SENSORY CONTROL OF CLUTCH SIZE IN THE ZEBRA FINCH (*TAENIOPYGIA GUTTATA*)

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ABSTRACT.—An analysis of the mechanism responsible for controlling clutch size was carried out in the Zebra Finch (*Taeniopygia guttata*) by manipulating the number of eggs present in the nest during laying. Sensory cues involved were also investigated. Stimulation from the eggs present in the nest during the second and third day of the egg-laying period determined how females cease to lay in this species. Disruption of ovarian follicular growth was triggered on the third day of laying, 6 ± 1 h after the onset of light (14L:10D), by tactile stimulation. Contact with eggs also was required to induce the onset of sensitivity to the stimulus responsible for ending laying. The hypothesis that individual variations in clutch size (four to six eggs) are caused by early disruption of follicular growth for smaller clutches versus late disruption for larger clutches was tested. The timing of follicular disruption showed no significant variation between females ($n = 12$) in relation to clutch size. There is good evidence that this result, established in domesticated Zebra Finches, holds true for wild Zebra Finches as well. Individual variation in clutch size resulted from the variable number of growing follicles that, once follicular disruption has been triggered, were able to complete the rapid-growth phase and ovulate. *Received 11 May 1992, accepted 30 October 1992.*

CONSIDERABLE PROGRESS has been made in our understanding of the evolution of clutch size since Lack (1947) first attempted to explain why birds lay the number of eggs they lay. Although it has been known for quite some time that clutch-size control mechanisms may differ between species (Cole 1917), how birds control the size of a clutch is still a very little known aspect of their breeding biology. Some species, classified as tactile indeterminate or semideterminate layers, have been shown to rely on eggs present in the nest during the laying period to cease laying whereas others, classified as determinate layers, do not need such stimulus (Haywood 1993a). The role of a contact between the female and her eggs in stopping laying has been substantiated, through egg-removal experiments, in a number of species, mostly nonpasserines (for a review, see Haywood 1993a). Studies carried out in gulls have demonstrated that the contact between the female and the first egg of a clutch results in disruption of ovarian follicular growth (growing follicles becoming atretic instead of ovulating) and then, after a few days, cessation of egg laying (Paludan 1951, Weidmann 1956).

The aim of my study was to analyze in the Zebra Finch (*Taeniopygia guttata*) how females control their clutch size by manipulating the number of eggs present in the nest during laying. Experiments were carried out to determine:

(1) whether the Zebra Finch is, like the few passerine species studied so far (Haywood 1993a), an indeterminate layer; (2) if yes, the number of eggs and the duration of contact required to induce the female to cease laying; (3) the type of stimulus perceived by the female that might be visual, tactile, olfactory, or auditory; and (4) the timing of the stimulus responsible for the ending of laying. Given that clutch size varies in this species, usually from four to six eggs, an attempt has also been made to uncover the mechanism responsible for individual variation in clutch size. If a contact between the female and her eggs is involved, it may be hypothesized that in females laying smaller clutches laying might be inhibited sooner by the eggs already present in the nest than in females laying larger clutches. This hypothesis was tested by determining for each of a dozen females the characteristic, average size of several successive clutches and the precise timing of disruption of ovarian follicular growth.

METHODS

Zebra Finches bred in captivity for many generations were kept in indoor cages (35 × 40 × 45 cm). All pairs were maintained at about 20°C and under a photoperiod of 14L:10D; with light on at 0800. Pairs were provided with fresh water, seeds, egg food, grit, and cuttlebone *ad libitum*. In addition, salad leaves for
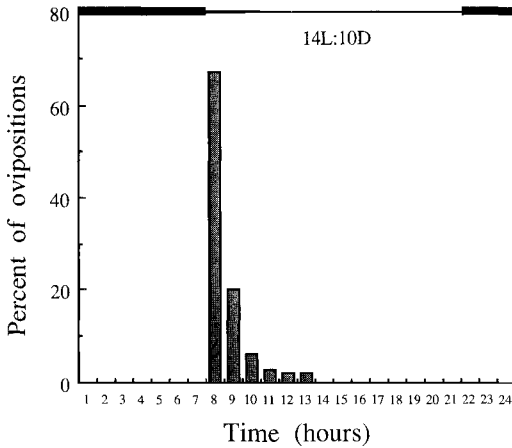
Fig. 1. Timing of egg laying in Zebra Finches maintained on lighting cycle of 14 h light and 10 h dark (14L:10D). Horizontal axis indicates particular time of day (e.g. 8 indicates 0800 to 0859). Percentages represent hourly ratio between number of ovipositions witnessed ($n = 21$) and number of visits to a nest box yielding a new egg ($n = 360$).
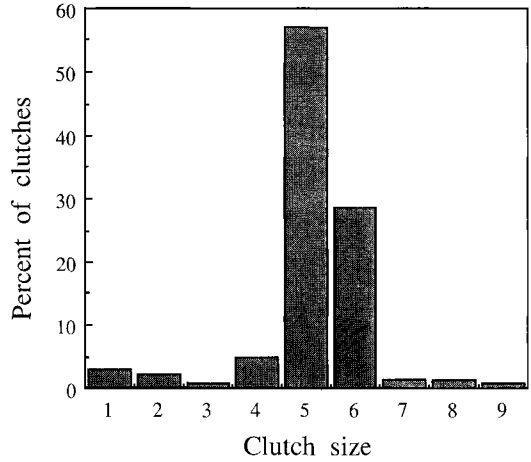

Fig. 2. Clutch sizes in domesticated Zebra Finches ($n = 140$).

green supplement and hay for nesting material were given about once a week. A single nest box was available to each pair. The contents of nests were checked daily before 1300. Most eggs were laid before that time (Fig. 1), but if an egg was laid that day after my visit it was generally detected on the next visit because, in contrast to freshly laid eggs which appear chalky, 24-h-old eggs often are shiny due to repeated contact with brood patches. Pairs were constantly induced to lay a new clutch by removing the previous one. Clutches were removed at the earliest on the fifth day of laying in order to prevent adverse effects on either oviposition or ovarian follicular growth (and, hence, on clutch size), but before the seventh day of the laying period in order to limit the impact of incubation on relaying and generate the shortest relaying periods. All pairs were kept under constant conditions throughout the study, and no change in clutch size was detected with its advancement. The same females were used to produce both control and experimental clutches. Control clutches were not interfered with except to weigh and measure the female and the eggs, as was done for experimental clutches. Clutches associated with the experiments 1–18 described below were produced at random. Overall, 25 pairs were involved in these experiments; not all pairs were used for each experiment.

Clutch size ranged from one to nine eggs, but most clutches comprise four to six eggs (Fig. 2). Clutches smaller than four eggs were discounted (5.7% of all clutches) because some of these were related to calcium deficiency since some eggs were thin shelled and renewing the old cuttlebone resulted in the female resuming the production of larger clutches.

Clutches greater than six eggs were also discounted (3.6% of all clutches) because there is some evidence that, as a consequence of removing clutches early during the incubation period, the natural tendency of males to incubate eggs during the laying of the following clutch was greatly enhanced. This alteration in the male behavior caused, in a few pairs, the female to spend less time on her eggs early during laying, thus occasionally delaying the cessation of egg laying. The following experiments were conducted:

Experiments 1–3.—In the first experiment, each laid egg was removed from the nest as soon as it was laid (this is noted as 0000 . . . on the basis of the number of eggs present daily in the nest, after visit), until the female had laid at least six eggs. In the second experiment, the first egg was left, but each subsequent egg was removed (i.e. a single egg was left throughout the laying period; 1111 . . .). In the third experiment, five eggs were added to the clutch on the day the first egg was laid (6789 . . .).

Experiments 4–7.—In the fourth experiment, in order to prevent tactile stimulation of the female by the eggs and allow visual contact with a clutch of eggs throughout the egg-laying period, eggs were removed as laid and a set of six eggs glued to one another was hung from the ceiling of the nest box, about 80 mm above the nest cup, on the first day of laying until laying stopped (or was stopped). In the fifth experiment, each egg as it was laid was replaced by a flat brownish button 10 mm in diameter. The aim was to provide the female with a tactile stimulus but no visual, olfactory, and auditory stimuli similar to eggs. In the sixth experiment, in order to test whether olfactory cues supplement tactile stimulus in cessation of egg laying, all eggs laid were replaced by eggs coated with a plastic film (acrylic white paint, Liquitex), which prevented any possible olfactory stimulus from the egg. A similar seventh experiment
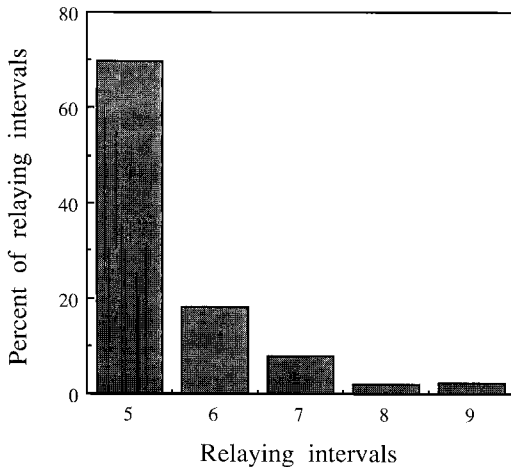
Fig. 3. Relaying periods in domesticated Zebra Finches (n = 195) calculated by subtracting date of removal of a clutch from laying date of first egg of following clutch.

was conducted to test the contribution of auditory cues with eggs coated with a thin layer of transparent rubber (silastic elastomer, Dow Corning), which prevented the female from hearing any normal sounds originating from contact between the birds' bill or claws and the eggs.

Experiments 8-11.—In these experiments, the timing of stimulus was established by comparing various periods during which eggs were left in the nest. In the test groups, eggs were removed (always before 1300) from the second day onwards. (experiment 8: 10000 . . .), the third day onwards (experiment 9: 12000 . . .), the fourth day onwards (experiment 10: 12300 . . .), and the fifth day of the laying period (experiment 11: 12340 . . .).

Experiments 12-14.—Here, the first egg to be laid was removed (experiment 12: 01234 . . .), the first two eggs to be laid were removed (experiment 13: 00123 . . .), and the first three eggs to be laid were removed (experiment 14: 00012 . . .).

Experiments 15-18.—Eggs were put into the nest one day (experiment 15: [1]234 . . .), two days (experiment 16: [12]345 . . .), three days (experiment 17: [123]456 . . .), and four days (experiment 18: [1234]567 . . .) before the first egg of the clutch was laid (the days during which eggs were added but no egg was laid are indicated in superscript). A rough idea of when to start adding eggs was provided by the consistency of relaying periods, which are mostly of five days (Fig. 3). Each clutch was attributed *a posteriori* to the experiments described above.

Experiment 19.—Among the 25 females used during this work only 12 were used to test the hypothesis that follicular disruption might be triggered significantly later in those females laying the largest clutches. All 12 females had in common the fact that they

had been reared (in a single batch) as part of a previous study (Haywood and Perrins 1992). Individual estimates of clutch size were calculated by taking the mean size of seven clutches successively laid by each female and controlled for the effect of (early) age. To relate these estimates of individual clutch size to the timing of follicular disruption, each female was subjected to the following egg-removal experiments. At different times on the third day of the laying period, complete sets of eggs were removed from the nest in order to determine whether females would lay in an indeterminate manner or not; eggs laid on subsequent days were also removed (before 1300) until at least six eggs had been laid. Sets of eggs were removed at 0800, 2200, and 1400, respectively. Females systematically responded by indeterminate laying when egg removal started at 0800, by determinate laying when egg removal started at 2200, and by either indeterminate or determinate laying when egg removal started at 1400. Consequently, females that responded in an indeterminate manner at 1400 were subjected to egg removal at 1500, whereas those that responded in a determinate manner at 1400 were subjected to egg removal at 1300. The results obtained in this way were confirmed by further egg-removal experiments carried out at 1400 (repeat experiments) and 1200. The timing of these removal experiments was such that in most cases determinate and indeterminate responses alternated. The latest time at which the female responded in an indeterminate manner and the earliest time that brought about a clutch of four to six eggs give, for each female, an estimate of the interval during which the disruption of follicular growth occurs. Each interval was transformed into a single middle value, so that the degree to which the timing of follicular disruption covaries with mean individual clutch size could be estimated.

Statistical analyses.—For each of the experiments 1-18, means of clutch sizes of control and experimental groups were tested for statistical differences. In total for these experiments, 239 control and 208 manipulated clutches were laid by 25 females. Since not all 25 females were involved in each of the experiments, the mean clutch size of controls is computed only for the females used in a given experiment so as to form matched pairs. When several, control or experimental, clutches were obtained from a single female, an average clutch size for that female was kept in the calculation of the mean clutch size of the control or experimental groups. Clutch size obtained for the experimental females and the corresponding controls were tested for the similarity between means (two-tailed t-test for matched pairs; Sokal and Rohlf 1981).

RESULTS

Quantitative nature of stimulus.—Females left with no egg in the nest during the laying period

TABLE 1.   Mean clutch size ± SD of control and experimental females for experiments 1 to 18.

Experiment	Sample size[a]	Control	Experimental	t-test (df)
Quantitative nature of stimulus				
1 Egg removed as laid (0000...)	7 (63, 32)	5.28 ± 0.34	13.43 ± 4.37	4.62 (6)**
2 Single egg left (1111...)	7 (60, 14)	5.01 ± 0.50	5.00 ± 0.60	0.07 (6)ns
3 Five eggs added (6789...)	6 (60, 12)	5.20 ± 0.32	5.03 ± 0.48	0.75 (5)ns
Qualitative nature of stimulus				
4 No tactile stimulus	4 (59, 5)	5.40 ± 0.15	9.50 ± 1.50	4.55 (3)***
5 No olfactory, auditory, or visual stimuli	4 (48, 4)	5.42 ± 0.16	5.75 ± 0.43	2.29 (3)ns
6 No olfactory stimulus[b]	4 (4, 4)	5.75 ± 0.43	5.75 ± 0.43	0.00 (3)ns
7 No auditory stimulus[b]	4 (4, 4)	5.75 ± 0.43	5.75 ± 0.43	0.00 (3)ns
Timing of stimulus				
8 Egg removal from 2nd day (10000...)	8 (70, 8)	5.34 ± 0.34	7.38 ± 2.00	2.74 (7)*
9 Egg removal from 3rd day (12000...)	18 (197, 33)	5.26 ± 0.32	9.42 ± 1.81	9.42 (17)***
10 Egg removal from 4th day (12300...)	20 (212, 39)	5.23 ± 0.34	4.74 ± 0.54	3.78 (19)**
11 Egg removal from 5th day (12340...)	6 (51, 9)	5.09 ± 0.50	4.83 ± 0.62	1.16 (5)ns
Experimental delay of stimulus				
12 Egg removal until 2nd day (01234...)	5 (47, 9)	5.39 ± 0.26	5.28 ± 0.39	0.58 (4)ns
13 Egg removal until 3rd day (00123...)	8 (68, 9)	5.32 ± 0.34	6.19 ± 0.79	2.55 (7)*
14 Egg removal until 4th day (00012...)	9 (77, 13)	5.34 ± 0.31	7.08 ± 0.33	12.60 (8)***
Experimental advance of stimulus				
15 Egg addition one day in advance ('234...)	4 (46, 4)	5.47 ± 0.11	5.25 ± 0.43	0.88 (3)ns
16 Egg addition two days in advance ('²345...)	5 (48, 5)	5.23 ± 0.37	4.40 ± 0.49	2.35 (4)ns
17 Egg addition three days in advance ('²³456...)	4 (35, 4)	5.43 ± 0.18	3.75 ± 0.43	5.31 (3)**
18 Egg addition four days in advance ('²³⁴567...)	3 (25, 5)	5.47 ± 0.19	2.78 ± 0.31	8.64 (2)*

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, $P > 0.05$.
[a] Number of control and experimental females, with numbers of clutches for controls and experimentals, respectively, in parentheses.
[b] Control was test group in experiment 5.

laid on average significantly more eggs than the controls (Table 1, experiment 1). One female laid a single clutch of 39 eggs, with nine single-day gaps in the sequence. When, after the first egg, further eggs were not allowed to accumulate in the nest through the laying period, experimental clutch sizes were not significantly different from the controls (Table 1, experiment 2). When a full clutch (five eggs) was placed in the nest on the first day of laying, clutch sizes of experimental females also remained unchanged (Table 1, experiment 3).

Qualitative nature of stimulus.—Females that were given the opportunity of prolonged visual contact with a clutch during laying, but lacked tactile stimulation from eggs, laid significantly more eggs per clutch than the controls (Table 1, experiment 4). Females in contact with buttons instead of eggs during the laying period had clutch sizes not different from the controls (Table 1, experiment 5). Some females laid extra eggs, but they were not taken into account because these birds, or their mates, systematically ejected the buttons from the nest. Females whose newly laid eggs were replaced by eggs coated with a plastic film or a thin layer of transparent rubber did not lay significantly larger clutches than birds whose eggs were replaced by buttons (Table 1, experiments 6–7).

Timing of stimulus.—When egg removal started on the second or third day of the laying period, females laid significantly more eggs per clutch than the controls (Table 1, experiments 8–9). When egg removal started on the fourth or fifth day of the laying period, however, females did not lay significantly more eggs than the control (Table 1, experiments 10–11). For the 20 females where eggs were removed on the fourth day of the laying period, none laid a clutch greater than six eggs. By contrast, the proportion of females ($n = 18$) laying clutches greater than six eggs when eggs were removed on the third day of the laying period was 100%.

In experiments 8–9, some females interrupted laying altogether as a result of the start of egg removal instead of continuing laying beyond their normal clutch size. Among all 81 clutches manipulated before the third day of the laying

period, 9.9% were smaller than seven eggs ($n = 21$ females), whereas among 217 control clutches of the same 21 females, 96.8% were smaller than seven eggs. Although the proportion of manipulated clutches smaller than seven eggs was greater when egg removal started on the second day of the laying period, by comparison with clutches where egg removal started on the first or third day, this difference is not significant ($X^2 = 4.49$, 2 df, $P = 0.106$).

Slightly smaller clutches than expected were on average laid by females manipulated on the fourth day of egg laying (Table 1). Lack of contact with eggs at this stage sometimes prevents the last large yolky follicle from completing the rapid-growth phase and ovulating. Hence, this causes a reduction in clutch size in the Zebra Finch.

Experimental delay of stimulus.—Females for which only the first egg laid was removed did not lay significantly more or fewer eggs per clutch than the controls (Table 1, experiment 12). Females in which the first two eggs were removed did significantly increase their clutch size (Table 1, experiment 13), although not as much as females in which the first three eggs were removed (Table 1, experiment 14). Removal of the first two eggs induced the female to lay an average of one extra egg, whereas removal of the first three eggs induced the female to lay an average of two extra eggs.

Experimental advance of stimulus.—Eggs added one or two days before females started laying did not significantly affect the clutch size laid by experimental females (Table 1, experiments 15–16), whereas eggs added three or four days before females started laying did (Table 1, experiments 17–18). Results in Table 1 show that addition of eggs two, three, and four days before the first was laid induced females to lay on average one, two, and three fewer eggs, respectively, than the controls.

Individual variation in clutch size.—Among the 12 females tested, the timing of disruption of ovarian follicular growth was restricted to an interval starting 5 h (1300) after the onset of light (0800) and lasting a maximum of 2 h. The individual timing of follicular disruption was not correlated with mean individual clutch size ($r_{11} = 0.437$, $P > 0.05$); across females, the time of follicular disruption tended to decrease slightly as clutch size increased: $Y = 16.516 - 0.506X$ (95% confidence limits of slope were -0.889 and -0.288).

DISCUSSION

Results presented here show that female Zebra Finches require contact with at least one egg during laying to lay a normal clutch (four to six eggs). A single egg actually is sufficient to trigger the cessation of egg laying although, under natural conditions, most females have already laid three eggs when the egg stimulus ending laying occurs. Clearly, such stimulus received by the female is independent of the number of eggs in the nest since five eggs added on the first day of laying does not lead to smaller clutch size. When eggs are removed as they are laid, close visual contact with a clutch is not sufficient to stop females from laying eggs. When I replaced eggs as they were laid with buttons (in order to provide the female with a tactile stimulus but no visual, olfactory, and auditory stimuli similar to eggs), experimental clutch sizes did not differ from the controls (Table 1). Thus, only tactile stimulus is required to induce females to stop laying. This finding is confirmed by experiments involving eggs coated with plastic to prevent egglike olfactory stimulus or coated with rubber to prevent egglike auditory stimulus, which suggest that neither olfactory nor auditory factors are involved in synergy with tactile stimulus in ending laying in this species. To sum up, following the classification of clutch-size control mechanisms proposed for the birds investigated to date (Haywood 1993a), the Zebra Finch is a tactile indeterminate layer of type S.

It has often been speculated that in species responding to egg removal, females may be using a visual stimulus from the eggs (alone or in connection with tactile stimulus) to trigger cessation of egg laying (Lack 1947, Chappell 1948, Jones 1969, Steen and Parker 1981, Lea et al. 1981, Kennedy 1991). Until now, however, only Steen and Parker (1981) have attempted to test the involvement of visual cues. They substantiated their view that such cues are in use in bantam hens (*Gallus gallus*) by putting a wire netting over the clutch in order to prevent females from having tactile contact with their eggs. Experimental clutch sizes (15.17 ± SD of 5.15) and control clutch sizes (14.67 ± 4.78) obtained from the same females ($n = 12$) were not statistically different ($t_{22} = 0.236$, $P > 0.05$). This experiment is, in my opinion, invalidated by the fact that females were allowed to sit on the floor next to the eggs and, hence, actually re-

ceived the tactile stimulus needed to trigger the cessation of egg laying. To date, it is only among parasitic species of cuckoos and cowbirds that there is good evidence that visual stimulus (probably related to the availability of suitable host nests) may be involved in controlling clutch size (Haywood 1993a).

Egg-removal experiments started on the second to fifth day of the egg-laying period (Table 1, experiments 8–11) show that the disruption of ovarian follicular growth occurs on the third or fourth day of laying. Further egg-removal experiments (experiment 19) demonstrate that follicular disruption is irreversible sometime after 1300 but before 1500 on the third day of laying (i.e. 5–7 h after dawn [14L:10D]). In other respects, the period during which females are responsive to the tactile stimulus ending laying can be experimentally delayed or advanced by changing the day when egg(s) first appear in the nest. Removing eggs for n days from the start of laying increased the clutch by $n - 1$ eggs (Table 1). In contrast, eggs added before the first egg is laid bring about a reduction of the size of the clutch. Adding eggs n days prior to egg laying reduced the clutch by approximately $n - 1$ eggs (Table 1). These results show that, although follicular disruption occurs on the third day of laying, the timing of this event relative to the onset of laying is determined on the second day of the laying period. Thus, eggs not only provide a stimulus responsible for the disruption of ovarian follicular growth, but they also provide stimulation for the onset of sensitivity to the stimulus responsible for follicular disruption. The fact that the timing of follicular disruption can be moved back and forth during the laying period demonstrates that the timing of tactile sensitivity to eggs is not internally related to the onset of egg laying.

It has been suggested that some species may alter their clutch size in response to egg removal, but not to egg addition (e.g. Common Kestrel [*Falco tinnunculus*], or vice versa, Rock Dove [*Columba livia*]; Kennedy 1991). Hence, the hypothesis that such species categorized as "removal indeterminate" or "addition indeterminate," respectively, have independently evolved mechanisms allowing them to cope with egg loss or egg parasitism (Kennedy and Power 1990, Kennedy 1991). This distinction is based primarily on artifacts; evidence that separate responses have evolved due to egg removal or egg addition per se is yet to be found. Common

Kestrels control their clutch size in such a way (Beukeboom et al. 1988, Haywood 1993a) that contact with an almost complete clutch days before the first egg is laid will be required to induce a significant response to egg addition. Rock Doves respond to egg addition to the extent that some females will incubate a clutch added prior to laying (Poulsen 1953), but egg formation and therefore laying, even of a reduced clutch, become de facto physiologically impossible. As shown here in the Zebra Finch, changes in clutch size that some species can produce as a result of egg removal or egg addition are mere consequences of the way they control their clutch size. Any tactile indeterminate layers (i.e. species in which egg stimuli are needed to trigger the disruption of ovarian follicular growth), therefore, will respond to both egg-removal and egg-addition experiments.

In Zebra Finches the sensitive period, during which tactile stimulation builds up to reach a stage where follicular disruption can effectively occur, lasts less than two days. Thereafter, females will remain responsive to any prolonged, tactile stimulation of the brood patch for several days. Females whose eggs were removed as they were laid for a period of up to 12 days, subsequently ceased laying within three to four days after egg removals were stopped. It was nonetheless difficult to assess rigorously the precise maximum duration of the sensitive period because, as mentioned earlier, the male who also incubates the clutch, often prevents the female from getting sufficient contact with the eggs left in the nest. This sensitive period and the factors that affect its duration therefore would be more easily investigated in a species where the male does not take part in incubating the clutch.

The present data on Zebra Finches demonstrate that the disruption of ovarian follicular growth is not triggered significantly later in females laying the largest clutches. The hypothesis that variation in the timing of the stimulus provided by eggs accounts for individual variation in clutch size, therefore, is not valid. It may be argued that the lack of variation in the timing of follicular disruption in relation to clutch size in 12 females bred in captivity for many generations might have resulted from a bottleneck effect when captive breeding was initiated and/or from subsequent inbreeding. If we assume that some significant variation of the timing of follicular disruption exists in the
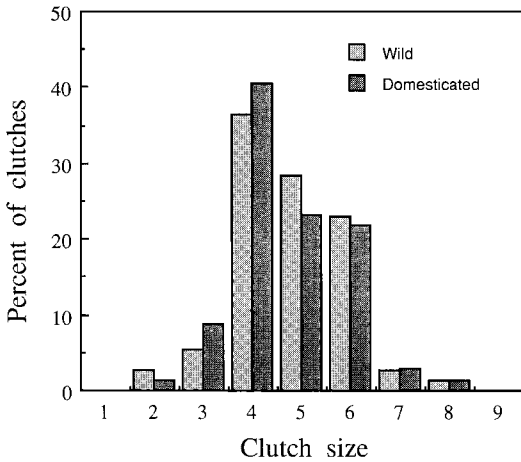
Fig. 4. Clutch size from wild and domesticated Zebra Finches maintained under the same conditions in captivity. Wild females ($n = 10$) and domesticated females ($n = 16$) laid 74 and 69 clutches, respectively, over three seasons (data from Sossinka 1970).

wild, clutch size likewise would be more variable. For instance, variable timing of follicular disruption, which has been reported for wild Blue Tits (*Parus caeruleus*), allows them to lay clutches varying from 6 to 13 eggs (Haywood

1993b). In this species, a lack of variation in the timing of follicular disruption would limit clutches to three or more likely two sizes, according to the number of yolky follicles undertaking rapid growth simultaneously. In Zebra Finches, data collected by Sossinka (1970) do not support the view that significantly more variation occurs in the wild. Distributions of clutch sizes from 10 females taken from the wild ($n = 74$ clutches) and 16 domesticated females ($n = 69$), both maintained under the same conditions in captivity, were not statistically different (Kolmogorov-Smirnov test for goodness of fit, $D = 0.0519$, $P > 0.05$; Fig. 4). As expected if a steady timing of follicular disruption is the rule in the Zebra Finch, the vast majority of clutches were restricted to three sizes. Clutches ranging from four to six eggs represented 87.8 and 85.5% of all clutches laid by wild and domesticated females, respectively. Therefore, it is likely that, as for the variable timing of clutch-size determination uncovered in Blue Tits, a steady timing is characteristic of the way Zebra Finches as a species control their clutch size.

Knowing that the timing of follicular disruption shows no positive relationship with clutch size, how are individual variations in clutch size generated? In theory, egg stimulus could act at two different stages of oocyte development: fol-
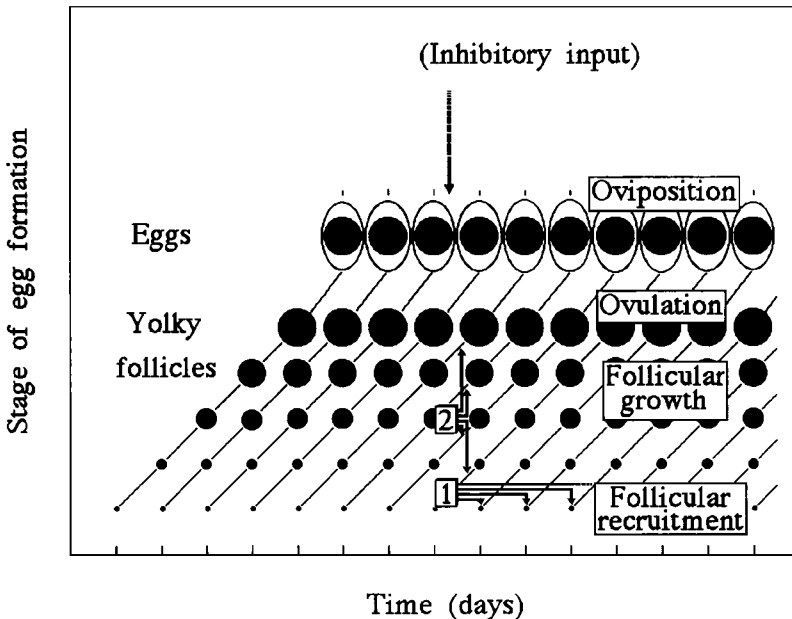

Time (days)

Fig. 5. In theory, how inhibitory input from eggs present in nest affects ovarian activity may either result in (1) disruption of follicular recruitment, or (2) disruption of follicular growth.
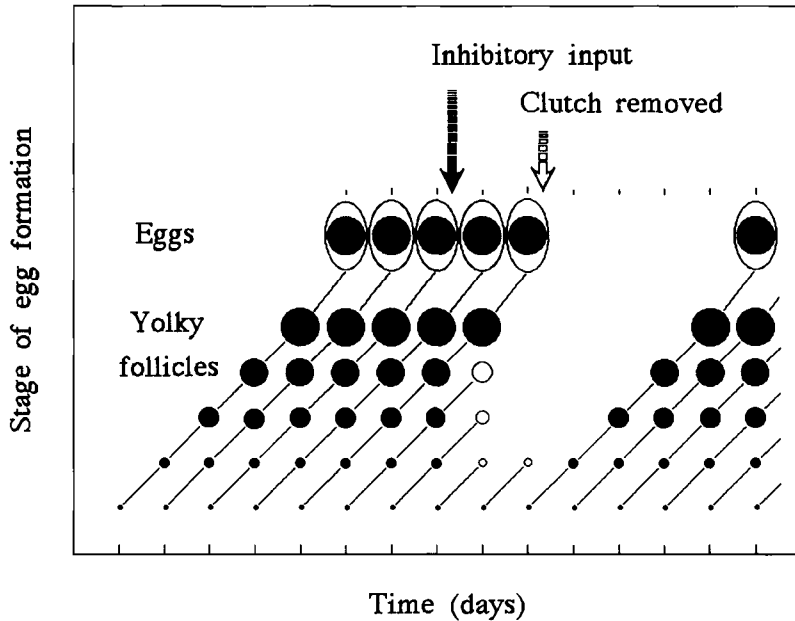
Fig. 6. Representation of a five-egg clutch determination in the Zebra Finch. Inhibitory input provided by eggs present in nest and responsible for disrupting growth of smaller yolky follicles (empty circles) occurs on third day of laying, 6 ± 1 h after dawn (14L:10D). Removal of clutch on fifth day of laying allows follicular growth to resume on same day.

licular recruitment and follicular growth (Fig. 5). Cessation of egg laying through disruption of follicular recruitment would inevitably produce clutches of at least eight eggs (Fig. 5), since five days are required to form an egg in the Zebra Finch (S. Haywood unpubl. data). As this prediction does not match the observed range of clutch sizes, the hypothesis that egg stimulus acts on the ovary by disrupting follicular recruitment must be rejected. The impact on follicular recruitment during follicular disruption is in fact minor or null. In effect, the bulk of relaying periods are as short as five days (Fig. 3), which implies that in most cases, at the time of follicular disruption, follicular recruitment is continued without interruptions; the follicle corresponding to the egg laid after such five-day periods is recruited into growth within a day of the removal of the clutch (Fig. 6).

The range of clutch sizes observed in Zebra Finches implies that the mechanism responsible for individual variation in clutch size specifically involves disrupting follicular growth. If all growing follicles up to the one in its last day of growth become atretic, the clutch size will be four eggs. Similarly, if all growing follicles up to the one in its third day of growth

become atretic, the clutch size will be five eggs (Fig. 6), and so forth. The greater the number of growing follicles affected by the female contact with eggs, the smaller the clutch. Since the timing of follicular disruption shows no variation between females in relation to clutch size, the depressive action brought about by the contact with eggs affects differently growing yolky follicles of different ages. Growth of follicles in their first or second day of development is systematically disrupted since no normal clutches reach a size of eight or seven eggs, respectively, but the extent to which follicles in their third and fourth day of development are affected by the inhibitory input from eggs is responsible for clutch-size variation in the Zebra Finch. Which factor(s) determines whether the growth of these large yolky follicles is disrupted is not known. However, it is known that conditions experienced by female Zebra Finches at an early age (nestling stage) have considerable effect on individual variation in clutch size (Haywood and Perrins 1992). Investigating the endocrine control of follicular disruption and its regulation at the level of the brain would help answer how clutch-size variation are generated in this species.

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