

EFFECTS OF PARENTAL EFFORT ON SECOND BROOD, MOULT AND SURVIVAL IN THE GREY WAGTAIL *MOTACILLA CINEREA*

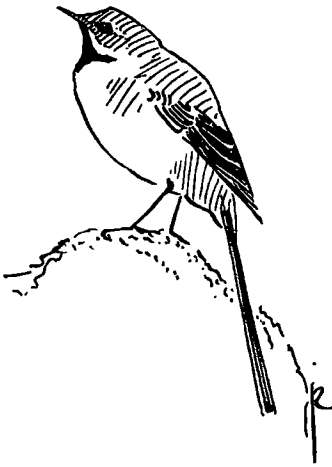
SVERRE KLEMP

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Negative effects of current reproductive effort on components of future reproduction, called the 'cost of reproduction', have been shown experimentally in a wide range of avian species. A possible mechanism for the mediation of these costs between successive breeding seasons may be the impairment of the postnuptial moult. Here I report the results of an experiment designed to test the hypotheses that a high reproductive effort leads to (1) a delayed onset and (2) an accelerated speed of moult. In the Grey Wagtail *Motacilla cinerea* I experimentally altered the size of 44 first broods by adding or removing two nestlings. Parental effort of both males and females, as measured by feeding rates and nestling time, differed between the two treatments. Frequency, timing, size, and success of second broods were not affected by the experiment neither in females nor in males. During moult, 18 experimental males, but none of the females could be re-captured. Males that raised reduced broods had significantly higher primary moult scores as compared to males with enlarged broods if re-capture date is controlled for (= Residual Moult Score). Residual Raggedness Value, a good estimator of moult duration, was not affected by the manipulation. Return rates of males in the year after manipulation were not significantly different between the treatments, while none of the females returned and none of the experimental offspring were recruited into the study population. In contrast to a number of earlier studies, these results are in agreement with the hypotheses that there is a trade-off between the investment in reproduction and the timing of postnuptial moult.

Key words: *Motacilla cinerea* - reproductive effort - brood size manipulation - moult start - moult rate - second broods - survival

Zoologisches Institut, Universität Bern, CH-3032 Hinterkappelen; Present address: Rahlaukamp 4, D-22045 Hamburg, Germany, E-mail: klemp@gmx.de



INTRODUCTION

The investment in current reproductive attempts may affect components of future reproduction negatively. This 'cost of reproduction' is a key issue in life-history theory. In various species, especially in birds, experimental manipulations of reproductive effort have shown to influence parental survival and/or future reproductive success (Roff 1992; Stearns 1992). Less is known of the ways in which reproductive costs are mediated. Nutrient and energy turnover rates of small

passerines are high and unlikely to cause long-lasting effects on survival and future reproduction: brood size manipulations had no effect on energy expenditure in raptors (Jönsson *et al.* 1996; Green & Ydenberg 1994) and Great Tits *Parus major* (Verhulst & Tinbergen 1997). In contrast, a changed allocation of resources or time into conflicting processes and activities could cause reproductive costs. Parental effort has been shown to reduce immuno-competence (Gustafsson *et al.* 1994) and parasite resistance (Oppliger *et al.* 1996) that, in turn, affects health and fecundity (Dufva

1996). A further mechanism that may underlie reproductive trade-offs in birds may be a postnuptial moult under stress-conditions (Langston & Rohwer 1996; Siikamäki *et al.* 1994). In the annual cycle of passerine birds of northern temperate regions the reproduction, moult and migration periods are separated from each other (Ginn & Melville 1983; Jenni & Winkler 1994). The costs of overlapping in these processes are various and include the impairment of flight capability, thermoregulation, feather durability and signalling (Earnst 1992; Jenni & Winkler 1994). Stressed individuals should therefore delay their moult from breeding to avoid these costs. Recently, Siikamäki *et al.* (1994) have shown experimentally, using clutch size manipulations (one or two eggs), that a high parental effort can, in fact, cause a delayed onset of moult in (female) Pied Flycatchers *Ficedula hypoleuca*. Thereby they confirmed the results of many observational studies that demonstrated a delay in postnuptial moult of birds with large clutches, second breeding attempts or late-hatched broods (see Jenni & Winkler 1994 for references).

On the other hand, late moult may conflict with migration (Kjellén 1994) or, in sedentary species, with other autumnal activities (e.g., fat storing, winter territoriality). European passerines do not start migration before they are in the final stages of moult (Jenni & Winkler 1994). Therefore, late-moulting individuals face yet another conflict, i.e. between the timing of moult and migration. One strategy could be to speed up feather regeneration and thereby finish moult before migration starts. A high moult rate may, however, be disadvantageous in terms of feather quality (durability, thermoregulation, signalling; Nilsson & Svensson 1996) and flight capability during moult (Haukioja 1971).

In this paper I report the results of an experiment designed to test the hypotheses that a high reproductive effort leads to (1) a delayed onset of moult and (2) to faster moult rates (i.e., higher number of simultaneously replaced feathers). I conducted this study with the partially migratory Grey Wagtail *Motacilla cinerea* since in this spe-

cies moult duration is much longer (*c.* 65 days) and more variable than in long-distance migrants such as the closely-related Blue-headed Wagtail *M. flava* (40-45 days; Glutz von Blotzheim & Bauer 1985; Sondell 1993). Therefore, a reduction of moult duration could be realised if selection would be strong enough.

MATERIAL AND METHODS

Grey Wagtails are small passerines (15-20 g body mass), distributed mainly in mountainous regions throughout Europe and Asia. Migrants return to the breeding grounds during March and April, depending on altitude and weather conditions. Breeding territories are highly restricted to (running) water. In favourable habitats, up to three clutches are laid between end of March and end of July, but most commonly there are one or two breeding attempts per year. First broods have on average five or six eggs, but later ones are somewhat smaller. Clutches are incubated for 11-13 days; the nestling period is 11-14 days (Glutz von Blotzheim & Bauer 1985). After the breeding season adults perform a complete moult of all body and wing feathers (Jenni & Winkler 1994).

This study was conducted along streams and rivers in the Emmental region (46°56'N, 07°53'E), Cantons of Berne and Lucerne, Switzerland. The study site lies between 690 and 920 meters a.s.l. The rivers are 3-26 meters in width and characterised by fast-running water, large gravel banks and bordering rock-faces frequently used as nest sites by Grey Wagtails (see Hirschi 1987 for a detailed description of the study area). During the breeding period, Grey Wagtail density is high in this area in comparison to sites at similar altitudes. A large proportion of the population (*c.* 70% in 1997) is marked with individual colour ring combinations.

In 1997, the size of 44 first broods was manipulated by removing two nestlings 1-3 days after hatching from one nest (reduced group; '-2') and adding them to one of the same hatching date and clutch size (enlarged; '+2'). The fate of the nests

and the parents was then followed until mid-September (end of the moult period), at least twice a week. On the day of maximum food delivery to the offspring (day 11 after hatching; *cf.* Schifferli 1972; Marti & Breitenmoser-Würsten 1991), feeding rates of both males and females were recorded at each experimental nest. Between 09:00 and 12:00 or between 14:00 and 17:00 hours, a video camera was placed in front of the nest for one hour to film all nest visits. For data analysis, the first 10 minutes and the last 5 minutes of each tape record were discarded to exclude disturbance effects.

During moult (July to mid-September), experimental parents were re-captured as often as possible with mist-nets. Feather length was measured using the method of Berthold & Friedrich (1979). The moult stage of the primary feathers was measured using the moult scoring scheme proposed by Ginn & Melville (1983): old feathers were scored as '0', new feathers as '5' and growing ones between '1' and '4', depending on size. The sum of these scores for all nine primaries (excluding the outermost reduced feather) is called the moult score. To control for different recapture dates both capture date (days after 1st January) and experimental treatment were included in a logistic regression of the actual moult scores divided by the maximum value of 45 (Residual Moult Score = RMS). For individuals re-captured more than once the data point closest to day 200 (19th July) was included, but successive RMS values of one individual at different control dates are significantly correlated (Kendall's rank correlation, $\tau = 0.63$, $P = 0.004$). Additionally, I estimated the onset of moult for each individual re-captured during active moult under the assumption of a fixed moult rate. Moult rate was calculated for 12 individuals with more than one monitoring date during moult and was 0.41 ± 0.02 (mean \pm SE) moult scores per day. To assess moult speed I used the Residual Raggedness Value (RRV), that is highly correlated with moult duration (Bensch & Grahn 1993). A positive value corresponds to higher moult speed due to the replacement of more feathers at a time (and therefore reduced

wing surface area).

All P -values are two-tailed and the significance level was $\alpha = 0.05$, unless otherwise specified. I used parametric tests only if the Kolmogorov-Smirnov-test ($\alpha = 0.2$) gave no deviation from normality. For small samples ($n < 10$), I used non-parametric tests in all cases since the underlying assumptions could not be tested adequately (Bortz 1985). Power values were calculated using *G-Power* 2.0 software (Faul & Erdfelder 1992).

RESULTS

For data analysis I included only parents that had been marked before fledging of the young (excluding 4 males and 7 females in '-2'; 4 males and 2 females in '+2'). Results have been analysed separately for males and females because of the different samples arisen from this procedure and because of the marked differences in reproductive strategies (e.g., second brood frequency, high proportion of mate change after first brood) and moult patterns between the sexes (Klemp unpubl. data). Only a small fraction of the experimental individuals could be followed throughout the entire season, but the re-capture rate was comparable in both experimental groups (males: 7 recaptures of 15 manipulated in '+2', 9/17 in '-2'; females: 5/17 in '+2', 4/14 in '-2'). There were no differences between the two treatments in the body size of the parents, the timing of the brood, or the brood size before manipulation (Table 1).

The mean brood size at day 8 after hatching was more than two nestlings larger in the '+2' group (Table 1). Given the range of manipulation (difference of 4 nestlings between the two treatments) this difference is, however, smaller than expected because enlarged broods did not differ in size from the original brood sizes (Wilcoxon signed rank test, one-tailed; $z = 1.25$, n.s.). Males of '+2' broods fed their broods twice as often as '-2' males (Fig. 1); feeding rates per nestling were not different between the treatments (t -test; $t = 1.48$, $df = 29$, n.s.). The feeding rates of females were slightly, but not significantly higher in enlarged

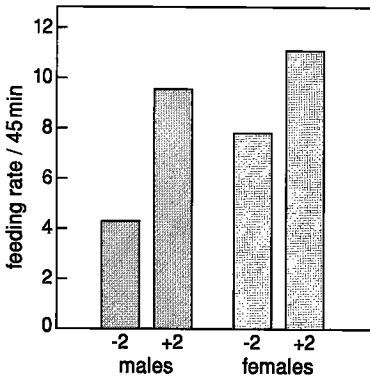


Fig. 1. Feeding rates of males and females in reduced ('-2') and enlarged ('+2') broods (mean \pm SE). *t*-Test males $n_{-2} = 16$, $n_{+2} = 15$, $t = -3.96$, $df = 29$, $P = 0.0004$; females $n_{-2} = 13$, $n_{+2} = 16$, $t = 1.35$, $df = 27$, $P = 0.189$.

broods (Fig. 1). There were, however, a significant experimental effect on nestling time with nestlings in enlarged broods fledged *c.* one day later (Table 1).

Second broods

Nearly 70% of the females left the study area after their first breeding attempt. There was no effect of the experiment neither on the probability of disappearance ($\chi^2_1 = 0.003$, n.s.; power analysis, $w = 0.0$, power = 0.0) nor on the frequency of second broods ($\chi^2_1 = 0.003$, n.s.; $w = 0.0$, power = 0.0). The delay between hatching (and also, fledging) of the first brood and the start of incubation of the second brood was independent of the experimental manipulation ('+2': 27.0 ± 19.1 d, $n = 5$; '-2': 16.0 ± 5.4 d, $n = 4$; *U*-test: $z = 0.37$, n.s.), as was clutch size, brood size and breeding suc-

Table 1. Characteristics of manipulated broods and parents in samples of the Grey Wagtail. Test statistics shown are results of *t*-tests (*t*) and *U*-tests (*z*).

Parameter	mean \pm SE		test statistic	<i>P</i>
	-2	+2		
Body size of male parent				
sample size	17	15		
tarsus length (mm)	21.1 \pm 0.0	21.1 \pm 0.0	$t = 0.0$.999
body mass (g)	17.5 \pm 0.1	17.1 \pm 0.1	$t = 0.8$.436
feather length (mm)	65.3 \pm 0.1	64.5 \pm 0.1	$t = 1.2$.223
Body size of female parent				
sample size	14	17		
tarsus length (mm)	20.7 \pm 0.1	20.7 \pm 0.0	$t = -0.2$.821
body mass (g)	17.7 \pm 0.1	17.6 \pm 0.1	$t = 0.1$.941
feather length (mm)	60.8 \pm 0.2	60.6 \pm 0.1	$t = 0.2$.878
Manipulated broods¹				
sample size	16	17		
start of incubation ²	104 \pm 3.7	108 \pm 4.1	$t = -0.7$.493
clutch size	5.3 \pm 0.1	5.3 \pm 0.1	$t = 0.1$.912
brood size after hatching ³	5.3 \pm 0.1	4.9 \pm 0.7	$z = -1.26$.207
brood size at day 8 ⁴	2.9 \pm 0.2	5.4 \pm 0.3	$z = -4.61$.000
Nestling time (d)	12.4 \pm 0.2	13.2 \pm 0.2	$z = -2.65$.008

¹ only broods with at least one (marked) parent in the sample; ² days after 1st January; ³ before experimental manipulation; ⁴ after manipulation

cess of the second brood and all subsequent broods (*U*-test; all n.s.; power under *t*-test assumptions 0.01 - 0.24). Males disappeared slightly less often than females from the study site (in seven out of 15 cases, '+2', and 12 of 17 cases, '-2', respectively), but again no experimental effect on disappearance was evident ($\chi^2_1 = 1.83$, n.s.; $w = 0.2$, power = 0.69). Characteristics of second broods did not differ between the two treatments (time-lag between first and second brood: '+2', 28.6 ± 20.8 d, $n = 7$; '-2', 27.4 ± 15.6 d, $n = 9$; other variables as above; *U*-test, all n.s.; power 0.05 - 0.10).

Primary moult

In all monitored males, primary moult started between end-June and mid-July (Fig. 2). Individuals with reduced broods had a relatively higher primary moult score than '+2' males when controlling for capture date by using a logistic regression model (=RMS; Fig. 2 and 3b). The same trend appeared in the calculated (absolute) date of the start of moult, but was non-significant (Fig. 3a). There was no difference between the two groups if moult onset was related to the start of incubation of the manipulated brood (*U*-test: $n_{-2} =$

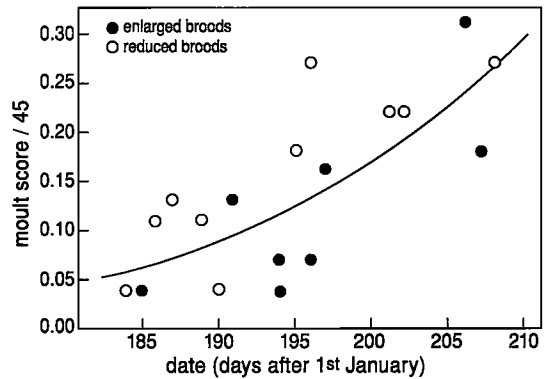


Fig. 2. Progress of moult (actual moult score divided by the maximum value of 45) in relation to capture date in male parents from the enlarged and reduced broods. Logistic regression: $F = 16.31$, $df = 16$, $P = 0.001$.

8, $n_{+2} = 10$, $z = 0.13$, n.s.). Moult rate, as measured by Residual Raggedness Value, was not affected by the manipulation (Fig. 3c). Controlling for second brood effort (variables as above) did not markedly change the probability level of the experimental effect on moult (Kendall partial rank-order correlation coefficient; moult start and RRV: $P \geq 0.4$ each). Only few experimental fema-

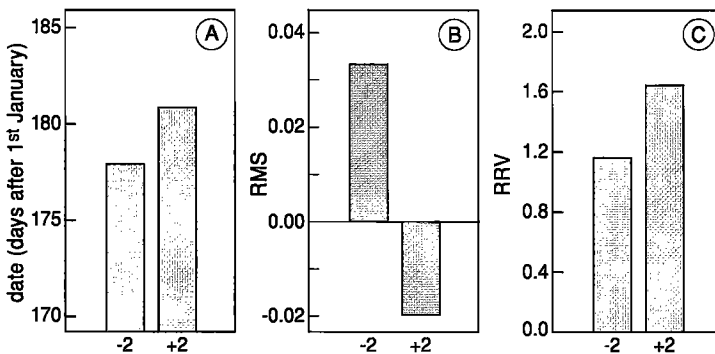


Fig. 3. Moulting patterns in males that reared reduced ('-2') and enlarged ('+2') first broods, respectively (median \pm SE; see text for explanation of variables). (A) Calculated start of moult (days after 1st January). *t*-test: $n_{-2} = 10$, $n_{+2} = 8$; $t = -0.70$, $P = 0.492$; power analysis $d = 0.75$, power = 0.109. (B) Residual Mould Score (RMS, see text). Likelihood Ratio Test on Logistic regression: control date $\chi^2_8 = 24.4$, $P = 0.02$, experimental manipulation $\chi^2_8 = 22.0$, $P = 0.05$. (C) Residual Raggedness value (RRV). *t*-test: $n_{-2} = 10$, $n_{+2} = 8$; $t = -1.15$, $P = 0.266$; power analysis: $d = 0.064$,

les could be re-captured after the breeding period. All these females started moult late in the season and most re-captures took place before the start of active moult (moult score = 0); therefore, experimental effects on female moult could not be analysed.

Return rate of adults and offspring recruitment

In the breeding season following the experimental manipulation (until 30 June 1998) seven of 17 males with reduced broods returned into the study area, but only three of the 15 males in the '+2' treatment did. This difference is, however, not significant (Fisher's exact test). None of the experimental females could be observed in 1998 and there was also no recruitment of experimental offspring.

DISCUSSION

In about half of the enlarged broods, nestling mortality led to brood sizes (at day 8) as small as or smaller than immediately after hatching. However, in this paper the experimental manipulation was successful in creating broods of different sizes and in modifying parental effort. Male feeding responses differed between the two treatments with higher rates in enlarged broods (Fig. 1) and both sexes suffered an extended nestling period in the enlarged brood treatment (Table 1). The failure of creating larger broods in sufficient numbers might have caused many of the results to be non-significant.

The data are consistent with the hypothesis that parental effort, at least in males, affects moult (Fig. 3b). Beyond that, the present study is the first to investigate effects of reproductive effort on the progress of moult, but no evidence has been found for an impairment of moult rate (Fig. 3c). The significant difference in the Residual Moult Score could principally be caused by two factors: an advanced or a faster moult in males with reduced broods or both. Moult rate, however, seems not to be affected by the experiment since

there were no differences in Residual Raggedness Value, an adequate estimate of moult rate. The trend in the data set (see Fig. 3c) hints in the opposite direction, towards accelerated moult rates in '+2' males, while the effect size is near zero. I conclude that the difference in RMS is caused most likely by an advanced onset of moult in '-2' males in relation to '+2' males. In the year of this study, first broods started exceptionally early and, therefore, there might have been no necessity to speed up moult rate.

Recent field experiments on the variation of start of moult in relation to breeding effort have revealed non-uniform results. Neither in Greater Canada Geese *Branta canadensis* nor in Willow Tits *Parus montanus* did brood size manipulations influence the onset of moult (Lessells 1986; Orell *et al.* 1996). Sanz (1997) also found no effect on the number of Pied Flycatchers in Spain that moulted before fledging of the young. In contrast, females (but not males) of this species in Finland started primary moult less frequently before completion of the brood if their broods had been enlarged (Siikamäki *et al.* 1994). Therefore, the delay of moult may be a strategy only in harsh environments, as in high latitude or in mountain habitats, since the assistance of both parents is necessary for the successful raising of the brood.

A large proportion of manipulated individuals in both groups could neither be observed nor be re-captured during moult. Since their response to the experiment is not taken into account, the results may be biased towards specific moult or spatial strategies, e.g. early moulting birds may more readily leave the study area. All field experiments face this problem because, with reasonable effort, only the close surroundings of a study site can be searched for individuals that have disappeared. In this case the fate of unobserved individuals is unknown. Within the study area the frequency of intra-seasonal territory shifts was very low and in all cases the immediately bordering territories were chosen (pers. obs.). Therefore, it is unlikely that individuals who 'disappeared' bred once again in the surroundings of the study site. The frequency of 'disappearance' was the

same in both experimental groups and there is no evidence that the experiment affected the probability of re-capture. I conclude that the bias due to non-random re-capture can be neglected.

The experiment had no effect on second broods. In various populations of Great Tits, brood size manipulations have reduced the probability of second broods and delayed egg-laying (Lindén 1988 for Gotland; Smith *et al.* 1987 in South-Sweden; Tinbergen 1987 for Holland). The same was found by Deerenberg *et al.* (1996) for captive Zebra Finches *Taeniopygia guttata*, but see Finke *et al.* 1987 for House Wren *Troglodytes aedon*). From a life history point of view, short-lived passerines should invest in breeding attempts especially during their first breeding season. In the Grey Wagtail population under study, opportunities for reproduction seem to be limited by the scarcity of breeding territories (unpubl. data), breeding started exceptionally early in 1997 (see above) and the main mortality occurs most likely in winter, between the breeding periods. In this case parental effort during first broods should hardly affect second broods, because parents can trade-off first against (expected) second brood effort before the first attempt starts. The data are in agreement with this expectation since there was no experimental effect on second broods neither in respect to size nor in respect to its timing, but due to small sample sizes the power of these tests is low. Reproductive costs should be compensated for after the breeding season, e.g., during moult. However, the delay in moult did not cause any (significant) survival effect. There are several possible reasons for this: firstly, a delay in moult may be disadvantageous in terms of survival only in years with severe (weather) conditions. Secondly, as Graves (1991) has pointed out, the usually small survival differences may not be detectable with samples of this size. And, finally, the local return rate may not be a reliable estimator of survival.

REFERENCES

- Bensch S. & M. Grahn 1993. A new method for estimating individual speed of moult. *Condor* 95: 305-315.
- Berthold P. & W. Friedrich 1979. Die Federlänge: Ein neues nützliches Flügelmaß. *Vogelwarte* 30: 11-21.
- Bortz J. 1985. *Lehrbuch der Statistik*. 2. Aufl. Springer, Berlin.
- Deerenberg C., C.H. de Kogel & G.F.J. Overkamp 1996. Costs of reproduction in the Zebra Finch *Taeniopygia guttata*: manipulation of brood size in the laboratory. *J. Avian Biol.* 27: 321-326.
- Dufva R. 1996. Blood parasites, health, reproductive success, and egg volume in female Great Tits *Parus major*. *J. Avian Biol.* 27: 83-87.
- Earnst S. L. 1992. The timing of wing moult in Tundra Swans: energetic and non-energetic constraints. *Condor* 94: 847-856.
- Faul F. & E. Erdfelder 1992. GPOWER: A priori, post-hoc, and compromise power analyses for MS-DOS. Bonn University, Bonn.
- Finke M.A., D.J. Milinkovich & C.F. Thompson 1987. Evolution of clutch size: an experimental test in the House Wren (*Troglodytes aedon*). *J. Anim. Ecol.* 56: 99-114.
- Ginn H. B. & D.S. Melville 1983. *Moult in Birds*. BTO Guide No. 19. British Trust for Ornithology, Tring.
- Glutz von Blotzheim U.N. & K.M. Bauer 1985. *Handbuch der Vögel Mitteleuropas*, 10/2. Aula-Verlag, Wiesbaden.
- Graves J. 1991. Comments on the Sample Sizes Used to Test the Effect of Experimental Brood Enlargement on Adult Survival. *Auk* 108: 967-969.
- Green D. J. & R.C. Ydenberg 1994. Energetic expenditure of male Ospreys provisioning natural and manipulated broods. *Ardea* 82: 249-262.
- Gustafsson L., D. Nordling, M.S. Andersson, B.C. Sheldon, & A. Qvarnström 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. *Phil. Trans. R. Soc. Lond. B.* 346: 323-331.
- Haukioja E. 1971. Flightlessness in some moulting passerines in Northern Europe. *Ornis Fennica* 48: 101-116.
- Hirschi W. 1987: Siedlungsdichte der Bergstelze *Motacilla cinerea* an Fließgewässern des Oberemmentals. *Ornithol. Beob.* 84: 63-65.
- Jenni L. & R. Winkler 1994. *Moult and Ageing of European Passerines*. Academic Press, London.
- Jönsson K.I., E. Korpimäki, I. Pen. & P. Tolonen, P. 1996. Daily energy expenditure and short-term reproductive costs in free-ranging Eurasian Kestrels. *Funct. Ecol.* 10: 475-482.

- Kjellén N. 1994. Moulting in relation to migration in birds - a review. *Ornis Svecica* 4: 1-24.
- Langston N.E. & S. Rohwer 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. *Oikos* 76: 498-510.
- Lessells C.M. 1986. Brood size in Canada Geese: a manipulation experiment. *J. Anim. Ecol.* 55: 669-689.
- Lindén M. 1988. Reproductive trade-off between first and second clutches in the Great Tit *Parus major*: an experimental study. *Oikos* 51: 285-290.
- Marti C. & C. Breitenmoser-Würsten 1991. Nestlings-nahrung und Fütterungsfrequenz der Bergstelze (*Motacilla cinerea*) im Saanenland. *Ornithol. Beob.* 88: 265-285.
- Nilsson J.-A. & E. Svensson 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proc. R. Soc. Lond. B* 263: 711-714.
- Oppliger A., P. Christe. & H. Richner 1996. Clutch size and malaria resistance. *Nature* 381: 565.
- Orell M., S. Rytkönen, K. Koivula, M. Ronkainen & M. Rahiala 1996. Brood size manipulations within the natural range did not reveal intragenerational cost of reproduction in the Willow Tit *Parus montanus*. *Ibis* 138: 630-637.
- Roff D.A. 1992. *The Evolution of Life Histories*. Chapman & Hall, New York.
- Sanz J.J. 1997. Clutch size manipulation in the Pied Flycatcher: effects on nestling growth, parental care and moult. *J. Avian Biol.* 28: 157-162.
- Schifferli L. 1972. Fütterungsfrequenz am Nest der Bergstelze (*Motacilla cinerea*) in verschiedenen Biotopen und Brutmonaten. *Ornithol. Beob.* 69: 257-274.
- Siikamäki P., M. Hovi & O. Rätti 1994. A trade-off between current reproduction and moult in the Pied Flycatcher - an experiment. *Funct. Ecol.* 8: 587-593.
- Smith H.G., H. Källander & J.-A. Nilsson 1987. Effect of experimentally altered brood size on frequency and timing of second clutches in the great tit. *Auk* 104: 700-706.
- Sondell J. 1993. Moulting strategies of White Wagtail *Motacilla alba* and Yellow Wagtail *M. flava* in central Sweden. *Ornis Svecica* 3: 107-116.
- Stearns S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, New York.
- Tinbergen J.M. 1987. Costs of reproduction in the Great Tit: intraseasonal costs associated with brood size. *Ardea* 75: 111-122.
- Verhulst S. & J.M. Tinbergen 1997. Clutch size and parental effort in the Great Tit *Parus major*. *Ardea* 85: 111-126.

SAMENVATTING

Voortplanten brengt kosten met zich mee, zeker bij soorten als de Grote Gele Kwikstaart *Motacilla cinerea* waar de oudervogels lange tijd voedsel naar de jongen moeten brengen. De belangrijke vraag is hoe die kosten betaald worden. Anders geformuleerd: hoe leidt een verhoogde ouderlijke inspanning voor het huidige broedsel tot een verlaging van de kans om in de toekomst nog nageslacht te kunnen grootbrengen? Om daar achter te komen werden individueel gemerkte Grote Gele Kwikstaarten bestudeerd die langs beken en riviertjes in het Zwitserse Emmentalgebied broedden. Een deel van de paren kreeg twee extra kuikens (+2), die van een andere deel van de paren waren weggehaald (-2). De oudervogels van beide experimentele groepen verschilden niet van elkaar, net zo min als de originele legselgrootte en legdatum. Acht dagen na het uitkomen hadden de vergrootte legfels duidelijk meer jongen dan de verkleinde legfels, al was het verschil niet 4, maar 2,5 jong. Zowel vrouwtjes als mannetjes brachten vaker voer naar de jongen bij de experimenteel vergrootte broedsels, maar dit verschil was alleen significant voor de mannetjes. Hoewel er tussen de twee experimentele groepen geen aantoonbaar verschil was in het aantal voedingen per jong per dag, duurde het toch een dag langer voordat de jongen in de vergrootte broedsels uitvlogen. Er kon geen effect van de experimentele manipulatie van het eerste broedsel op het tweede broedsel worden aangetoond. Een groot probleem bij deze conclusie was echter dat bijna 70% van de vrouwtjes en bijna 60% van de mannetjes uit het studiegebied verdween na de eerste broedpoging. Omdat geen enkel vrouwtje en maar een klein aantal mannetjes het volgende broedseizoen naar het studiegebied terugkeerden, kon niet worden vastgesteld of de experimentele ingreep ook gevolgen had op de overleving tijdens de winter. Het is echter goed mogelijk dat mannetjes die zich meer hadden ingespannen voor de jongen, een lagere overlevingskans hadden. Het experiment bleek namelijk bij de mannetjes een duidelijk effect op de rui te hebben. Mannetjes met een vergroot broedsel begonnen later aan de rui dan mannetjes met een verkleind broedsel. Door sneller te ruien zou een later ruitijdstip gecompenseerd kunnen worden, maar er werden geen verschillen in ruisnelheid gevonden tussen de beide groepen mannetjes. (BJE)

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