food resources, which have rarely been documented (De Steven 1980; Stutchbury & Robertson 1988; Arnold 1993; but see Bryant 1978), or nonheritable variation in parental condition (Price, Kirkpatrick & Arnold 1988), which has rarely been supported (Winkler & Allen 1996). The egg viability hypothesis suggests that a seasonal decline in clutch size and increase in asynchrony occurs because the benefits of laying additional eggs are offset by the decline in hatchability with increasing temperatures (Arnold 1993; Stoleson & Beissinger 1995). Ambient temperatures typically exceed physiological zero at many temperate sites during late spring and summer, and seasonal decreases in hatchability have been reported (Koenig 1982). Models of the trade-off between the onset of incubation, egg viability and brood reduction showed that advancing the onset of incubation from penultimate to middle eggs resulted in higher fitness as the season progressed (Stoleson & Beissinger 1995). Although avian embryos are more tolerant of extreme cold than heat (Batt & Cornwell 1979), birds that breed where temperatures drop below freezing might also be subject to the constraints of egg viability. The egg viability hypothesis suggests that such species should also show trends towards smaller clutch sizes or an earlier onset of incubation.

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