

SHORT- AND LONG-TERM FITNESS CORRELATES OF REARING CONDITIONS IN BARN OWLS *TYTO ALBA*

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During a 12-year study of the Barn Owl *Tyto alba* I investigated the short- and long-term fitness correlates of hatching date, brood size and hatching rank. Observations showed that nestling survival was lower at the end of the breeding season and in larger broods, and that chicks born late in a hatching sequence died more often than their older siblings. Survivors also developed longer tarsi in larger broods and when positioned at the top of the within brood size hierarchy. Pairs breeding earlier in the season and producing larger broods more often recruited at least one of their offspring in the local breeding population. I did not detect any association between the reproductive success of yearling recruits and birth date, the size of the brood out of which they fledged, and their within-brood hatching rank. This study therefore lends support for the prediction that the rearing conditions experienced by nestlings are rather more strongly correlated with fitness components expressed early than later in life.

Key words: *Tyto alba* - brood size - hatching rank - laying date - rearing conditions

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INTRODUCTION

In birds, the quality of rearing conditions is a major determinant of nestling body condition, nestling survival and recruitment probability (Martin 1987). When food becomes short, sibling competition increases (Mock & Parker 1997), growth is depressed (Smith *et al.* 1989), and chicks are more vulnerable to environmental stress factors (Hoffmann & Merila 1999). Although the effect of rearing conditions on nestlings has received much attention (Gebhardt-Heinrich & Richner 1998), little is known of the long-term fitness consequences of rearing conditions (Lindström 1999; Metcalfe & Monaghan 2001).

Few studies have investigated the extent to which reproductive success and adult survival are correlated with rearing conditions experienced as a nestling. In Western Gulls *Larus occidentalis* and Crimson Rosellas *Platycercus elegans* the

position of nestlings in the hatching sequence predicted nestling survival but not, or only weakly, adult survival (Spear & Nur 1994; Krebs 1999). In female, but not male Great Tits *Parus major*, nestling condition affected recruitment probability but not reproductive success (Verboven & Visser 1998; Visser & Verboven 1999) or to a low extent (Haywood & Perrins 1992). Thus, rearing conditions appear to often alter nestling condition, survival and the degree of recruitment (referred to as short-term effects) to a larger extent than reproductive success of recruits (long-term effects). I am aware of only one study reporting striking long-term effects of rearing conditions on fitness. In Little Egrets *Egretta garzetta* last-hatched chicks enjoyed a lower reproductive success than their older siblings (Thomas *et al.* 1999). Their results may be explained by a pronounced hatching asynchrony resulting into a fixed dominance hierarchy that strongly penalises last-hatched

chicks. Altogether these studies indicate that long-term effects of rearing conditions measured by hatching date, brood size or hatching rank may differ between species depending on both life-history traits and ecological requirements.

My objective in the present study is to determine whether in the Barn Owl *Tyto alba* the quality of rearing conditions assessed by hatching date, brood size and hatching rank correlates with nestling condition and survival better than with reproductive success and adult survival. These life-history traits are particularly interesting because they exhibit large variation in the barn owl (Roulin 2002a). More specifically, I examine the prediction that rearing conditions are better for nestlings born early than late in the breeding season, for nestlings in smaller broods and for senior than junior nestlings.

METHODS

The study was carried out between 1988 and 1999 in western Switzerland (46°49' N; 06°56' E) in an area covering 30 x 7 km². One hundred and ten nest-boxes were fastened to barns and regularly checked to record breeding parameters and to ring or measure nestlings and their parents. Breeding females were distinguished from males by the presence of a brood patch.

Assessment of breeding parameters

The date at which the first offspring hatched (defined as hatching date) was determined by estimating the age of the older nestling using wing length (Schönfeld & Girbig 1975; Taylor 1993). Laying date was defined as hatching date minus 32 days of incubation (Baudvin 1986). In this species incubation usually starts when the first egg is laid. As Barn Owls do not evict non-hatched eggs from their nest, brood size at hatching is defined as clutch size minus number of non-hatched eggs. Brood size at fledging is defined as the number of nestlings that survived at least up to 55 days of age. Fledging success is the proportion of hatched nestlings that fledged.

Hatching ranks were determined by ranking nest-mates according to wing length. Rank 1 was assigned to the largest nestling, rank 2 to the second largest nest-mate, and so on. Wing length reflects hatching ranks accurately because wing growth rate does not differ between female and male nestlings and is not affected by food-deprivation (Durant & Handrich 1998; Roulin unpubl. data). To take into account the covariance between brood size and hatching ranks while analysing the relationship between hatching rank, nestling condition, nestling survival and recruitment probability, I assigned nestlings to the category 'senior' if they hatched at a rank below the mean hatching rank of their brood. Individuals that hatched at a rank above this mean were assigned to the category 'junior'. For broods of five chicks the third-hatched individual belonged to the category 'junior'.

Statistical procedures

To investigate the effect of size hierarchy on tarsus length, this trait was measured on 55-day-old nestlings in 1997, 1998 and 1999, and for each nest I calculated the Pearson correlation coefficient between nestling tarsus length and hatching rank. A negative coefficient indicates that nestlings that hatched later in a hatching sequence developed shorter tarsi. A similar procedure was applied for body mass measured at 44 days of age in 1998 and at 25 days of age in 1996. Note that I did not analyse the relationship between body mass of nestlings and their future reproductive success because this trait was not measured at the same age throughout the study period. Residuals from the regression of nestling body mass on nestling age may indeed not be reliable, since environmental effects have different impacts on nestling body mass depending on nestling age. For instance, brood size manipulation experiments altered body mass before 40 days of age but not thereafter (Roulin 1998).

When analysing the probability of an individual recruited into the breeding population, I applied a stepwise backward procedure of a logistic regression with a binomial error distribution. I

fitted a full model including all the explanatory variables, that is year, laying date and brood size. A quadratic term of laying date (laying date²) was included to test for non-linear effects. Significance of variables was tested using the chi-squared-distributed change in both deviance and number of degrees of freedom when the variable was dropped from the full model including significant and non-significant terms. The logistic model that contained only significant terms was called 'final model'.

It is worth mentioning that for two reasons I did not control for female and male identity and for nest sites in the statistical analyses. First, bird identity was not always known. Second, the aim of the present study is to investigate short- and long-term fitness correlates of brood size, hatching date and hatching rank, factors that can be themselves correlated to other uncontrolled variables. Therefore, if I would have controlled for bird identity and nest site, it would still not be possible to conclude whether brood size, hatching date and hatching rank causally affect short- and long-term fitness components. In statistical analyses, I also did not consider whether a given brood was a first or second breeding attempt. The reason is that late broods are usually second broods, and hence there is a strong covariation between laying date and brood number. Furthermore, 46% of females that produce a second annual brood abandon their first brood half through the rearing period to their mate and start a new breeding attempt elsewhere with a previously unmated male (Roulin 2002b). Therefore, many broods that are said to be second broods are in fact a first breeding attempt for males. Reproductive success at the first and second nest of deserting and non-deserting females did not differ significantly (Roulin 2002b).

Statistical analyses were carried out using the Statistix statistical package (Analytical Software 1989). All tests are two-tailed and *P*-values smaller than 0.05 are considered as significant. Non-parametric analyses were performed when data sets were not normally distributed. Means are quoted with \pm 1 SE.

RESULTS

Short-term correlates of rearing conditions

Mean hatching date was 30 April \pm 1.7 d (range 5 March to 30 July). Figures 1 and 2 show that there was an overall trend for clutches to increase in size as the season progressed, and for broods to decrease in size. This indicates that fledging success declined at the end of the breeding season (Spearman correlation: $r_s = -0.17$, $n = 393$ broods, $P < 0.001$). This seasonal pattern of reproductive success was also found among double-brooded females. Second annual clutches were larger than first ones (6.1 ± 0.3 versus 5.2 eggs ± 0.3 ; paired *t*-test: $t_{15} = 3.17$, $P = 0.006$) and fledging success decreased from the first to the second annual breeding attempt ($71 \pm 7\%$ of hatched nestlings fledged vs. $48 \pm 5\%$; $t_{15} = 2.86$, $P = 0.01$).

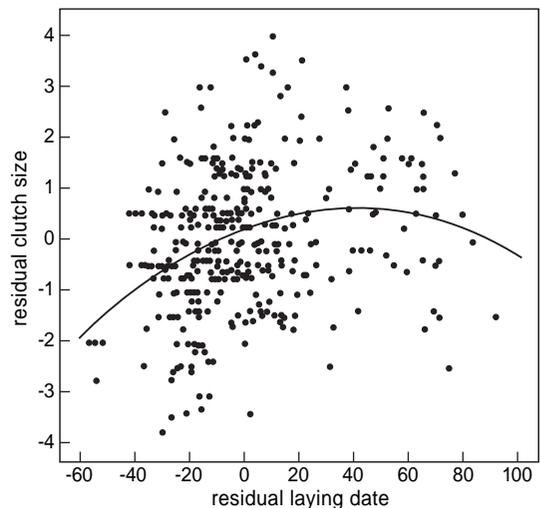


Fig. 1. Relationship between residual clutch size and residual laying date. Residuals were calculated from an ANOVA including clutch size as the dependent variable and year as a factor. The same procedure was applied for laying date. A second-order curve is fitted. In a multiple regression analysis, clutch size is significantly explained by year ($F_{11,386} = 7.40$, $P < 0.001$), laying date ($F_{1,386} = 22.20$, $P < 0.001$; standardised $\beta = 1.73$) and laying date² ($F_{11,386} = 16.50$, $P < 0.001$; $\beta = -1.49$).

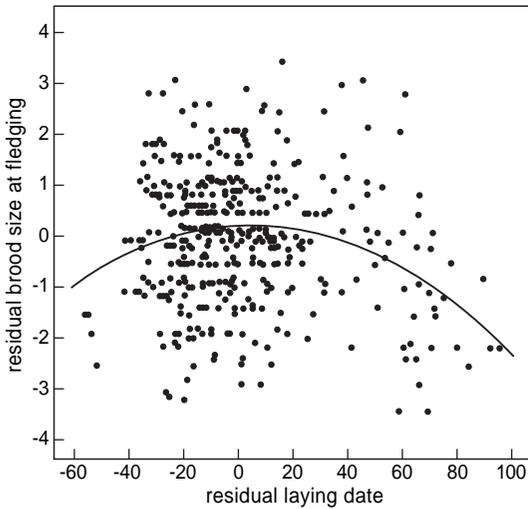


Fig. 2. Relationship between residual brood size at fledging and residual laying date. Residuals were calculated from an ANOVA including brood size as the dependent variable and year as a factor. The same procedure was applied for laying date. A second-order curve is fitted. In a multiple regression analysis, brood size at fledging was significantly explained by year ($F_{11,378} = 3.22$, $P < 0.001$), laying date ($F_{1,376} = 5.99$, $P < 0.01$; standardised $B = 0.88$), laying date² ($F_{1,376} = 9.34$, $P < 0.01$; $B = -1.09$) and brood size at hatching ($F_{1,376} = 104.18$, $P < 0.001$; $B = 0.49$).

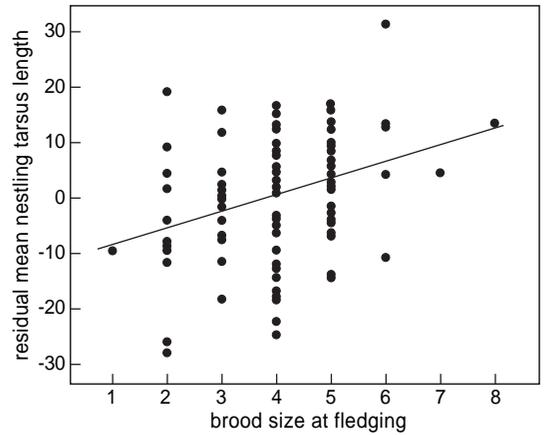


Fig. 3. Relationship between mean nestling tarsus length and the size of the brood out of which nestlings fledged. Tarsus length is expressed by residuals from the regression of mean nestling tarsus length on mean tarsus length of their parents. Regression line is drawn.

Mean clutch size was 6.0 ± 0.07 ($n = 405$, range 2-11), mean brood size at hatching was 5.6 ± 0.07 ($n = 403$, range 1-11) and mean brood size at fledging was 4.1 ± 0.06 ($n = 477$, range 1-8). Although fledging success was lower when the number of hatchlings was larger ($r_s = -0.40$, $n = 397$, $P < 0.001$), survivors developed longer tarsi when raised in larger broods ($F_{1,95} = 10.65$, $P = 0.0015$;

Table 1. Logistic regression of the probability that a nest produced at least one local recruit in relation to year, laying date, and brood size at fledging. The final model is the model with all predictor variables that explained a significant part of the deviance. Rejected terms did not explain a significant part of the deviance.

Parameter	Change in Deviance	df	P
Null model	335.39	355	
Final model	267.76	343	
Constant		1	
Year	44.5	10	< 0.001
Laying date	16.56	1	< 0.001
Brood size at fledging	7.17	1	< 0.01
Rejected term			
Laying date ²	2.38	1	> 0.10
Brood size at hatching	0.57	1	> 0.30

Fig. 3) after controlling for the tarsus length of their parents ($F_{1,95} = 33.15$, $P < 0.001$), laying date ($F_{1,95} = 0.33$, $P = 0.57$) and year ($F_{2,95} = 0.61$, $P = 0.54$).

In 76 out of the 80 nests (95%) in which brood reduction occurred, at least one junior nestling died, whereas in only 4 of these 80 nests (5%), did at least one senior nestling die. Among the survivors, older nestlings developed longer tarsi than their younger nest-mates (mean Pearson correlation between tarsus length and hatching rank: -0.40 ; sign test by comparing coefficients with zero: $n = 100$ broods, $P < 0.001$). In addition, they also had a lower body mass at 25 days of age (-0.35 ; sign test: $n = 32$, $P = 0.031$), although this was not the case at 44 days (-0.03 ; $n = 41$, $P = 0.64$).

Long-term correlates of rearing conditions

Early breeding pairs more often produced at least one local recruit than late pairs (Table 1). This finding is not biased by differential dispersal of birds born at different dates in the season. Indeed, in an ANOVA where log-transformed distance between birth site and the site where recruits bred in their first-year of age was entered as a dependent variable, hatching date did not explain a significant part of the variance ($F_{1,118} = 1.14$, $P = 0.29$) after controlling for sex ($F_{1,118} = 14.20$, $P < 0.001$), since females disperse at larger distances (median is 15 km) than males (7 km).

Pairs producing larger broods more often had at least one of their offspring recruiting into the local breeding population (Table 1). This relationship is not biased by differential dispersal by nestlings raised in broods of a different size. After controlling for sex the log-transformed distance was not significantly related to brood size at fledging (ANOVA: $F_{1,123} = 0.007$, $P = 0.93$).

Hatching rank did not predict recruitment probability of those recruits, since recruits hatched at a similar mean rank as their non-recruiting nest-mates that successfully fledged (2.75 ± 0.13 versus 2.87 ± 0.07 ; paired t -test: $t_{124} = -0.77$, $P = 0.44$). This result is not biased by differential dispersal by senior and junior offspring (ANOVA with log-transformed distance as a dependent variable and controlling for sex; hatching rank: $F_{1,97} = 0.006$, $P = 0.94$). Senior and junior recruits were issued from broods hatching at a similar date and of a similar size, and they were as often males as females (Table 2).

Reproductive success of yearling recruits was not correlated with their birth date and hatching rank, and the size of the brood from which they fledged (Table 3). Note that although tarsus length was negatively correlated to hatching rank among fledglings (see above), this relationship disappeared among recruits ($r = -0.08$, $n = 47$, $P = 0.58$).

Table 2. Logistic regression of the probability that a senior or a junior nestling recruited in relation to sex, laying date, and brood size at fledging. Senior chicks hatched at a rank below the mean hatching rank of their brood, whereas junior chicks hatched at a rank above this mean.

Parameter	Change in Deviance	df	P
Null model	165.83	121	
Constant		1	
Rejected terms			
Sex	0.9	1	> 0.30
Laying date	1.09	1	> 0.20
Laying date ²	1.14	1	> 0.20
Brood size at fledging	1.48	1	> 0.20

Table 3. Relationship between rearing conditions experienced by nestlings (measured by year when born, birth date, size of the brood out of which they fledged, hatching rank defined as senior or junior) and the reproductive success they achieved in their first breeding attempt (measured by laying date, clutch size and brood size at fledging). ANCOVA analyses were performed with reproductive parameters entered as dependent variable, sex and year as factors and birth date, brood size and hatching rank as covariates. The significant effect of sex on laying date indicates that yearling females breed on average earlier in their first breeding season (25 April) than yearling males (8 May).

Characteristics of recruited individuals	Reproductive parameter of recruited individuals at their first reproduction								
	Laying date			Clutch size			Brood size at fledging		
	<i>F</i> -value	<i>df</i>	<i>P</i>	<i>F</i> -value	<i>df</i>	<i>P</i>	<i>F</i> -value	<i>df</i>	<i>P</i>
Sex	7.6	1,71	0.008	0.7	1,78	0.42	0.02	1,75	0.89
Year when born	1.6	8,71	0.14	1.2	9,78	0.30	0.8	9,75	0.64
Birth date	0.3	1,71	0.85	0.8	1,78	0.40	0.2	1,75	0.68
Brood size at fledging	0.8	1,71	0.37	0.6	1,78	0.40	0.1	1,75	0.83
Hatching rank	0.3	1,71	0.60	0.5	1,78	0.47	1.4	1,75	0.24

DISCUSSION

The present study provides a series of results (Table 4) and a survey of the Barn Owl literature is worth considering in order to determine whether these results are specific to Swiss Barn Owls or whether they are applicable to other populations. I restricted this comparison to the subspecies *Tyto alba alba* and *T. a. guttata* that both occur in Switzerland. The finding that clutch size increases as the season progressed and slightly declines at the end of the breeding season has been reported in a *guttata* population in Germany (Schönfeld & Girbig 1975) and a mixed *guttata* and *alba* population in France (Baudvin 1986). It is therefore not surprising that second annual clutches were larger than first ones in German and Czech *guttata* populations (Schönfeld & Girbig 1975; Kaus 1977; Brandt & Seebass 1994; Poprach 1996) and in mixed *guttata* and *alba* populations (Baudvin 1986; Chanson *et al.* 1988; Muller 1991; present study). In stark contrast are the studies performed in *alba* populations. In Scotland, clutch size decreased as the season progressed (Taylor 1994), and both in Scotland and Spain first clutches were

larger than second ones (Taylor 1994; Martinez & Lopez 1999). These geographical variations merit further investigations to understand their cause. Nestlings were more likely to be recruited when born early than late in the season, a similar finding as the one reported by Taylor (1994) in his Scottish population. Nestling survival was lower in larger brood suggesting that clutch size is not necessarily the most optimal one and that parents are frequently too 'optimistic'. However, after brood reduction occurred I found that offspring in larger broods developed longer tarsi and were more often recruited in the local breeding population. This may indicate that parents producing

Table 4. Summary of the results.

Negative effects are represented by the symbol -, positive effects by +, and no detectable effects by 0.

Parameters	Nestling survival	Recruitment	Reproduction
Laying date	-	-	0
Brood size	-	+	0
Hatching rank	-	0	0

larger broods are of higher quality or occupy high quality territories.

Short- and long-term correlates of hatching date and brood size

Hatching date and brood size were both correlated with fledging success and recruitment probability, but not with the reproductive success of recruits. These results can be explained by the fact that these two breeding parameters covary with environmental factors like food availability (Taylor 1994) and weather conditions (Baudvin 1986; Marti 1997). As a consequence, if birds face harsh conditions as nestlings, their fledging success and recruitment probability may be low. Since reproductive success is closely linked to environmental factors, it is therefore not surprising that variation in this breeding parameter is explained by environmental conditions prevailing at the time of the first breeding attempt rather than by conditions that prevailed in the previous year when recruits were still at the nest. In contrast, in cases where environmental conditions are stable over years and across territories, the likelihood of detecting long-term effects may be greater because the conditions that breeders experience should create less noise when analysing the relationship between rearing conditions and fitness components measured at adulthood. For instance, based on more than 1000 Great Tit recruits, Haywood & Perrins (1992) found a weak correlation between rearing conditions and the clutch size of recruits. In contrast, they detected a strong effect in a captive population of Zebra Finches *Taeniopygia guttata* with only eleven data points. Since environmental conditions strongly vary in wild populations, but not in captive ones, this example suggests that a low spatial and temporal heterogeneity in the quality of the environment could be crucial to detect long-term fitness effects of rearing conditions. Variation in environmental conditions (as observed in Scotland, Taylor 1994) may explain why I did not detect long-lasting effects of hatching date and brood size in the Barn Owl. Because these two breeding parameters varied annually, breeding success may be so strongly dependent on pre-

vailing environmental conditions that the effects of past rearing conditions can be difficult to detect.

Short- and long-term correlates of hatching rank

Long-term effects of a size hierarchy resulting from a pronounced hatching asynchrony may occur in species in which food provisioning is mainly governed by competitive interactions among siblings (Mock & Parker 1997; Ostreier 1997). The poor competitive ability of junior chicks induces a reduced growth that in turn impairs the development of crucial organs and physiological functions (Lesage & Gauthier 1998). Therefore, being a junior may be so detrimental that long-term fitness effects of size hierarchy should be detectable. In contrast, if parents control food allocation despite large size disparities among the offspring, junior chicks may not incur pronounced long-term fitness penalties. In other words, the extent to which junior chicks are outcompeted for food may determine whether size hierarchy imposes large or weak long-term fitness effects. For instance, in Crimson Rosellas hatching asynchrony is pronounced, with the first-hatched chick being up to seven days older than its last-hatched sibling. However, growth of survivors was not related to their place in the within brood size hierarchy (Krebs 1999) because parents allocated food equally among the offspring (Krebs *et al.* 1999). In contrast, in the Little Egret offspring size hierarchy appeared to strongly influence within brood food allocation and as a consequence junior chicks achieved a reduced breeding success (Thomas *et al.* 1999).

The Barn Owl is one of the bird species that shows extreme hatching asynchrony. For instance, in the year 2000 I observed a pair that successfully raised a brood of nine in which the last-hatched offspring was three weeks younger than its oldest sibling. Although nestlings that hatch late in a sequence are in poorer condition than their older siblings (Wilson *et al.* 1987; Roulin 1998; present study), this size disadvantage did not translate into a significantly reduced perfor-

mance after fledging. The lack of detectable long-term fitness effects of size hierarchy suggests that parents control within brood food allocation or, alternatively, senior nestlings do not monopolise most food items. The finding that siblings vocally negotiate priority of access over the impending food resource (Roulin *et al.* 2000; Roulin 2002c) indicates that senior chicks may indeed not monopolise a much larger than equal share of the resources. This is further supported by the observation that in experimentally created two-chick broods the younger chicks acquired the first prey item delivered of the night in approximately half of the cases (25 out of 53 cases, 47%, pers. obs.).

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SAMENVATTING

Van 1988-99 werd in het westen van Zwitserland een populatie Kerkuilen *Tyto alba* intensief gevolgd, die de beschikking had over 110 verschillende nestkasten. Gedurende het broedseizoen werden de kasten regelmatig gecontroleerd, werden uitgekomen jongen geringd en werd de groei van de kuikens intensief gevolgd om te onderzoeken of de datum en de volgorde van uitkomen en de grootte van het broedsel gearrelateerd waren aan lichaamsgrootte en overleving. De overleving van de kuikens nam af met de grootte van de broedsels, en was aan het einde van het broedseizoen lager dan aan het begin. Binnen een nest hadden de laatst geboren kuikens een kleinere kans om te overleven dan de eerste kuikens. Echter, de overlevenden uit grotere broedsels hadden grotere poten (langere tarsus) dan die uit kleinere broedsels. Binnen een nest werden de meest dominante uilskuikens het grootst. Paren die vroeg broedden en de grootste broedsels produceerden, hadden de meeste kans om aan een volgende generatie bij te dragen. Hoewel er dus allerlei verbanden lijken te bestaan tussen geboortedatum, broedselgrootte en rangorde en de vroege overleving, werden er geen aanwijzingen gevonden dat deze factoren van grote invloed zijn op hun latere broedsucces. (TP)

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