Trade-off between moult and brood size in the blue tit - an experiment.

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Abstract

Life history theory predicts that whenever two (or more) energetically expensive activities overlap, there will be a trade-off between the activities. An increased allocation of energy/resources to one activity will lead to reduced allocation to the other(s), and the other way around. Two of these opposing activities in the life of a passerine bird are reproduction and renewal of the plumage (i.e moult). In this experiment, we wanted to test whether changed parental work-load during reproduction (after day 5 after hatching) due to experimentally changed brood size would be reflected in moult frequency, moult score and moult speed and whether the sexes reacted to such a changed condition differently. Both increased and reduced clutch sizes were produced. We also wanted to test whether moulting individuals would invest less in the current brood than non moulting individuals as measured by proportion of feedings by the sexes. This experiment clearly showed that males were able to quickly react to changed (reduced brood size) parental responsibilities and initiate or speed up moult, while we found no such effects of the experiment among the females. What was remarkable was that there was no statistically significant difference between the experimental groups at day 7 after hatching, but at day 14 the difference was obvious. Even when only birds that had started moulting at day 7 were analyzed, the difference was highly significant between the groups. We found no evidence of reduced reproductive effort among moulting males, however, but this may be related to that the most intensively moulting males were attending broods of only two chicks. With such a reduced work load they could probably do their fair share of the feedings and still commence moult at the same time. No difference could be discerned between the age groups in neither sex.

Innhold

1 Introduction

Life history theory predicts trade offs to occur whenever two activities simultaneously competes for a limited amount of resources, that is when a beneficial change in one trait is linked to a detrimental change in another (Stearns 1989, 1992). This is in line with Levins' principle of allocation: "If resources are limited, and if the organisms can only acquire a limited amount of resources and energy for which two or more processes compete directly, then an increase in energy allocated to one must result in a decrease in energy allocated to the other(s)"(Levins 1968).

Trade offs can be either physiological (Calow 1979) or ecological (Partridge 1989) in origin. One of the classical tradeoffs is the cost of reproduction, that is; breeding activities may have consequences for other functions and activities in a birds` yearly cycle. The costs could be e.g survival costs or fecundity costs. In this study, we wanted to investigate one of the less documented trade-offs, namely the trade-off between reproduction and moult.

In most species where post-breeding moult has been studied, sexual differences in moulting performance have been noted and the males commonly initiate moult ahead of the females, especially in passerines (e.g Verbeek 1973, Dhondt 1981, Bensch et al. 1985, Slagsvold & Lifjeld 1989, Morton 1992, Hemborg 1998, 1999, Hemborg et al. 1998, Hemborg & Merilä 1998, 1999, Strinella et al. 2015, but see Gow & Stutchbury 2013), while the norm is the opposite in other bird groups. For instance, in many raptors, the females commonly moult earlier than the males. The males provide food to the female and the young nestlings while she incubates the eggs and broods the hatchlings. The females of these species commonly starts to moult while in this period (Newton & Marquiss 1982, Arroyo & King 1996). The most special example is probably in hornbills (*Bucerotidae*) where the females take the opportunity to moult while being walled into the nest cavity (Kemp 1995). In addition, yearlings often start ahead of older birds (e.g Morton & Morton 1990, Siikamäki et al. 1994, Hemborg & Merilä 1999). In many of these species, from a wide array of geographical zones, some temporal overlap between breeding and moult has been documented (e.g Verbeek, 1973, Foster, 1975, Orell & Ojanen 1980, Tiainen 1981, Bensch et al. 1985, Morton & Morton 1990, Zaias & Breitwisch 1990, Hemborg 1999, Gardner et al. 2008, Echeverry-Galvis & Hau 2012, 2013). In fact, some overlap between these activities has been recorded in more than 100 species (Payne 1972). In this lies potential conflict of interests between the sexes if one of the sexes' moulting activities results in reduced allocation of effort to parental duties, which may lead to e.g increased nestling mortality, lowered future survival or realized fecundity to the mate (e.g Svensson & Nilsson 1997, Hemborg & Merilä 1998). The most extreme "reduced allocation of effort to parental duties" is of course if onset of moult results in nest desertion by one of the parents, as shown in the hooded warbler (*Setophaga citrina*) (Mumme 2018), some pied flycatcher males (Hemborg 1999) and possibly also in the great reed warbler (*Acrocephalus arundinaceus*) (Ezaki 1988).

Breeding and moult are both energy demanding activities in the bird`s yearly cycle and are traditionally considered temporally mutually exclusive events (Payne 1972). Most temperate species of altricial birds renew their plumage at least once a year (Jenni & Winkler 1994), usually shortly after breeding, the so-called post nuptial / post breeding (or pre basic) moult. Costs associated with moult include energy and nutrient use for the synthesis of new feathers and the metabolic changes involved in maintaining the tissues necessary for feather synthesis (e.g Murphy & King 1992, Lindström et al. 1993), reduced wing lift (Pennycuick 1975), flight efficiency (Tomotani et al. 2017, Hedenström & Sunada 1999, Bowlin et al. 2011) and flight maneuverability/performance (Swaddle & Witter 1997). Some may even temporarily lose the ability to fly (Haukioja 1971), and consequently, increased vulnerability to predators due to reduced wing area (Slagsvold & Dale 1996) as well as impaired insulation in combination with increased periferal blood flow (the growing feathers are highly vascularized), causing excessive heat loss during moult (Ginn & Melville 1983). Moult, as such, may be regarded as a handicap to a bird, and it has been shown that, in the pied flycatcher (*Ficedula hypoleuca*), the diet of a bird with induced moult (a few feathers plucked) have more restricted diets (Lifjeld & Slagsvold 1988). If the time available to moult is constrained, for instance because of delayed broods, birds may have to speed up the moult rate. This may have serious consequences since it may result in reduced feather quality (Dawson et al. 2000, Vágási et al. 2012, Möller & Nielsen 2018). Overlapping breeding and moult may have the same effect (Echeverry-Galvis & Hau 2013). This in turn may reduce over winter survival (Nilsson & Svensson 1996). Since moult is an energy consuming activity, it is hardly surprising that it usually takes place in late summer/early autumn after breeding, when the resources are still abundant and the birds have no parental responsibilities. Timing and temporal segregation of breeding and moult have probably evolved as an ecological adaptation to a seasonably variable food source and demand. In this way, both activities can be fitted into the annual cycle while minimizing energetic stress. Since the seasons are very predictable in the temperate zone, selection has ample "opportunities" to favour individuals that times these energetically expensive activities to the very productive northern summer and minimizes their overlap.

Apart from sex and age, a number of other factors have been shown to be of importance for the initiation and duration/rate of moult. Among these are:

1) Physiological condition

In the Laysan albatross (*Phoebastria immutabilis*), moult varies with parasite load (Langston & Hillgarth 1995). Male starlings (*Sturnus vulgaris*) delayed moult when they experienced a period of food shortage (Meijer 1991) and severe malnutrition may make white-crowned sparrows (*Zonotrichia leucophrys gambelli*) interrupt or postpone moult until conditions improve (Murphy et al. 1988).

2) Endocrine function

In the white crowned Sparrow, initiation of moult closely follows refracturing of the gonads, in the males measured as decreasing testicular length, in the females indirectly measured as the time when the female will no longer engage in further reproductive attempts if the current clutch for some reason results in failure, for instance by predation (Morton 1992). This suggests an endocrine control of moult, and different hormones have been shown to have effects on moulting performance. Sex hormones seem to inhibit moult, while thyroid hormones (e.g thyroxin) seem to stimulate it (Schleussner et al 1985, Hahn et al. 1992).

3) Photoperiod and genetics

Several studies have shown that the photoperiodic regime may influence initiation and duration/rate of moult (e.g Blackmore 1969, Dolnik & Gavrilov,1980, Dawson 2008) Special genotypes (Clock) exhibit delayed moult in the wintering quarters compared to other genotypes in the barn swallow (*Hirundo rustica*). The Clock-genotype seems to be involved in photoperiodic control of both moult and breeding (Saino et al. 2013)

4) Clutch or brood size

Clutch and brood size size experiments have shown that parents attending experimentally increased clutches tend to delay moult in comparison with control clutches (Bensch et al. 1985, Slagsvold & Lifjeld 1989, Siikamäki et al. 1994, Svensson & Nilsson 1997, but see Sanz 1999).

5) Stage in breeding cycle

Some studies indicate that initiation of moult is determined by breeding schedule and not on absolute date. Date of breeding did not have any effect on whether the birds initiated moult during breeding or not. Often this is linked to sex, as in pied flycatcher (Siikamäki et al. 1994, Hemborg 1998, Hemborg 1999, this study). While the female seems closely tied to the breeding schedule, the male is more flexible and can react to changed parental responsibilities and adjust their allocation of resources accordingly. Contrary to the above, some species show that date influences the probability of moulting while breeding. However these studies often involve failed or induced delayed broods. E.g as in the blue tit (Svensson & Nilsson 1997)

6) Ecology

In a study from northern Finland, the Willow tit (*Parus montanus*) was more likely to initiate moult while breeding than the Great tit (*Parus major*). They also terminated moulting earlier. The authors suggest that the difference may arise because of the species`different ecologies. The Willow tits start and terminate the moult earlier because they must have time to collect their winter food storages in autumn. (Orell and Ojanen 1980).

7) Latitude

Especially for migratory species that ideally can squeeze in both reproduction and moult in a narrow time window while food availability is at a maximum in the very productive northern summer, an overlap between reproduction and moult may be a good strategy (Hemborg et al. 2001). This time window becomes narrower with latitude, so a relationship between latitude and moult is commonly assumed (Eeva et al. 2000). Moult breeding overlap seems to be more common among species and populations breeding far north (e.g Dhondt 1981), but exceptions to this rule exist (e.g Hemborg et al. 2001).

Moult is therefore a multivariate and probably a somewhat plastic/variable phenomenon, and it is tempting to write, as Jenni & Winkler do in their seminal work "Moult and ageing of European passerines, 1994": "Within a species, it appears that the timing, rate and extent of moult can be adjusted according to a bird's individual circumstances. Within the time window set by endogenous annual cycle and modified by the photoperiod, the precise timing and rate of the post-breeding moult is thought to be fine-tuned by feedback from perceived environmental factors (e.g food availability, temperature), social cues (e.g breeding success, number of broods, parental care activities, interaction between mates) and factors modifying moult once started (e.g bad weather, unpredictable onset of breeding)". (Jenni & Winkler 1994).

1.1 Income versus capital breeders

The Blue tit is an income breeder, that is: eggs, feathers etc are produced from a daily surplus of energy (Drent & Daan 1980). High metabolic rates therefore rapidly eliminate physiological traces of reproduction. It is a small, sedentary, cavity nesting passerine. Blue tits are normally single brooded in our population. Pairs with two broods are rare, and in some seasons none have been recorded (Slagsvold & Rohwer 2000). The species has one annual moult (Svensson 1992, Flegg & Cox 1969, Jenni & Winkler 1994). The plumage is completely renewed in summer, usually shortly after breeding. Hence, the new plumage will be kept until next summer.

Earlier studies on reproductive effort versus moult have either manipulated clutch size in the egg stage (Siikamäki et al. 1994), compared enlarged versus control clutches (Svensson & Nilsson 1997), induced delayed breeding by performing clutch removal (Svensson & Nilsson 1997), or studied moult in birds with a known breeding history. In this study, we manipulated breeding effort in the nestling stage. Both enlarged and reduced nests were produced, and we wanted to investigate whether this influenced onset and speed of moult (intraindividual trade off). (A similar experiment with clutch sizes was conducted with the grey wagtail (*Motacilla cinerea*), but here speed of moult was not recorded (Klemp 2000)). Feeding frequencies were analyzed to see whether individual differences in parental effort could be accounted for by the differing stages of moult. We also performed a small scale nest removal experiment in combination with the clutch size experiment in order to see which factor is the most important for the initiation of moult; time of breeding or brood size. We predicted that parents attending small broods, having a comparatively leisurely time, would react rather quickly to their changed parental responsibilities and be more likely to have initiated moult at the time of fledging. Furthermore, among the individuals that had already started moulting at day 7, we predicted parents attending small broods to show higher moult rates. Reducing brood size could also have consequences for the male`s parental effort. One might expect that a brood of only two chicks would be of little value to the male because of potentially higher survival rate in general (life history aspect) and that we would observe reduced proportional feeding frequencies from these males compared with males attending large broods. On the other hand, feeding only two chicks probably means only marginal energetic expenses from the male. Since absolute feeding frequencies are dependent on brood size (Nur 1984), the males may take their share of the parental responsibilities and still have work loads significantly smaller than males attending large broods. Contributing to rearing chicks from small broods to fledging may also have an additional advantage. These chicks may receive more food and thus have higher quality and therefore have larger than average probability of becoming a local recruit to the population since sibling rivalry is also minimized.

To sum up, the present study of blue tits had 4 main objectives:

- To investigate whether there are sexual differences in the initiation and speed of moult in our population, i.e to check whether the males start moulting ahead of the females and if they moult faster.
- When brood sizes change, and the parental responsibilities change accordingly, does this have any impacts on the parents' moult strategies, and are there any differences between the males and the females?
- Among the individuals that had already started to moult at day 7, did brood size have any impact on moult speed?
- Did moult score of a parent at the end of the nestling period have any effect on the amount of food provisioning to the brood?

2 Methods

2.1 Study area and general methods

This study was carried out in a nestbox breeding population of blue tits (*Cyanistes caeruleus*) in Sørkedalen, just north of Oslo, Norway during spring/summer 1997. The blue tit is a small passerine, common in deciduous and mixed forests in most of the norwegian lowlands. It is a primarily sedentary species, but mostly juveniles may make massive invational movements or short-distance migrations in some years. In summer the main diet is arthropods, e.g spiders or insects and their caterpillars, but in autumn and winter their diet shifts to a vegetarian one and it is a common visitor to bird feeders during winter. Most birds are monogamous (but see Kempenaers 1995). It breeds in different kinds of premade natural or artificial cavities.

The study area consists of mixed lowland coniferous and deciduous forests surrounded by large areas of coniferous forests. Cavity-breeding birds can choose from hundreds of nestboxes placed in all sorts of woodland habitats present in the area. We performed regular nestbox inspections in the breeding season to record dates of egglaying, number of eggs, start of incubation and hatching date.

2.2 Clutch removal

Early pairs, (i.e pairs that started egg-laying earlier than 10 May) had their first clutches removed. Both eggs and nests were removed, and the female were caught, aged, weighed, measured and banded for future identification. Very few pairs moved to another nest box in another part of the study area and produced replacement clutches shortly after removal. These experimentally delayed pairs were later subjected to the clutch size experiments referred to below and were treated as a subgroup (delayed = D).

Removal of early clutches served two purposes. First, recent investigations on the blue tits from the study area have shown that early pairs may become double brooded (Tore Slagsvold, unpublished data). This might influence the results if for example, while rearing the first brood, one or both of the parents reduced its/their parental investment, or delayed moult in anticipation of a prolonged breeding period.

Second, clutch removal also potentially gave us the opportunity to investigate the effect of delayed breeding in combination with clutch size experiments on moult and parental investment. This approach could also potentially give us some idea about what is most important for the initiation and rate/duration of moult; delayed/not delayed breeding or brood size, i.e the capacity to moult while feeding young (see e.g Svensson & Nilsson, 1997). Unfortunately, very few delayed pairs eventually became a part of this study.

2.3 Clutch size experiments

Shortly after completion of egg laying (i.e 1-2 days after the female started incubating), all experimental pairs had their clutch size adjusted to contain 7 eggs. This was done to give all experimental pairs similar workloads early in the nestling period.

To investigate whether moult in the blue tit is influenced by brood size, broods with the same hatching date where manipulated when the chicks were 5 days old.

A few days prior to manipulation, i.e 2 days after presumed hatching date, the nestboxes were checked for hatching success and the chicks were weighed and aged according to weight curves for blue tit young. These weight curves are closely matched by blue tits in the study population (Tore Slagsvold unpublished data). Broods with the same hatching date were assigned to two treatment groups. One group got their brood sizes reduced to contain only 2 chicks (reduced group = “Small”). The remaining chicks where moved to another nest box with the same hatching date. This group consequently had their brood sizes enlarged and constituted the enlarged group (enlarged group = “Large”). Because of hatching losses, it eventually consisted of broods containing 9 to 12 chicks. We chose 9 as the lower limit for the enlarged group. In two cases, hatching success was so low that the broods, originally assigned to the enlarged group, eventually consisted of 7 or 8 chicks. This was considered to be too low to be included in the enlarged group and these pairs were excluded from the analysis.

The treatment for the broods was randomized, although a completely randomized design was impossible, because not all clutches hatched at the same day. Because of relatively low overall number of suitable broods, we chose not to have a control group. Note that our experimental pairs eventually belonged to one of 4 groups: delayed and enlarged, delayed and reduced, natural and enlarged, and natural and reduced. Very few pairs eventually belonged to the two delayed groups, however (see above), so these were omitted from the statistical analysis. Clutch removal did, however, serve one of the original purposes; to avoid double brooded pairs that could confound the analysis.

2.4 Quantification of moult

In this study we wanted to investigate whether brood size had any effect on both timing and speed of moult. We therefore caught the parents twice. In passerine birds, moult is usually initiated by the shedding of the innermost primary – by tradition denoted as primary one out of ten (Fig 1). The primaries constitute the “hand” of a bird and is as such very important for flight performance. After shedding primary one, moult commences ascendantly, ending with the reduced/rudimentary primary number ten. Moult of other feather tracts (e.g the secondaries, coverts and body feathers) overlap with primary moult. While the secondaries are the main feather tract giving lift, the primaries provide thrust and propel the bird through the air. At any one time during the time of primary moult, a blue tit needs to maintain wing lift and flight ability, so the “moult gap” can not be too extensive. In line with this, in our experiment, no individual had more than three primaries simultaneously growing in different stages (moult scores, see below).

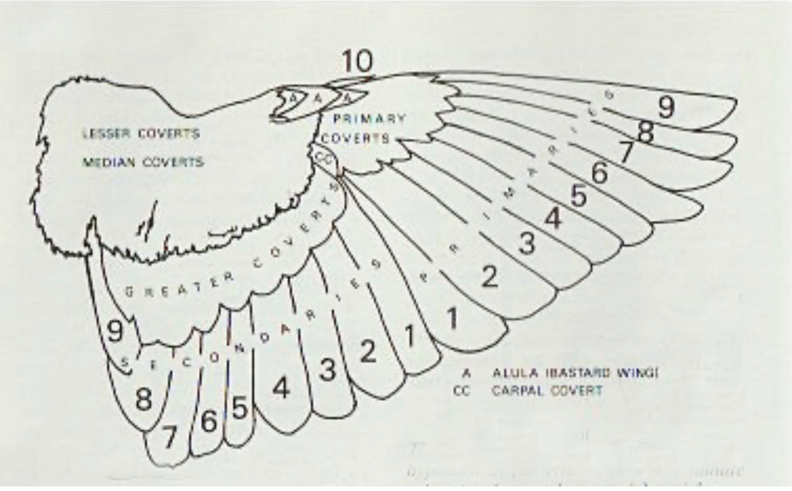
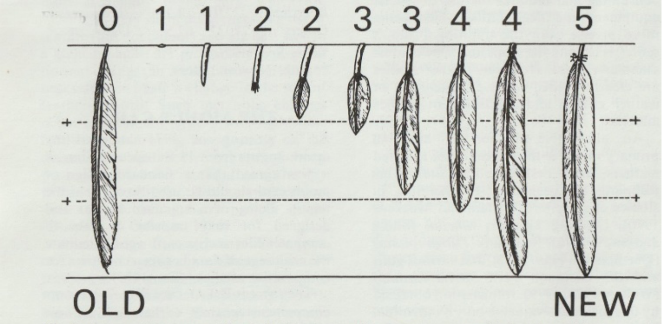


Figure 1
The topography of a birds' wing. Note the different feather tracts. In the present experiment, the primaries, constituting the "hand", is the relevant tract. Moult is usually initiated by the shedding of the innermost primary no. 1 (P1). *Reproduced from Ginn & Melville (1983), with permission of the British Trust for Ornithology*

When the chicks were 7 days old, both parents were trapped, aged, measured, ringed and colour banded (or identified if already ringed/banded). They were then scored for their stage of primary moult according to Ginn & Melville (1983) (Fig 2).



The feather scoring system. The dashed horizontal lines represent one third and two thirds growth. The numerical scoring system is:

0 Old feather remaining.
1 Old feather missing or new feather completely in pin.
2 New feather just *emerging from the sheath up to one third grown.*
3 New feather between one and two thirds grown.
4 New feather more than two thirds grown and with remains of waxy sheath at its base.
5 New feather fully developed with no trace of waxy sheath remaining at base.

Figure 2
The system for giving individual feathers moult scores.The dotted lines represent 1/3 and 2/3 of full length of the feather. *Reproduced from Ginn & Melville (1983), with permission of the British Trust for Ornithology*

Each individual primary on both wings was given a score between 0 (= old feather) and 5 (= fully developed new feather with no waxy sheats), and the total primary score was calculated as the sum of the scores of the individual feathers. Because the progress of moult on the left and right wings was often not symmetrical, total primary score here refers to the sum of both wings combined. An individual was recorded as having started to moult by the shedding of the 1st (innermost) primary.

When the chicks were 14 days old, the parents were trapped again and the primary moult score recorded a second time to be able to record the change in moult scores from day 7 to day 14. The nest boxes were then checked for the number of living chicks for calculation of mortality rates. When analyzing the results, both total sample and analysis restricted to only those individuals that had started to moult at day 7 were conducted. This was done because we predicted that if the blue tits responded to the clutch size manipulations (performed at day 5), we would see very little or no difference between the groups at day 7 – just two days later, but that the effect would be more pronounced at day 14. If the difference between the groups was significantly different also among birds that had already started moulting at day 7, it would strengthen the hypothesis that the manipulation was indeed the most important factor explaining individual moult scores and changes in moult scores from day 7 to day 14.

2.5 Registration of feeding frequencies

When the chicks were 13 days old, the parents were filmed for 1.5-3 hours during the morning hours by discreetly placing a video camera on a tripod, 3-7m from their nest boxes. The tapes were later analyzed and the sexes` feeding frequencies recorded. To aid in distinguishing between the sexes, one of the parents (which one was decided by flipping a coin beforehand) was given a red spot on its ear coverts by use of a permanent marker when checked for primary score at day 7. When analyzing the tapes, feeding frequencies were not recorded before it was evident that neither sex took notice of the camera, something that (confirmed by personal observation) in all cases happened very quickly. We used proportion of feedings since both total and per nestling feeding rates are dependent on brood size.

2.6 Biometrical measurements

The parents were sexed according to the presence/absence of a brood patch.

To test whether we by chance had chosen males with superior physical condition to the “small” experimental group and that this could be confounding factors or even explain possible differences in moult scores later in the breeding season, we checked size and weight measurements so that we could be able to compare these against experimental group:

At first catch at day 7, wing length and tarsus length were recorded. The wing-length was measured down to the nearest half millimeter as the length from the wing bend to the tip of the longest primary, with a flattened wing and with a ruler with a stop at the wing bend. (Svensson, 1992). The tarsus was measured with a sliding caliper to the nearest tenth of a millimeter. Both at day 7 and day 14, the individuals were – in addition to be checked for primary moult score, also weighed with a 50 g Pesola spring. They were also checked for subcutaneous fat deposits according to the scale developed at Ottenby bird observatory (Petterson & Hasselquist 1985).

2.7 Statistical tests

Most statistical tests were performed with the SPSS statistical package, but some tests were also performed with the data analysis package in MS Excel. Because most data critical to this study were not normally distributed, most tests were non-parametric (Mann Whitney U-test), but tests involving normally distributed (biometrical) data were submitted to parametric tests, e.g t-tests. Tests were two-tailed with a significance level of $\alpha = 0.05$.

3 Results

3.1 Binomial logistic regression

A binomial logistic regression was performed to ascertain the effects of age, sex, experimental group and proportion of feedings (day 13) on the likelihood that the subjects had initiated moult at day 14. The logistic regression model was statistically significant, $\chi^2(4) = 26.99$, $p < 0.001$. Of the four predictor variables only two were statistically significant: sex and experimental group (as shown in Table 1). Males had 58.23 (p=0.001) times higher odds to have a positive moultingstatus (i.e initiated moult) at day 14. Subjects being in the experimental group with two hatchlings had 14,17 (p=0.027) times higher odds to have a positive moultingstatus at day 14.

Table 1

Logistic Regression Predicting Likelihood of moult initiation at day 14 based on age, sex, proportions of feeding day 13 and experimental group.

	B	SE	Wald	*df*	*p*	Odds Ratio	95% CI for Odds Ratio	
							Lower	Upper
Sex	4.064	1,231	10.906	1	.001	58.23	5.21	649.66
Age	-.637	.926	0.474		.491	.05	0.09	3.24
Experimental Group	2.651	1.202	4.869	1	.027	14.17	1.35	149.38
Proportion of feedings	-.570	3.251	0.031	1	.861	.57	.001	330.57

3.2 Effects of sex

The results showed clearly that the males were much more likely to start moulting during the breeding season while feeding chicks than the females, and that, among moulting individuals, the moult scores were significantly higher. No females had started moulting on day 7 and only two had started moulting on day 14. Conversely, 13 (of 23) males had started moulting on day 7 and 16 on day 14. Consequently, the difference in moult scores on day 7, day 14 and change in moult score from day 7 to day 14 were dramatically different between the sexes and highly statistically different (Table 1).

Table 2: Mean moult score and SD at day 7, day 14 and change in moult score from day 7 to day 14 among male and female blue tits in the two experimental groups. “Small” group attending 2 nestlings and “large” group attending ≥ 9 nestlings.

		Males		Females			
		Experimental group		Experimental group		U-test between sexes	
Stage		Small (n=10)	Large(n=13)	Small (n=10)	Large (n=13)	z	P
Day 7	mean (SD)	2.90 (4.70)	1.62 (1.98)	0 (-)	0 (-)	-4.14	<0.001
Day 14	mean (SD)	9.8 (7.35)	2.92 (3.28)	0.50 (1.09)	0 (-)	-4.37	<0.001
Change Day 7-14	mean (SD)	6.9 (3.75)	1.31 (1.49)	0.50 (1.09)	0 (-)	-4.25	<0.001

3.3 Effects of age

In males, no difference between the yearlings and the older males were found in the values relevant to this study (moult scores at day 7 and day 14, and change in moult scores from day 7 to day 14). The data from the age groups were therefore lumped for the statistical analysis. (U-test day 7: z = -0.55, P = 0.61, day 14: z = -0.03, P = 0.98, change in moult score from day 7 to day 14: z = 0.28, P = 0.78). Of the two females that had started to moult their primaries at day 14, one was a yearling and the other was an older female. This, of course, constitutes a far too little sample to reveal any differences between the age groups.

3.4 Effect of brood size

Among males, at day 7, we found no significant differences in moult score between birds attending small or large broods. At day 14, however, the males attending small broods had significantly higher moult scores than the males attending large broods. There was also a significant difference in the change in moult score from day 7 to day 14 between these groups. The males attending small broods had significantly higher increase in moult score than males attending large broods.

If the analysis were restricted to only the males that had started moulting at day 7, we found the same pattern, namely that there is no difference in moult score at day 7, but that males attending small broods have a significantly higher moult score at day 14 and also have a significantly higher increase in moult score from day 7 to day 14. (Table 2, Fig 1 a, Fig 1 b).

Table 3: Mean moult scores at day 7, day 14 and change in moult score from day 7 to day 14 (Change 7-14) among blue tit males in the experimental groups attending small (2 nestlings) and large (≥9 nestlings) broods; all males, and analysis restricted to only males that had initiated moult at day 7 . Statistics (z and P-value) refer to Mann Whitney U tests.

	All males (n=23)				
		Experimental group		U-test between exp groups	
		Small (n=10)	Large (n=13)	z	P
Stage					
Day 7	mean	2.90	1.62	-0.34	0.78
	SD	4.70	1.98		
Day 14	mean	9.8	2.92	-2.55	0.01
	SD	7.35	3.28		
Change Day 7-14	mean	6.9	1.31	-3.41	<0.001
	SD	3.75	1.49		
	Males with moult score > 0 Day 7 (n=13)				
		Small (n= 6)	Large (n=7)		
Day 7	mean	4.83	3.0	-0.15	0.95
	SD	5.34	1.73		
Day 14	mean	14.00	5.42	-2.80	0.002
	SD	6.36	2.37		
Change Day 7-14	mean	9.17	2.43	-3.04	0.001
	SD	2.48	1.13		

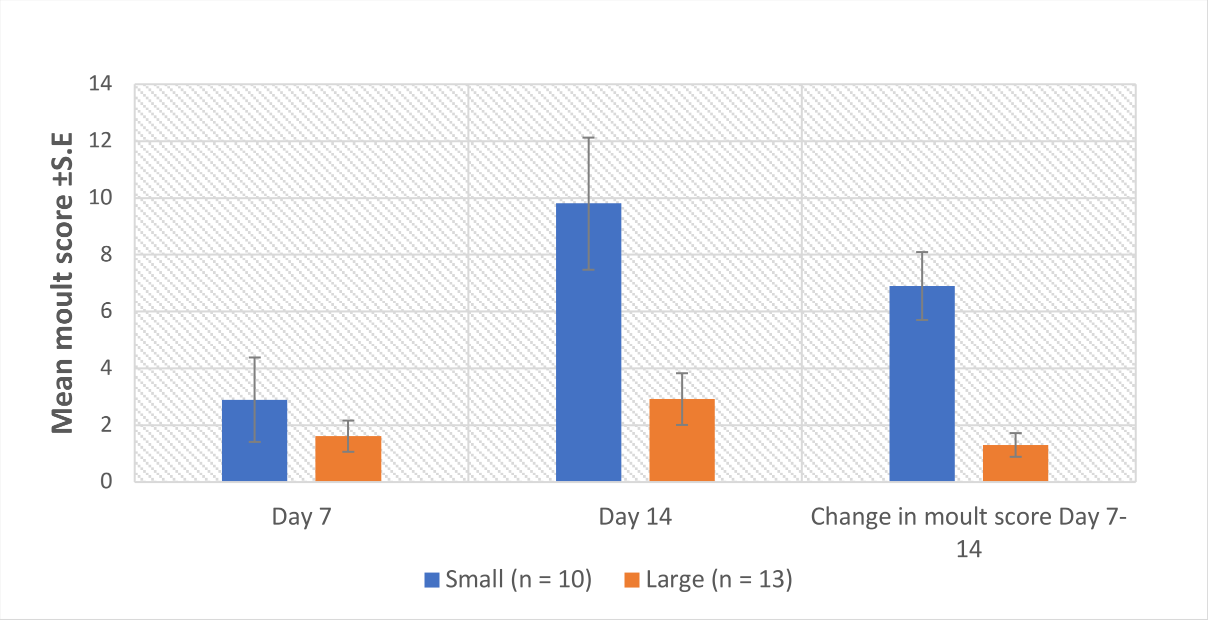


Fig 3 a

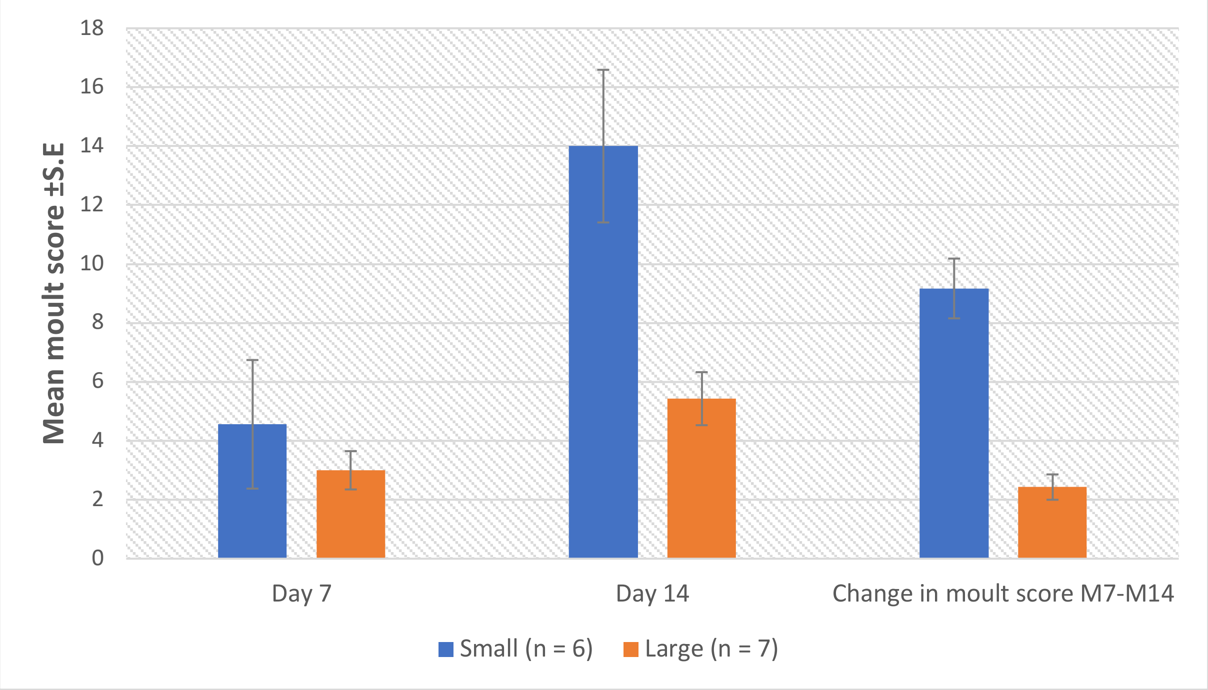


Fig 3 b

Fig 3 a: Mean moult scores ± S.E (vertical bars) of male blue tits on day 7, day 14 and change in moult score from day 7 to day 14 among males attending small (2 nestlings) and large (≥9 nestlings) broods.
Fig 3 b: Same presentation where the analysis were restricted to the males that had actually initiated moult at day 7.

At day 7, no females (n = 23) had started to moult, and at day 14 only two females had initiated moult, both having just started moult by shedding P1 and having a moult score of 2 and 3 respectively. Both females that had started moulting primaries at day 14 (i.e while rearing young) were rearing small broods.

3.5 Effect of date on male moult score

Linear regression showed that date was not a significant factor either on day 7 or day 14:

Fig 4a)

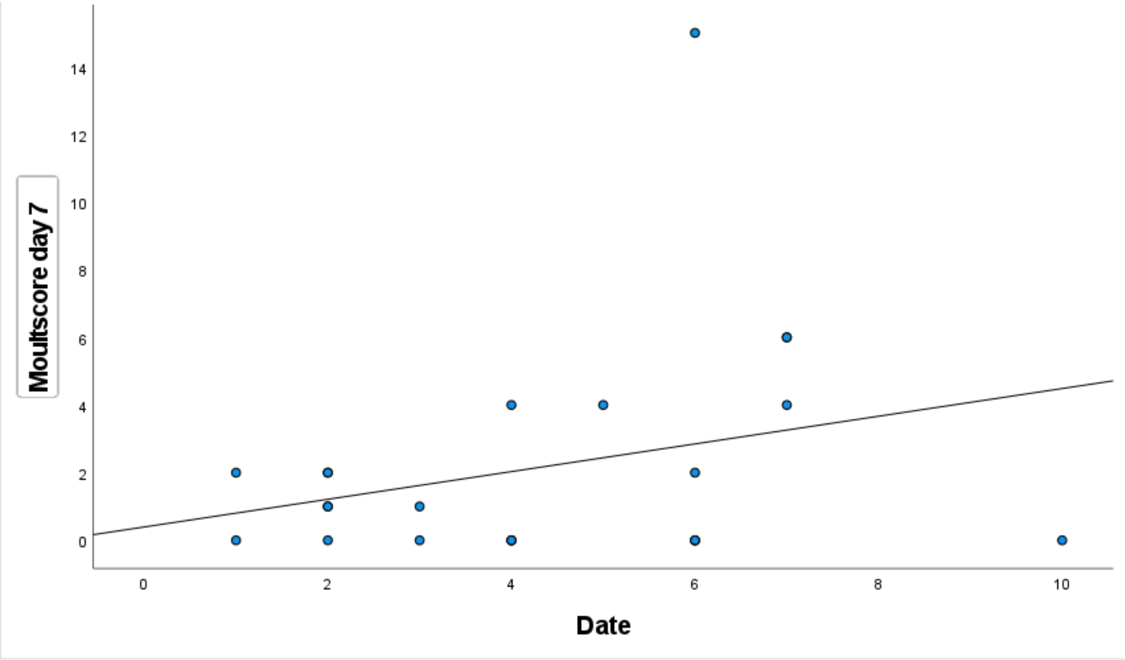


Fig 4b)

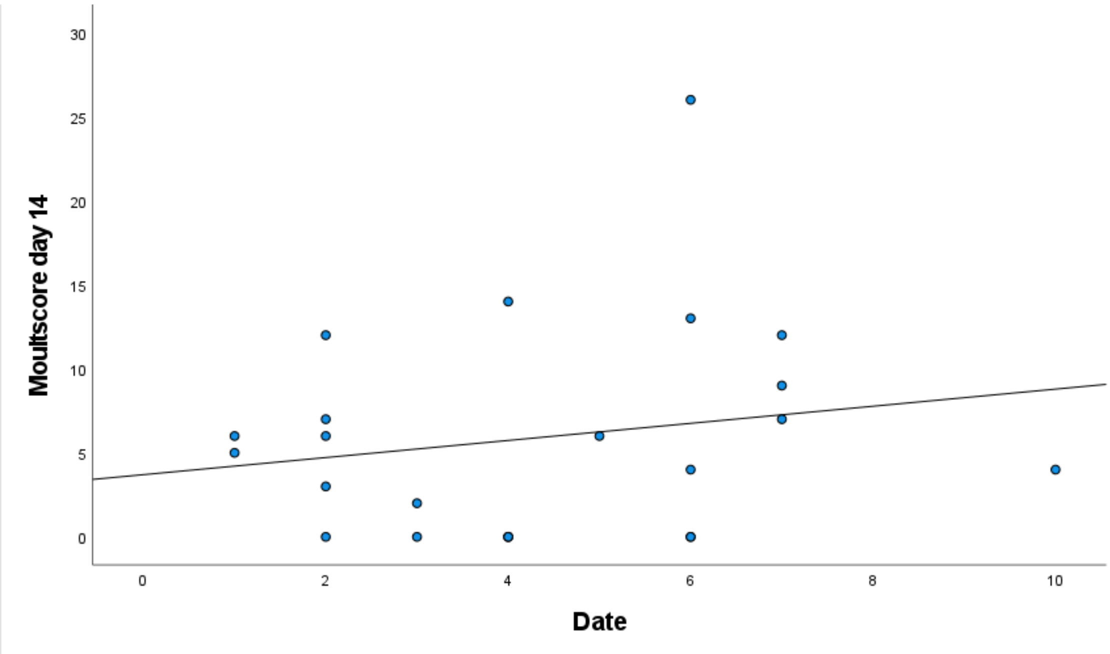


Figure 4: Linear regression of date of first catch (date 1 is June 14) vs male moult score on both day 7 (**Fig 4a**) and day 14 (**Fig 4b**). We found no significant relationship between date and moult score on neither day 7 or

day 14. (Linear regression of date of first catch vs male moult score; Day 7: *$y = 0.4x + 0.4$, $r^2 = 0.08$, $P = 0.19$, Day 14: $y = 0.51x + 3.7$, $r^2 = 0.04$, $P = 0.39$ (n= 23 on both tests)*

3.6 Proportion of male feeding visits

At day 13 , the nestboxes were filmed, and the proportion/percentage of feeding visits to the nest boxes of the two sexes were recorded by analyzing the tapes. For males, we found no differences between the individuals that had started to moult (n = 16) and those that had not (n = 7) in terms of percentage of feeding visits (mean = 47% vs 44%, t-test: t = 0.51, P = 0.52). Males contributed on average with a smaller percentage of feedings than the females, independent of what experimental group they belonged to, but the difference was very marginally non-significant: t-test: Average percentage of feedings F/M: 54%/46%,
P = 0.053 (n = 23).

When proportion of feedings were plotted against number of hatchlings at day of filming (day 13), no significant differences were found, but there seemed to be a much larger spread among males attending small broods (two hatchlings). This is reflected in a statistically significant difference of the variances between the groups. F-test $_{(12, 9)}$: F = 6.15, $P < 0.05$.

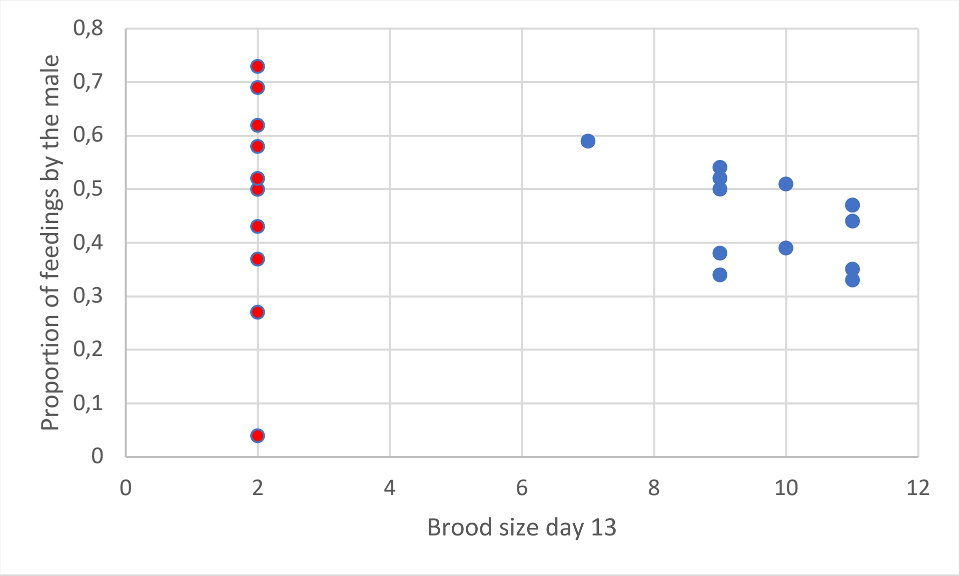


Figure 5: Male proportion of feedings against number of chicks on the day of filming (day 13). Red circles: Males attending small (two hatchlings) broods: mean: 0.48, SD = 0.21,
Blue circles: Males attending large (9-12 hatchlings) broods: mean: 0.45, SD = 0.08.

3.7 Effects of biometry

We found no significant differences in the size measurements , but body mass among the males of the experimental groups were significantly different both at day 7 and at day 14. The body mass of males attending small broods were significantly higher than that of males attending large broods both at day 7 and at day 14. (Table 3).

Table 4: Wing length, tarsus length and body mass at day 7 and day 14 among male blue tits from the experimental groups ("small" attending broods with only two nestlings, "large" attending broods with ≥9 nestlings).

	Experimental group					
	Small (n=10)		Large (n=13)		t-test	
	mean	SD	mean	SD	t	P
Wing length (mm)	68.85	1.31	68.88	1.16	0.07	0.95
Tarsus length (mm)	19.99	0.63	19.63	0.50	1.49	0.15
Weight (g) day 7	11.83	0.48	11.1	0.46	3.71	0.001
Weight (g) day 14	11.88	0.34	11.02	0.67	3.49	0.002

Here, we also found that adult males had significantly longer wings than yearling males (t-test: t = 2.85, P = 0.01). This is not a very extraordinary find, though. The first set of primaries often tend to be shorter than consecutive sets. (See e.g. Alatalo et al, 1984 for possible explanations for this phenomenon).

3.8 Chick mortality

There was a strong statistically significant difference between the experimental groups in this respect. Chick mortality was only recorded in large broods. Mean mortality rate (large group) 0 0.06, SD = 0.1, n = 10. Small group no mortality. Between groups: Mann-Whitney U-test, U = 475, P = 0.001.

4 Discussion

The present study showed that among blue tits, there was a strong difference between the sexes regarding the flexibility of the timing of the initiation of moult, and also of the speed of moult. The males may respond very quickly to changed parental responsibilities and initiate moult or speed it up (if the parental responsibilities are reduced), while the females seem more strongly tied to the breeding schedules. Brood size clearly had a very strong impact on both the frequency of males initiating moult during breeding, moult score on day 14, and also on the speed of moult. Males attending small broods had significantly higher moult speeds. This indicates that the males have a finely tuned ability to adjust their allocation of resources between the two energy demanding processes reproduction and moult, depending on the work load, an ability the females seem to lack, at least in the same degree.

Among females, no difference was found between individuals attending small or large broods and we could not discern any increase in moult speed either. The females' moult seemed therefore more tied to where they were in the current breeding cycle and they did not seem to take advantage of reduced parental responsibilities and to start moult when the daily work load was reduced (see also Hemborg 1998a & 1998b).

Contrary to our predictions, male initiation of moult showed no effect in reduction of reproductive effort, measured as proportion of feedings, but see below.

4.1 Effects of sex

In line with several other studies from a wide array of species (e.g Hemborg & Merilä 1999), the males in this experiment were much more likely to initiate the post breeding moult while attending young, i.e. show moult breeding overlap. There are alternative explanations to this tendency. One explanation may be that the females are more energy limited early in the breeding period. They do have to produce eggs, lay them, incubate them and brood the young. These are in blue tits responsibilities solely tied to the female. Many males started moulting while the females where in this phase and it may be difficult for a female to initiate moult while having these intense parental responsibilities. At the time were many males started their moult, the females spend a lot of time in the nest incubating eggs or brooding the newly hatched young. Heat production (for heating eggs/hatchlings) and reduced time available for foraging may be important restricting parameters for the female. (Mertens 1980, Walsberg 1983)

Second, the males may value the brood less because of reduced certainty of paternity (Kempenaers et al. 1992, Møller & Birkhead 1993, Westneat & Sherman 1993, Sheldon et al. 1997, Queller 1997). While the female "knows" that all the nestlings are her offspring, the male can really never know if any of the nestlings actually is his. The brood may therefore always be considered to be more valuable to the female than it is to the male, no matter how large it is. However, as blue tits are short lived, this may of be his only chance of reproduction, so he should naturally invest in every brood.

In addition, males tend to live longer in these species (Breitwisch 1989). Hence, the male may spare himself and reduce his reproductive effort and start to moult while breeding instead, as a consequence of him having a – on average – larger number of reproductive events ahead in the years to come. A longer life span of males than females may be an effect of dominance hierarchies, maybe especially in the winter, within the species, and the females has indeed been shown to be subdominant to conspecific males in this population (Hansen & Slagsvold 2004). Higher over winter survival could also be an effect of lower heat loss due to higher volume to surface ratios, an effect of the males being larger. Both of these explanations (the males value the brood less/spare himself because of longer life span) constitute an obvious source of sexual conflict in species where there is a difference in the overlap between reproduction and moult between the sexes if this manifests itself in reduced investment in the current brood by one of the parents (most often the male). In addition, males may have to finish their moult earlier than the females because there can be a strong density dependent competition for territories among males in the early autumn when they have to be able to defend a territory against the new recruits, the juveniles of the year (Gauci & Sultana 1981).

4.2 Effects of age

As opposed to other studies (e.g Siikamäki et al. 1994, Hemborg & Merilä 1999), in this experiment no effects of age were found either among the females or among the males. Yearlings and adults were not statistically different from each other in any parameter relevant to this study. This was a bit surprising, since one may expect, with the same reasoning as for the males above, the current brood for a yearling to be of less value than it is to an adult because they have, on average, more reproductive events ahead, regardless of sex. However, the blue tit is a short-lived species (Haftorn 1971), and it may very well be no other option but to “go all in” in every reproductive event.

4.3 Effects of brood size

It may be argued that a brood size of only two chicks may be considered artificially low. However, small broods also occur in nature, for instance because of low hatching success. We did demonstrate in this experiment that brood size may be a very important parameter for both initiation and speed of moult for a temperate passerine species, at least for the males. The experiment also shows the different responses of the two sexes. No females had started moult at day 7 and only two were in the initial phases at day 14, so it could be argued that they didn´t respond at all. The males, on the other hand, were able to respond quickly to the reduced work load. At day 7 we found no significant differences between the groups, but at day 14, merely a bit more than a week since manipulation, the difference were clearly evident. The effect of brood size manipulation was obvious at day 14 and, even if the statistical tests were restricted to only birds that had actually initiated moult at day 7, in this subgroup the effect was still highly statistically significant. The males attending small broods had a much higher (statistically) increase in moult score from day 7 to day 14. This result in essence rules out that the males’ moult were tied to where they were in the breeding cycle. If this where the case, the speed of moult would not have increased for only the males attending small broods. This probably means that the sexes have different “sensors”. The females´ moult scheme seem to be tightly tied, not to the number of chicks and parental responsibilities, but to the breeding schedule, while males are able to respond quickly to changed parental responsibilities and increase the speed of moult if the work load involved in raising chicks is reduced. In the blue tit, it can therefore be argued that, in line with Hemborg's study of pied flycatchers (Hemborg 1998a) "there are sexual differences in the mechanisms controlling allocation of resources to reproductive and somatic investments". This may be beneficial to the male if it results in increased over winter survival, increased fecundity or increased numbers of mating partners the following years. It could, on the other hand, be detrimental to the female (e.g Hemborg & Merilä 1998).

Moult certainly also involves costs, maybe especially during breeding, since it reduces the wing area – and consequently lift of the wing and flight ability. This in turn may increase the individuals' vulnerability to predators and impede their ability to catch food for themselves and the chicks. In addition, in the blue tit, the parents tend the young for two to three intensive weeks after fledging (Slagsvold et al. 2013) and the female seem to take more care of the smaller offspring than the male (Slagsvold et al. 1994). There may therefore also after fledging be different work loads to the two sexes that may influence onset and speed of moult. More research are needed to conclude on this point, however.

Since production of feathers is an energy demanding process (Lindström et al. 1993), the physical condition during moult can also be expected to be reduced and the daily energy surplus as well. When moult overlaps with breeding, both being energy demanding processes, it is to be expected that either moult or breeding may suffer as a consequence. This also strongly suggest an intraindividual trade-off (Stearns 1989, 1992) between these processes when birds attend more normal sized broods, since this increased frequency and speed of moult were confined to males attending small broods. With no such trade-off, we should have seen similar moult scores and moult speeds across the experimental groups.

Another effect of brood size was that only large broods experienced chick mortality. This is hardly surprising, though, since raising two chicks compared to e.g twelve should be very little demanding to the parents. At least the risk of starvation among the hatchlings should in theory be minimized in these small broods. Diseases could of course potentially cause mortality also for small broods. However, it didn't seem to happen during the nestling stage in the present study.

4.4 Effect of moult score on male proportion of feeding visits

One might expect that males that has started their post breeding moult while rearing young may reduce their share in the rearing of the chicks. This has been shown in other studies where the pairs have been delayed by removing the first clutch and as a result have become time limited (Svensson & Nilsson 1997). In this experiment, however, we did not see any evidence of this. Males on average contributed less than females, but this was not related to moult score. One explanation of this may of course be that the most intensively moulting males attended very small broods (two chicks). This probably constitutes a low work load. They could therefore do their fair share of the feedings of the brood, and at the same time have enough surplus energy to commence moult. What was rather interesting regarding the male proportion of feedings was that the males attending small broods had a much larger spread in the proportion of feedings than the males attending large broods. The difference in variance between the groups were statistically highly significant. It was as if the brood was regarded as worthless or very valuable (and everything in between) for males attending small broods, while most males attending large broods usually contributed closer to approximately 50 % share of the feedings. This effect is difficult to interpret and understand. However, it is beyond the scope of this experiment.

4.5 Effect of biometry

Size measurements showed no correlations to the moult scores of the groups. Males attending small broods, however, had a significantly larger body mass than males attending large broods. This was the case both at day 7 and at day 14. It is very probable that this difference was caused by reduced parental responsibilities and that raising two chicks was such a little work load that the males attending these small broods were able to not only increase moult speed, but also to build up body mass during the breeding period.

5 Conclusions

Life history theory predicts that trade-offs occur whenever two energetically expensive activities compete for a limited amount of resources. This study of blue tits strongly supports this prediction and gives support to other studies that has shown trade-off between reproduction and somatic maintenance, i.e moult in birds. It also shows that there are clear sex-related differences in the control of moult. The males initiate moult earlier and are able to react quickly to changed parental responsibilities and start or increase speed of moult quickly (probably) as a consequence of reduced work loads, whereas the females do not seem to have this ability in the same way. Contrary to expectation, we did not find any differences between the age groups and we similarly could not discern any reduced parental effort as a consequence of ongoing moult among the males. The latter could possibly be explained by the very small brood size of the most intensely moulting males. It would have been interesting to follow up an experiment like this to see if the manipulations had any effect on survival of adults and whether the fledglings from the different groups differ in the probability of becoming a local recruit to the population.

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