

RESPONSES OF EGG-LAYING PIED FLYCATCHERS TO EXPERIMENTAL CHANGES IN CLUTCH SIZE: A RE-EXAMINATION¹

M. D. KERN

Biology Department, The College of Wooster, Wooster, OH 44691, e-mail: mkern@acs.wooster.edu

R. J. COWIE AND F. M. SLATER

School of Biosciences, Cardiff University, P.O. Box 915, Cardiff CF1 3TL, U.K.

Abstract. Previous studies with small numbers of clutches suggested that Pied Flycatchers (*Ficedula hypoleuca*) were determinate egg-layers whose clutch size was fixed before laying began. We found that females lay additional eggs of normal size if clutch size is experimentally reduced, but do not lay fewer eggs when clutch size is increased. In the terms of Kennedy and Power (1990), Pied Flycatchers are removal-indeterminate and addition-determinate.

Key words: determinate egg-laying, *Ficedula hypoleuca*, indeterminate egg-laying, Pied Flycatcher.

Birds are commonly grouped as determinate or indeterminate egg layers depending upon how they respond to alterations in clutch size while laying. Determinate layers do not respond to such changes, but lay a fixed number of eggs. Indeterminate layers, on the other hand, compensate for egg removal or addition by laying more or fewer eggs to keep clutch size approximately constant (Kennedy 1991).

Until recently, the Pied Flycatcher (*Ficedula hypoleuca*) was considered a determinate layer (Berndt 1943, von Haartman 1967). The evidence was slim, however, and led Haywood (1993) in a review of egg-laying patterns to conclude that the status of this species was still uncertain. Several facets of their natural history suggest that Pied Flycatchers may in fact be indeterminate layers. For example, the number of yolky follicles that develop in the ovary exceeds clutch size (Silverin 1980) and levels of luteinizing hormone, which is required for ovulation, are moderate to elevated throughout the laying and incubating phases of the breeding cycle (Silverin and Wingfield 1982). This would presumably enable the birds to produce additional eggs if circumstances warranted it. Furthermore, the clutch size of Pied Flycatchers is highly variable (< 4 to 10 eggs) (Järvinen 1989), not rigidly fixed by the genotype (Lundberg and Alatalo 1992), and flexible. Several proximate factors can influence it, including the type of woods in which the birds nest (Gezelius et al. 1984), food availability (Sanz and Moreno 1995), female size and condition (Askenmo 1982), population density (Alatalo and Lundberg 1984), and even the size of the nest box (Karlsson and Nilsson 1977). In other words, the potential for producing additional eggs is clearly present in this passerine.

It might, however, be in the flycatchers' best inter-

ests to limit the eggs they lay to a number below the most productive clutch size (Moreno et al. 1991), if it would improve their fitness. With a smaller clutch, they could keep egg size large, an important factor in the growth and survival of the chicks (Järvinen and Väisänen 1983, Järvinen and Ylimaunu 1984), and perhaps simultaneously enhance their own survival and fecundity in the future given that large clutches carry high immediate and future costs of reproduction for flycatchers (Nur 1988, Gustafsson and Pärt 1990).

In any event, previous studies suggesting that Pied Flycatchers are determinate layers involved only 9 (von Haartman 1967) and 17 nests (Berndt 1943) and few-to-no replicate manipulations of clutch size, and are therefore difficult to interpret. This and the evolutionary importance of egg-laying patterns led us to re-examine the status of Pied Flycatchers, to include a recently developed method of evaluating the laying pattern (Kennedy 1991), and to determine whether Pied Flycatchers enlarge their clutches by producing eggs that are smaller than normal, as Least Flycatchers (*Empidonax minimus*) do (Briskie 1985).

METHODS

The female Pied Flycatchers in our study used nest boxes in several deciduous or mixed deciduous-conifer woods, dominated by sessile oaks (*Quercus petraea*), within 10 km of Newbridge-on-Wye, Powys, Wales, U.K. (52°N, 3°W).

During the 1993 nesting season, we removed the first and all subsequent eggs as they were laid from 11 nests, a method commonly used in previous studies to determine egg-laying patterns. These were the first clutches of the females: egg laying began between 10 and 22 May.

In 1994, we removed, added, or switched two eggs in 73 nests as specified by Kennedy's (1991) method for determining egg-laying patterns. Two eggs were removed from a nest on the day they were laid, beginning with egg 1 ($n = 12$ nests), egg 2 (10 nests), or egg 4 (10 nests). Two eggs were added, one per day, to complete nests that were still empty and in which females subsequently laid (9 nests), or to nests after egg 1 (10 nests) or egg 4 (9 nests) was laid. Eggs 1 and 2 were switched in 13 additional (control) nests. The empty nests to which eggs were added had nest cups that were well molded, generally a sign that laying is about to start. Egg laying began in these nests one to several days later and the eggs we provided became a part of the clutch in all cases.

We used a similar experimental protocol in 1998. Two eggs were removed from a nest as laid, beginning

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with egg 1 ($n = 10$ nests) or egg 4 (10 nests). Two eggs, one per day, were added to other nests after the female had laid egg 1 (10 nests) or egg 4 (10 nests). Eggs 1 and 2 or 4 and 5 were swapped in another 20 (control) nests.

All of the egg sets studied in 1994 and 1998 were first clutches. Because the clutch size of Pied Flycatchers decreases during the nesting season at a rate of 0.07 eggs day⁻¹, at least in Finland where this well known "calendar effect" was first described by von Haartman (1967), we used only clutches in which egg laying began between 7 and 14 May. The mean dates of clutch initiation among our groups ranged from 10 to 13 May.

To be sure that the females in the 1994 and 1998 groups had finished laying, we continued to monitor their clutches during incubation, and in most cases until the chicks hatched. In 1994, 67 clutches hatched; the other 7 were either deserted ($n = 4$) or depredated ($n = 3$) during the incubation period. In 1998, 49 clutches are known to have hatched chicks and the other 11 to have been incubated for 2 or more days.

In all three seasons, we measured the dimensions of the eggs with digital calipers (± 0.01 mm) to determine their volumes (V_{egg}) by means of the equation $V_{\text{egg}} = 0.50 LB^2$ where L and B are the egg's length and maximum breadth, in cm (Kern and Cowie 1996).

MEASURES OF FEMALE CONDITION AND TERRITORY QUALITY

Age, previous breeding experience, physical condition, and territory quality are all factors that can influence the clutch size of female Pied Flycatchers (Lundberg and Alatalo 1992). We had enough ancillary information about the birds in our study populations to examine the possible influences of the females' condition and the quality of their territories on clutch size. We used egg size as an indirect measure of female condition because heavier birds, in better condition, lay larger eggs than lighter females (Järvinen and Väisänen 1984). We compared egg size in clutches of 6–7 and 8–9 eggs to determine whether differences in clutch size depended on the condition of the female.

We also examined the possibility that clutch size is related to territory quality at the two major study sites for which we have five or more consecutive years of data. Pied Flycatchers have type B territories, the value of which is reflected by how often each nest box has been used. Territory quality (Q) can be measured therefore using the equation $Q = u - a^{-1}$ (Potti 1993) where u = the number of years that a nest box was used by Pied Flycatchers and a = the number of years that the nest box was available (i.e., not occupied by another species). The value of Q increases with the number of years in which the nest box has been available, but for any given period higher values indicate better quality.

STATISTICAL ANALYSES

We compared responses to addition or removal of eggs with the control situation (egg swaps) using Mann-Whitney U -tests, 1-tailed because we expected differences in only one direction. In analyzing the 1994 data, we combined results from nests in which eggs were added on days 0–2 of egg laying into an "early ad-

ditions" group and results from nests in which eggs were removed on days 1–3 into an "early removal" group because of small sample sizes. In 1998, we combined data from nests in which eggs were swapped on days 1–2 or 4–5 into a single control group because the distribution of clutch sizes was similar in both cases (U -test, $P > 0.2$). We used single-factor analysis of variance to compare the mean V_{egg} of the groups in the 1994 and 1998 populations, and Student's t -tests and Spearman's rank correlation analysis to examine relationships between clutch or egg size and measures of the flycatchers' condition or the quality of their territories. The values reported are means \pm SD.

RESULTS

1993 EXPERIMENT

In the manipulated nests, one female laid a new egg on 18 consecutive days, but each of the other 10 flycatchers laid 5–8 eggs: 5 eggs (1 female), 6 eggs (1), 7 eggs (5), and 8 eggs (3). This distribution (not including the 18-egg clutch) is not significantly different from that of 17 unmanipulated nests that were initiated during the same 13-day interval in 1993 (U -test, $P > 0.2$). The clutch size of these 10 manipulated females averaged 7.00 ± 0.94 eggs, which was nearly identical to the clutch size of 6.71 ± 0.77 eggs in the 17 unmanipulated nests.

Egg volume was not related to the position of an egg in these 10 clutches: the largest egg within individual clutches varied, for example, from the first to the last egg laid. The mean volume was 1.61 ± 0.08 cm³ with ($n = 88$ eggs) or without ($n = 70$ eggs) the 18-egg clutch. Within the latter, V_{egg} averaged 1.57 ± 0.06 cm³ and showed distinct peaks in eggs 5, 10, and 15.

1994 AND 1998 EXPERIMENTS

Adding eggs to the nest had no effect on clutch size in either 1994 or 1998 (Table 1). Clutch size was, however, increased significantly when eggs were removed from the nest during early laying in 1998 (Table 1). With one exception, the only females that laid 9-egg clutches, rare in our area (Campbell 1955, pers. observ.), were those with eggs removed (Table 1). None of the other clutches in manipulated nests was outside the normal 4- to 8-egg range characteristic of our populations.

The average V_{egg} in the groups ranged from 1.53 to 1.61 cm³ in 1994, and 1.54 to 1.62 cm³ in 1998. Volume was not influenced by changes in clutch size during either year (ANOVA: $F_{4,62} = 0.6$ in 1994, $F_{4,54} = 1.0$ in 1998; $P > 0.5$ in both cases).

Although females in the early removal group responded significantly to manipulations in clutch size (Table 1), the average V_{egg} of those which laid clutches of 6–7 eggs was not significantly different ($P > 0.5$) from that of females which laid clutches of 8–9 eggs in either 1994 (1.57 vs. 1.60 cm³, 7 vs. 12 females) or 1998 (1.74 vs. 1.72 cm³, 4 vs. 6 females).

Territory quality averaged 79.2% and 77.1% of maximum possible values in 1994 and 1998, respectively. Clutch size was not significantly related to it in any of the 1994 groups. In 1998, however, clutch size was weakly correlated with Q in the "early removal"

TABLE 1. The effects of altering the number of eggs in the nests of Pied Flycatchers at various times during the egg-laying period.^{a,b}

Year	Treatment	Dates when egg laying began	Clutches (n)	Clutches (n) with sizes of					Clutch size	P-value ^c
				4	6	7	8	9		
1994	Swaps	7–11 May	13		3	7	3		7.00 ± 0.71	—
	Additions									
	Days 0–2	10–14 May	19	1	7	9	2		6.58 ± 0.90	ns
	Days 4–5	11–14 May	9		1	7	1		7.00 ± 0.50	ns
	Removals									
1998	Days 1–3	8–14 May	22		5	4	10	3	7.50 ± 1.01	0.07
	Days 4–5	7–14 May	10		2	5	3		7.10 ± 0.74	ns
	Swaps	9–13 May	20		2	12	6		7.20 ± 0.62	—
	Additions									
	Days 1–2	12 May	10		2	8			6.80 ± 0.42	ns
1998	Days 4–5	9–11 May	10		2	6	1	1	7.10 ± 0.88	ns
	Removals									
	Days 1–2	12 May	10		1	3	5	1	7.60 ± 0.84	<0.02
	Days 4–5	9–11 May	10		1	5	2	2	7.50 ± 0.97	0.07

^a "Swaps" = exchanges of 2 eggs between a pair of nests. This constitutes the control group in each year.

^b Day 0 = addition of eggs to finished nests prior to laying. Day 1 = first day of laying.

^c Mann-Whitney *U*-tests.

group ($r_s = 0.79$, $P = 0.06$, $n = 6$ nest boxes), and more strongly so in the "late additions" group ($r_s = 0.94$, $P = 0.04$, $n = 5$ nest boxes).

DISCUSSION

In the terms of Kennedy and Power (1990), Pied Flycatchers are addition-determinate, but removal-indeterminate egg layers. The addition-determinance may mean that females lay a minimal number of eggs under any circumstance, although that number can vary between individuals. The removal-indeterminance shown in Table 1 suggests that some females can apparently lay more than this minimal number. The results of the 1993 experiment are consistent with this interpretation assuming the one unusual clutch of 18 eggs was produced by a single female. Several factors suggest that only one bird laid this clutch in spite of its three peaks in V_{egg} . To begin with, there was no instance in which two eggs were laid in this nest box on the same day. In our experience, when a nest box is deserted by one female and taken over by another, the nest is usually refurbished and laying does not begin for several days. No such refurbishing occurred and there was no gap in laying—one egg was produced on each of 18 consecutive days.

Why some Pied Flycatchers lay more than the normal complement of eggs when clutch size is reduced early in the egg-laying period and others do not (Table 1) is unknown. Age, however, may play a role given that first-year birds often produce smaller clutches than older adults (von Haartman 1967, Järvinen 1991) and the optimal clutch size increases with age in the closely related Collared Flycatcher (*Ficedula albicollis*; Gustafsson 1990).

The bird's size and condition may also be important because large and heavy females produce larger eggs and clutches than small birds (Järvinen and Väisänen 1983, Potti 1993). Our study, however, provides no support for this possibility as there was no difference

in V_{egg} between females in the "early removal" group that laid clutches of 6–7 eggs and those that laid clutches of 8–9 eggs in either 1994 or 1998.

Territory quality could also be a factor, particularly because it is the most important criterion that female Pied Flycatchers use when selecting a mate (Alatalo et al. 1986). Högstäd (1980) has suggested for magpies that all females produce clutches of the most productive size, but that clutch size varies among individuals because they occupy territories of different quality. Recent work in which the nests of Pied Flycatchers were moved from deciduous to coniferous sites prior to egg laying without females deserting (Siikamäki 1995) supports this hypothesis. In general, the birds in our populations nested at high-quality sites in both 1994 and 1998. Furthermore, clutch size in 1998 was related to Q in two groups, one of which was the "early removal" group, i.e., the group which responded to egg removal by laying additional eggs (Table 1). Our data are then consistent with the premise that birds occupying superior territories are able to lay more than the minimal number of eggs. The quality of the nest box itself was probably not a factor in our study because all but two of our boxes are uniform in size and construction.

Breeding experience could also be a factor. Harvey et al. (1985) found that at least 40% of 2-year-old female Pied Flycatchers nesting in the Forest of Dean, Great Britain, had no breeding experience at all. More recently, Nur (1988) concluded that female flycatchers acquire the ability to adapt clutch size to prevailing environmental conditions gradually and that only prior experience in the nesting area enables them to adjust clutch size appropriately. It is therefore possible that experienced birds respond to egg removal, whereas first-time breeders do not.

The reason why indeterminate laying has not been observed in Pied Flycatchers previously may reflect differences in methods of assessing laying patterns. It

may be difficult to detect indeterminate responses in species like Pied Flycatchers that have highly variable clutch sizes unless large numbers of nests are manipulated. We believe this is why our findings differ from those of Berndt (1943) and von Haartman (1967) whose sample sizes were very small.

Haywood (1993) has proposed that egg-laying patterns are evolutionary responses to the amount of food available to female birds when the eggs are forming. That is, indeterminate responses will occur when the food supply in the nesting area varies in an unpredictable manner from year to year, whereas determinate responses will evolve when the food supply remains reasonably constant. As far as Pied Flycatchers are concerned, there is considerable support for this hypothesis because such proximate factors as habitat characteristics, the abundance of food when the birds are laying, female condition, and weather affect their clutch size (Lundberg and Alatalo 1992).

Kennedy and Power (1990), on the other hand, have proposed that nest parasitism and predation are ultimately responsible for indeterminate laying patterns and that they may act independently. As a result, a species may respond to either the addition or removal of eggs, both, or neither. As far as Pied Flycatchers are concerned, there is less support for this hypothesis. We have, for example, cases in which two females laid eggs in the same nest and in which nests suffered losses of one to several eggs to predators (mice and possibly jays or crows), and conspecific egg parasitism has been documented previously in Pied Flycatchers (Högstedt, cited in MacWhirter 1989). Unless parasitism is so infrequent that it does not affect fitness in clutches of large size (Power et al. 1989), we might therefore expect these flycatchers to be both addition- and removal-indeterminate, rather than addition-determinate and removal-indeterminate (Table 1).

Pied Flycatchers are certainly indeterminate layers in the sense that more yolky follicles develop in the ovary than are laid (Silverin 1980). The extra ones can be used to replace the first clutch if it is destroyed, but they might also be a source of additional eggs for the initial clutch. The moderate-to-high levels of luteinizing hormone that persist throughout the laying and incubating phases of the breeding cycle (Silverin and Wingfield 1982) would presumably enable flycatchers to produce these additional eggs if an occasion warranted it. Some do, but others apparently do not (Table 1). Nonetheless, even when females do respond to the removal of eggs from their nests, the clutch generally stays within the normal range for the species (Table 1) and egg size remains large.

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EGG RECOGNITION IN YELLOW-BILLED AND BLACK-BILLED MAGPIES IN THE ABSENCE OF INTERSPECIFIC PARASITISM: IMPLICATIONS FOR PARASITE-HOST COEVOLUTION¹

GINGER M. BOLEN²

Museum of Vertebrate Zoology, 3101 VLSB, University of California, Berkeley, CA 94720

STEPHEN I. ROTHSTEIN

Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106

CHARLES H. TROST

Department of Biology, Idaho State University, Box 8007, Pocatello, ID 83209

Abstract. Yellow-billed Magpies (*Pica nuttalli*) ejected 100% of nonmimetic eggs placed in their nests despite such behavior having no detectable present day benefits. They are not currently parasitized, nor is there any evidence of a recently extinct brood parasite. Furthermore, there was no molecular evidence of conspecific parasitism, and Yellow-billed Magpies accepted

eight of nine conspecific eggs transferred between nests, so recognition would rarely be of benefit if conspecific parasitism occurred. Thus, we suggest that egg recognition in Yellow-billed Magpies is a plesiomorphic trait, a primitive character inherited from a remote ancestor, its nearest relative, the Black-billed Magpie (*Pica pica*). The latter suffers from parasitism by Great Spotted Cuckoos (*Clamator glandarius*) in Eurasia and displays rejection behavior throughout Europe in populations that are allopatric and sympatric with this cuckoo. As would be expected if Yellow-billed Magpies inherited rejection behavior from the Black-billed Magpie, or the common ancestor of both species, we found that North American Black-billed

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² Current address: Conservation and Research Center, 1500 Remount Road, Front Royal, VA 22630, e-mail: gingerbolen@excite.com