Ann. Zool. Fennici 34: 229–234 ISSN 0003-455X
Helsinki 31 December 1997

Fat reserves and moult-migration overlap in goldcrests, *Regulus regulus* — A trade-off?

Juha Merilä

Merilä, J., Laboratory of Ecology and Animal Systematics, Department of Biology, University of Turku, FIN-20014 Turku, Finland; Present address: Department of Zoology, Section of Population Ecology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden

Received 1 August 1997, accepted 16 September 1997

Moult and migration are both recognised as highly energy-demanding activities of birds. I studied moult-migration overlap in migrating goldcrests *Regulus regulus* to see whether birds might be trading these activities off against each other. I found that in both sexes the size of subcutaneous fat reserves were greater in birds in later stages of moult. This indicates that birds in active moult were either: (1) not able to store as much fat as birds which have completed moult, or (2) that birds in active moult used up their fat reserves quicker than birds that had completed their moult. This suggests that moult-migration overlap is costly, and there exists a trade-off between energy allocated to moult and migratory fat deposits.

1. Introduction

When allocation of energy to one activity reduces energy available for another, an organism is said to be facing a physiological trade-off. Trade-offs are believed to be important in life history evolution, and a whole array of different kinds of trade-offs has been described (Roff 1992, Stearns 1992). Most of the known trade-offs involve energy allocated to reproduction as one demand, and energy allocated to some aspect of selfmaintenance as another (Stearns 1992). However, examples of physiological trade-offs involving conflicting demands between different aspects of self maintenance are still rare.

For migratory birds, the two most energetically demanding activities, other than breeding, are moult and migration (Jenni & Winkler 1994). In general, they do not overlap in adult passerine birds, suggesting that they are mutually exclusive (Hanh *et al.* 1992, Larsson 1993, Kjéllen 1994). However, in juveniles with a partial post-fledging moult, several species show moult-migration overlap to a varying degree (Jenni & Winkler 1994). During this moult, juvenile birds replace their downy plumage with adult feathers and grow a better insulating adult plumage (Ginn & Melville 1983). As both feather synthesis (King 1981, Blem 1990, Lindström *et al*. 1993) and migratory flight (e.g. Alerstam & Lindström 1990) are highly energy-demanding processes, birds can be expected to trade one for another when opportunities and time for feeding are limited.

In this paper my aim is to evaluate the hypothesis that the resources devoted to post-juvenile moult will be diverted away from fat reserves

This article is also available in pdf format at http://sekj.pc.helsinki.fi/Journals

in migrating goldcrests. If this is the case, we would expect that fat reserves are negatively correlated with degree of moult-migration overlap, i.e. that birds migrating in early moult stages have less fat than birds at later moult stages.

2. Methods

The material for this study was collected between 31 August and 16 October 1994 at Hoburgen Bird Observatory (56°55´N 18°08´E), at the southern tip of the island of Gotland, Sweden. Goldcrests were mist-netted during all mornings when weather conditions allowed for netting as part of a standardised ringing program (e.g. Averland & Elfström 1993). During this period, altogether 810 first-year goldcrests were captured, of which 761 were scored for the stage of post-juvenile moult. Birds were sexed and aged according to Svensson (1992), measured for wing length, and the size of their subcutaneous fat reserves was determined according to Petterson and Hasselquist (1985). Time of fat scoring was noted and the stage of post-juvenile moult was assigned according to Bensch and Lindström (1992). This moult scale ranges from 0 (a newly fledged juvenile in downy plumage) to 6 (post-juvenile moult completed). An important assumption made in this study is that birds in different stages of moult were actually on migration, and that birds in active moult were not, for example, locally born individuals in a early dispersal phase. However, for two reasons, I feel confident that this assumption holds. First, the distance from Hoburgen to the nearest large coniferous forest is about five kilometers, and therefore, most birds captured in Hoburgen are likely to be true migrants. Second, data from another Swedish bird station (Landsort), which is an isolated island, show that migrating goldcrests are frequently (35–62% of all captured goldcrests depending on the year) in moult stages 3 to 5 (Johan Nilsson, pers. comm.).

Table 1. Stage of postjuvenile moult in male and female Goldcrests *Regulus regulus* captured during autumn migration. *N* = number of individuals.

		Moult stage							
	N	0	1	2	3	4	5	0–5	6
Males	381	0	0	0	12	48	71	131	250
Females	380	0	0	0	6	58	95	159	221
Total	761	0	0	0	18	106	166	290	471
% total		0	0	0	2	14	22	38	62

All statistical analyses were carried out with StatView™ SE + Graphics package (Abacus Concepts Inc. 1988) or with a regression program written with Resampling Stats (Bruce 1991). With one exception, non-parametric statistics were used throughout as the dependent variables (fat score and moult stage) were not normally distributed. When I needed to control for time of the season and time of the day to test for an association between moult stage and size of fat reserves, a multiple regression analysis was employed, but the *P*-values were obtained with a randomisation procedure free from any distributional assumptions (Edgington 1980, Bruce 1991).

3. Results

The majority (61.8 %) of the 761 goldcrest scored for stage of post-juvenile moult had completed (= stage 6) their moult before arriving at Hoburgen (Table 1). In both sexes, individuals which had completed their moult had significantly larger fat reserves than moulting individuals (Table 2), and the size of fat reserves correlated positively with the moult stage in both sexes (Males: $r_s = 0.21$, $z = 4.22$, $P < 0.001$; Females: $r_s = 0.12$, $z = 2.28$, $P = 0.02$; Fig. 1). Fat scores were also positively correlated with the time of the season ($r_s = 0.33$, $z = 9.19$, $N = 763$, $P < 0.001$), and negatively with the time of the day ($r_s = -0.13$, $z = 3.35$, $N = 763$, $P < 0.001$). However, even after accounting for these confounding factors, the size of fat reserves increased with increasing moult score in both sexes, i.e. individuals in active moult had smaller fat reserves than individuals in more advanced stages of moult (Table 3A).

Table 2. Comparison of mean fat score of moulting and non-moulting Goldcrests *Regulus regulus*. *N* = sample size.

	Mean fat score (± *S.D.*)			
	Male	*N*	Female	*N*
Moulting	2.17 ± 1.76	131	2.25 ± 1.76	159
Moult complete	2.98 ± 1.73	250	2.65 ± 1.15	221
z [a)]	4.18***		2.28*	

[a)] Mann Whitney, $^*P < 0.05$, $^{***}P < 0.001$.

A problem with the interpretation of these results could arise if the moult stage was also season-dependent. However, moult stage was not correlated with the time of the season ($r_s = 0.04$, $z = 1.18$, $N = 761$, $P = 0.23$), but a closer look at data revealed that when the season is divided into 7-day periods, both the average moult score (Kruskall-Wallis: $H = 12.79$, *d.f.* = 4, $P = 0.012$), and the proportion of individuals that had completed their moult ($\chi^2 = 0.018$, *d.f.* = 4, $P = 0.018$) were lowest early in the season (Table 4). However, when early captured birds were excluded from the analyses, there was no evidence of seasonal variation in moult stage (average moult score: $H = 0.96$, *d.f.* = 3, $P = 0.81$; proportion of moulting individuals: $\chi^2 = 1.53$, *d.f.* = 3, $P = 0.68$). Furthermore, the relationship between size of fat reserves and the stage of moult remained unchanged even when the data obtained early in the season were excluded (Table 3B).

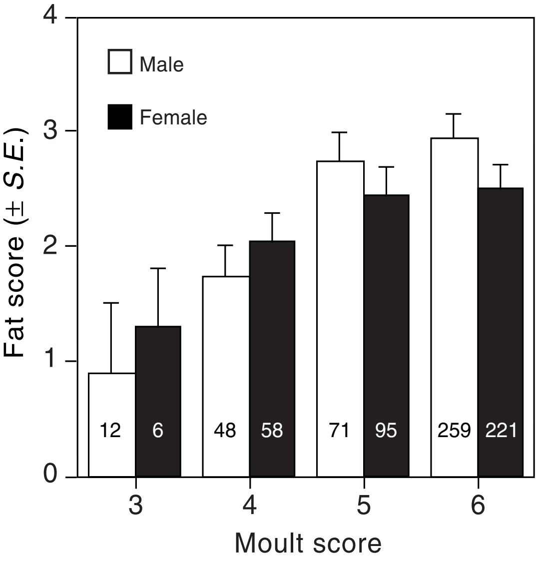

Fig. 1. Mean fat deposit size at different moult stages in male and female goldcrests *Regulus regulus* captured during autumn migration.

4. Discussion

When resources devoted to one activity trade-off with the resources available to another, a negative correlation between the two activities is to be expected (Stearns 1992). I found that goldcrests in the earlier stages of post-juvenile moult (= high energy demands) had smaller energy reserves than birds in the later stages of moult (= lower energy demands), indicating a trade-off between energy reserves and moult. Since migratory birds need large fat reserves to fuel energetically demanding flight and to buffer themselves against unpredictably in re-fuelling possibilities and weather conditions (e.g. Berthold 1993), this indicates that birds which had completed their post-juvenile moult were better off than birds that migrated and moulted simultaneously.

Although there is good evidence that moulting and feather synthesis in particular is costly (e.g. Payne 1972, Lindström *et al.* 1993), fat reserves do not normally become reduced during

Table 3. Results of multiple regression analyses of fat depot size on moult stage, time of the season and time of the day in male and female goldcrests *Regulus regulus*. *P*-values have been obtained with randomisation (see Methods); in all cases $P < 0.001$.

	b ± *S.E.* Males	*b* ± *S.E.* Females
A. All individuals		
Moult	0.68 ± 0.09	0.31 ± 0.10
Day	0.10 ± 0.01	0.25 ± 0.01
Time	– 0.21 ± 0.04	– 0.19 ± 0.05
N	383	384
B. Early captured individuals excluded		
Moult	0.70 ± 0.10	0.42 ± 0.10
Day	0.12 ± 0.01	0.10 ± 0.04
Time	– 0.22 ± 0.05	– 0.17 ± 0.04
N	379	367

Table 4. Proportion of individuals in active moult and mean moult score of juvenile Goldcrests at different times of season.

7-day period	*N*	% Moulting	Mean moult score (± *S.D.*)
31.08–18.09[a)]	21	71.4	4.85 ± 0.85
19.09–25.09	210	40.5	5.42 ± 0.80
26.09–02.10	225	35.6	5.45 ± 0.83
03.10–09.10	278	35.6	5.47 ± 0.78
10.10–18.10[b)]	34	41.2	5.41 ± 0.82

[a)] Data for weeks 35–37 pooled, [b)] Data for weeks 41–42 pooled.

the moult, but sometimes even increase (Payne 1972, Dhonth & Smith 1980, Norman 1991, Lindström *et al*. 1993). Such an increase in mass might indicate that birds try to buffer themselves against energetic stress during the period when much of the acquired energy has to be devoted to feather growth and regulation of body temperature when feather insulation is reduced (Ginn & Melville 1983). However, these observations concern birds moulting outside the migration period. In the case of migrating goldcrests, the small fat reserves of moulting individuals may indicate that the cost of moult becomes amplified as energy has to be devoted both to migration and moulting. In the case of post-nuptial moult, there seem to be several strategies to avoid moult-migration overlap (Kjellen 1994). For example, some species suspend their moult before migration and resume it after reaching the wintering grounds (Kjellen 1994). However, such a strategy may not be feasible in the case of post-juvenile moult in passerines wintering in northern latitudes as downy feathers provide poor insulation against cold weather.

It was shown that many (ca. 40%) of the goldcrests had not completed their post-juvenile moult when arriving at Hoburgen. The question is, therefore, why so many goldcrests initiate migration before completing their moult? Some light on this question may be shed by the observations that the moult stage is partly age dependent, at least in some other species (Bensch & Lindström 1992). Hence, it could be that late-hatched young and young from second clutches (e.g. Haftorn 1982) initiate their migration when still at earlier stages of moult. According to this scenario, moulting birds are late-hatched individuals which are making “the best of a bad job”. However, the proximate reason forcing late-hatched young to migrate earlier remains unknown.

An interesting finding was that there is no clear-cut relationship between time of the season and stage of post-juvenile moult. This might indicate that the onset and/or duration of post-juvenile moult is not strongly related to any particular calendar date (c.f. Berthold 1993), but that much of the individual variation in moult stage may be due to differences in environmental conditions experienced in the past. However, it also quite possible that the captured birds represent a mixture of individuals originating from different geographical regions which might differ in breeding time and onset of moult.

The results of this study differ from those obtained by Merilä and Svensson (1995) and Svensson and Merilä (1996) for migrating goldcrests and blue tits (*Parus caeruleus*), respectively. In the case of the goldcrest, the fact that we did not previously find any evidence for fat-moult association may be attributable to a much smaller sample size in that study. Large sample sizes are important as the size of fat reserves is affected by a multitude of factors, such as, for example, distance travelled, time spent at the stop-over site etc. (e.g. Hansson & Petterson 1989). Furthermore, the assessment of the post-juvenile moult stage is prone to some errors as birds on stage five sometimes can be misclassified as belonging to stage six (J. Merilä, pers. obs.). Such errors will act to homogenise any differences between moulting and non-moulting birds, especially when sample sizes are small. The fact that moulting blue tits seem to have similar-sized fat reserves as non-moulting individuals (Svensson & Merilä 1996) is not incompatible with the results of this study. It may be that the goldcrests, due to their smaller body size, and their consequently higher per-gram metabolic rate are more prone to energetic stress. In fact, Lindström *et al.* (1993) have shown that the energetic cost of feather synthesis increases steeply with mass-specific basal metabolic rate, and therefore, we should expect moult-migration overlap to be more costly to goldcrests than to blue tits. However, it is clear that more studies, preferably experimental, are needed to assess the magnitude of costs associated with moult-migration overlap in different species differing in their ecology.

The biochemical adjustments involved in the switch from mainly protein metabolism during moult to lipid metabolism during fat deposition have been studied by Jenni-Eierman and Jenni (1994). They showed that plasma triglyceride levels increased more rapidly during the course of the day in birds that had completed moult, as opposed to those that were still moulting. These results and our findings in this study suggest that fat deposition rates might be higher after moult, presumably since birds might then be relieved from the energetic cost of feather synthesis and hence be able to allocate more energy to fat deposits.

Last but not least, it is necessary to consider the fact that all results presented in this study are correlative, and even if extremely difficult to achieve, an experimental verification is urged. As moulting is probably controlled by hormones (Payne 1972), hormones involved with feather synthesis might at least theoretically have inhibitory effects on fat deposition. Consequently, smaller fat deposits among moulting birds might be a "forced" outcome where the hormones involved with moult process might work as physiological inhibitors for fattening. In such a case, the positive correlation between moult stage and fat reserves would not need to have anything to do with current energy balance, but be merely an inevitable outcome of physiological processes involved with the process of moult. However, even if this were the case, this scenario is perfectly compatible with the idea of trade-off between moult and size of energy reserves, as such antagonistic hormonal mechanisms might be viewed as a result of natural selection favouring a moult strategy which does not overlap with migratory activities.

In conclusion, the data show that moult-migration overlap in goldcrests is associated with smaller subcutaneous fat reserves, and indicates, although does not prove, a trade-off between resources devoted to migratory fat deposits and moulting. Such a trade-off is in line with recent suggestions (e.g. Hedenström & Petterson 1987, Ellegren 1993) that an overlap between moult and migration might slow down the speed of migration in birds.

Acknowledgements. I am in debt to several members of the Sundre Bird Ringing Group for their help in collecting the data. Special thanks are due to Thord Fransson, Christer Larsson, Nils Kjéllen, Ben Sheldon, Erik Svensson and Hannu Pietiäinen for insightful comments on an earlier draft of this manuscript, and Johan Nilsson for providing information on the moult status of migrating Goldcrests at Landsort Bird Station. This is report no. 32 from the Sundre Bird Ringing Group.

References

Abacus Concepts Inc. 1988: Statview™ SE + Graphics ver. 1.03. The solution for data analysis and presentation graphics. — Abacus Concepts Inc, Berkeley, CA.

Alerstam, T. & Lindström, A. 1990: Optimal bird migration: the relative importance of time, energy and safety. — In: Gwinner, E. (ed.), Bird migration: The physiology and ecophysiology: 331–351. Springer-Verlag, Berlin Heidelberg.

Averland, M. & Elfström, P. 1993: Sundregruppens verksamhet 1992. — Bläcku. 19: 1–16.

Bensch, S. & Lindström, Å. 1992: The age of young willow warblers Phylloscopus trochilus estimated from different stages of postjuvenile moult. — Ornis Svecica 2: 23–28.

Berthold, P. 1993: Bird migration: a general survey. — Oxford University Press, Oxford.

Blem, C. R. 1990: Avian energy storage. — Current Ornithology 7: 59–133.

Bruce, C. 1991: Resampling Stats: probability and statistics in a radically different way. User guide version 3.0. — Resampling Stats, Arlington.

Dhonth, A. & Smith, J. N. M. 1980: Postnuptial molt of the song sparrow on Mandarte Island in relation to breeding. — Can. J. Zool. 58: 513–520.

Edgington, E. 1980: Randomization tests. — Marcel Dekker, New York.

Ellegren, H. 1993: Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. — Ornis Scand. 24: 220–228.

Ginn, H. B. & Melville, D. S. 1983: Moult in birds. — BTO Guide 19. The British Trust for Ornithology, Hertfordshire.

Haftorn, S. 1982: Parental care of nestlings by the goldcrest Regulus regulus. — Ornis Fennica 59: 123–134.

Hanh, T. P., Wingfield, J. C. & Ramenofsky, M. 1992: Adjustment of prebasic molt schedule in birds. — Ornis Scand. 23: 314–321.

Hansson, M. & Petterson, J. 1989: Competition and fat deposition in goldcrests (Regulus regulus) at a migration stop-over site. — Vogelwarte 35: 21–31.

Hedenström, A. & Petterson, J. 1987: Migration routes and wintering areas of willow warblers ringed in Fennoscandia. — Ornis Fenn. 64: 137–143.

Jenni, L. & Winkler, R. 1994: Moult and agening of European passerines. — Academic Press, London.

Jenni-Eiermann, S. & Jenni, L. 1994: Physiological aspects of seasonal changes in fat deposition and fat utilization of migratory Passerines. — J. Ornithol. 135: 393.

King, J. R. 1981: Energetics of avian moult. — Proc. XVII Int. Orn. Congr.: 312–317.

Kjéllen, N. 1994: Moult in relation to migration in birds – a review. — Ornis Svecica 4: 1–24.

Larsson, C. 1993: Moult patterns in Passerine bird species. — Introductory Research Essay no. 53 Dept. Zoology, Uppsala Univ., Repro. HSC, Uppsala.

Lindström, A., Visser, G. H. & Daan, S. 1993: The energetic cost of feather synthesis is proportional to basal metabolic rate. — Physiol. Zool. 66: 490–510.

Merilä, J. & Svensson, E. 1995: Fat reserves and health state in migrant Goldcrests Regulus regulus. — Funct. Ecol. 9: 842–848.

Norman, S. C. 1991: Postjuvenile moult in relation to dispersal and migration in the Chiffchaff Phylloscopus collybita. — Ringing & Migration 12: 80–85.

Payne, R. B. 1972: Mechanisms and control of molt. — In: Farner, D.S., King, J. R. & Parkes, K. C. (eds.), Avian biology, Vol. 2: 104–155. Academic Press, New York.

Petterson, J. & Hasselquist, D. 1985: Fat deposition and migration capacity of Robins Erithacus rubecula and goldcrests Regulus regulus at Ottenby, Sweden. — Ringing & Migration 6: 66–76.

Roff, D. A. 1992: The evolution of life histories. Theory and analysis. — Chapman & Hall, New York.

Stearns, S. 1992: The evolution of life histories. — Oxford University Press, Oxford.

Svensson, L. 1992: Identification guide to European passerines. — Märsta Tryck, Mästa.

Svensson, E. & Merilä, J. 1996: Moult-migration overlap, migratory condition and plumage coloration in Blue Tits Parus caeruleus. — Condor 98: 825–831.