

Differences in Primary Molt and Biometrics between Adult and Second-year Black-headed Gulls in Puck Bay (Southern Baltic)

WŁODZIMIERZ MEISSNER

Avian Ecophysiology Unit, Department of Vertebrate Ecology & Zoology, University of Gdansk
Al. Legionów 9, PL 80-441 Gdansk, Poland
Internet: w.meissner@univ.gda.pl

Abstract.—Black-headed Gulls (*Larus ridibundus*) were caught on the southern Baltic coast during early phase of their autumn migration between 27 July and 9 August from 1992 to 1995. Due to involvement in breeding, adult Black-headed Gull started primary replacement later than second-year birds, but their molt was slightly faster during the studied two-week period. This suggests that the difference in primary molt score between the age classes may decrease toward the end of the molt period. There were no differences in primary molt between sexes. Adults had larger hole in wing area and they had higher body condition index than second-year birds. This might reflect higher cost of flight of adults due to their lower aerodynamic efficiency of the wing and their tendency to buffer themselves against increased energetic stress. Second-year Black-headed Gulls migrate for longer distances farther than adults on average and this might be a reason of their slower rate of primary replacement. Received 23 February 2006, accepted 5 January 2007.

Key words.—molt, autumn migration, Baltic, Black-headed Gull, *Larus ridibundus*.

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Gulls breeding in the Arctic zone start primary molt at the beginning of the breeding period due to a very narrow time window for incubation, chick rearing and migration (Ingolfsson 1970; Meissner 2002). However, some gull species from Central Europe also begin replacement of primaries quite early and two energetically costly events: molt of primaries and migration overlap to a great extent in this group (Walters 1978; Coulson *et al.* 1983). In a given species, the start of primary molt is determined genetically, but it is modified by many different factors, like timing of breeding, migration distance, climatic conditions and food abundance (Stresemann 1971; Verbeek 1977; Kjellén 1994).

The Black-headed Gull (*Larus ridibundus*) is a common species breeding in almost the whole of Europe and Central Asia (Gluz von Blozheim and Bauer 1982; Malling Olsen 2004). During autumn migration this species passes in large numbers along sea-coasts and inland regions of Europe (Gluz von Blozheim and Bauer 1982) and actively molts primaries (Malling Olsen 1993). Although comprehensive data about primary molt of this species were gathered near Amsterdam by collecting shed feathers and dead birds (Walters 1978), the course of primary molt remains poorly known.

In this paper primary molt and morphometrics of the Black-headed Gull migrating in autumn through Puck Bay were analysed, with special attention paid to possible age and sex differences.

METHODS

Fieldwork was conducted from mid-July to the end of September, 1992 to 1995, on Puck Bay coast (Southern Baltic) at a narrow sandy peninsula near Rewa village (54°38'N, 18°31'E) (Fig. 1). The main trapping method was cannon-netting. Some gulls were caught also by mist-nets at dusk and at dawn, mainly by flushing them out towards the nets. Birds in the age of at least second calendar year of life were used in the analysis, because first-year (juvenile) Black-headed Gulls do not molt primaries until their second summer of life (Gluz von Blozheim and Bauer 1982). In this period, molt data were collected for 216 adult and 52 second-year Black-headed Gulls, however over 90% of birds were caught between 27 July and 9 August. Only molt data from this period were included into analysis.

The total head length and bill depth at gonys were measured to the nearest 0.1 mm with calipers, while wing length (maximum chord method) with accuracy of 1 mm with a stopped ruler. Gulls were weighed with PESOLA spring balance with accuracy of 2 g. Two different discriminant functions were applied for sexing of each individual. The first function was based on measurements of Black-headed Gulls from a breeding colony in Bojano located about 40 km from the study area (Meissner and Bzoma 2005). The second function was calculated for birds breeding in The Netherlands and in Spain (Palomares *et al.* 1997). Only those birds in which sexing result was the same according to both functions were taken for further analysis.

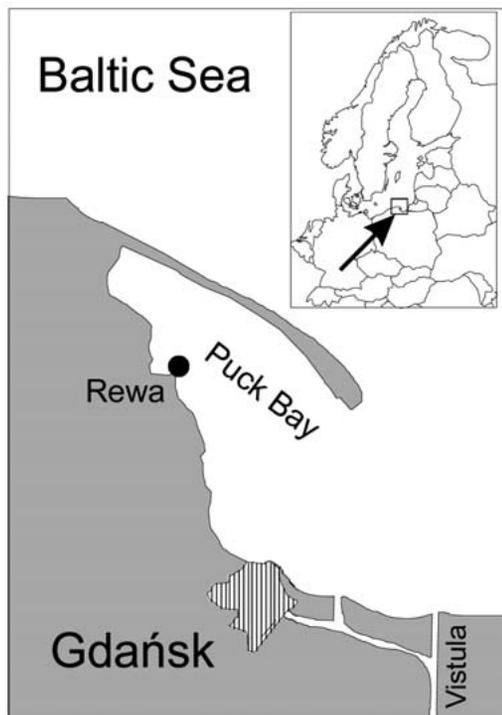


Figure 1. Location of the study area.

All adult and second-year Black-headed Gulls showed primary molt. Molt was scored according to Ashmole (1962) using a six score scale, where 0 corresponds to an old feather and 5 a new full grown one. Molt score was used as a measure of advancement of primary replacement and thus was not adjusted to varying masses of feathers. To estimate the size of a gap in the wing area of molting individuals the wing raggedness score was used (Haukioja 1971). This score was calculated for each primary as 5 minus the molt score for growing feather. The only exception was the case of a missing feather. Normally in such a case the raggedness score should be 4 (calculated as 5-1), but it leads to overestimating the gap size due to the presence of greater coverts which partly cover the gap in the wing area. Hence, the score of 3 (5-2) is given in such situation. Both old and new fully grown primaries are given the raggedness score of 0. Raggedness scores of all ten primaries were summed which gave the individual value of a gap size.

To assess the amount of energetic reserves in both age classes the body mass was regressed against the total head length and bill length, according to the equation: $BM = 4.41THL + 13.02BD - 198.44$ ($R^2 = 0.51$), where: BM—body mass, THL—total head length, BD—bill depth.

The total head length and bill depth were chosen as indicators of structural size, because these two measurements are highly correlated with overall size of a bird and they are the best predictor of the sex in many gull species (e.g., Hanners and Patton 1985; Bosch 1996; Torlaschi *et al.* 2000) including the Black-headed Gull (Palomares *et al.* 1997; Meissner and Bzoma 2005). Residuals from this regression were taken as predictor of

body condition carried by individual bird (body condition index). All analyses were done using STATISTICA 6.0 software (StatSoft 2001).

RESULTS

For 26 adult Black-headed Gulls (11.6%) and ten second-year birds (19.2%) two discriminant functions gave opposite results. All these birds according to Meissner and Bzoma (2005) were females, but according to Palomares *et al.* (1997) they should be males. These were dropped from analysis. In 232 Black-headed Gulls the same result of sexing were obtained by both functions. For further analysis 38 second-year and 180 adult gulls caught between 27 July and 9 August were used.

To check for possible differences in advancement of primary molt between both sex and age groups, two-way ANCOVA was performed with sex and age as independent variables and date (the number of a day, with 1 July = 1) as a covariate. Significant factors were the age (ANCOVA, $F_{1,213} = 121.4$, $P < 0.0001$) and day (ANCOVA, $F_{1,213} = 47.3$, $P < 0.0001$). The influence of sex was not significant (ANCOVA, $F_{1,213} = 0.01$, $P = 0.91$). There was no interaction between sex and age (ANCOVA, $F_{1,213} = 1.1$, $P = 0.30$). In general, adults were less advanced in primary molt than second year birds (post-hoc Tukey test, $P < 0.001$). During the 14 days of the studied period this difference was on average about ten points of primary molt score.

There was a significant progress in molt scores within the studied period over the 14 days. In second-year birds it was 0.56 points of molt score per day and in adults 0.73 points. The slopes of the linear regression between day and molt score differed significantly between adult and second-year birds (ANCOVA, $F_{1,214} = 4.7$, $P = 0.003$). The progress of molt during the two weeks of study was slightly faster in adults than in the second-year birds (Fig. 2).

Body condition did not differ between sexes, but only between age classes (two-way ANOVA, $F_{1,221} = 0.45$, $P = 0.50$; $F_{1,221} = 12.44$, $P = 0.0005$, respectively). Body condition index of adults (mean 2.94, SD = 17.28, N = 185) was higher than for second-year birds

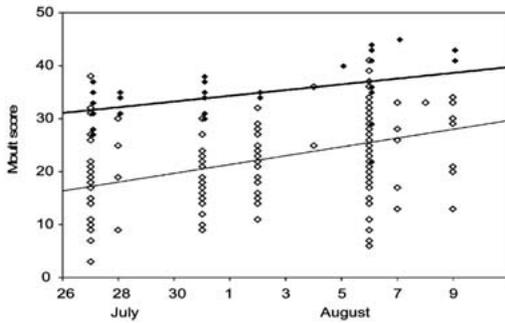


Figure 2. Regression between primary molt score and days (day 1 = 1 July) for second-year (black squares, thick line) and adult (open squares, thin line) Black-headed Gulls caught during autumn migration in Rewa between 27 July and 9 August in years 1992-1995. Slopes of regression lines differ significantly (ANCOVA, $F_{1,214} = 4.7$, $P = 0.003$).

(mean -7.87 , $SD = 21.05$, $N = 40$) (Tukey post-hoc test, $P < 0.001$). The number of primaries growing simultaneously varied between two and eight and did not differ between both age groups (t -test, $t = 1.07$, $P = 0.29$). However, the gap size was significantly larger in adults (t -test, $t = 2.15$, $P = 0.03$). Except for wing length there were no significant differences in linear measurements between age classes within a given sex (Table 1).

The molt score was negatively correlated with gap size (Pearson correlation coefficient, $r = -0.33$, $P < 0.05$; $r = -0.56$, $P < 0.05$ in second-year birds and in adults respectively) and number of growing primaries ($r = -0.40$,

$P < 0.05$; $r = -0.30$, $P < 0.05$ in second-year birds and in adults, respectively). This means that the gap size in both age groups decreased towards later stages of molt when the number of primaries growing simultaneously became lower.

DISCUSSION

Large numbers of adult gulls from north-eastern Baltic countries perform molt migration in July and August along the southern part of the Baltic coast using rich summer food resources (Alerstam 1993; Meltofte 1993). At least up to mid-July the majority of adult Black-headed Gulls from Finland, Estonia and Latvia stay close to their breeding colonies (Viksne 1968). In that time the overall speed of their migration is low, but after about two months when molt is finished or close to the end, adults start to migrate faster (Alerstam 1993) and the bulk of wintering Black-headed Gulls arrive at British wintering sites between mid-September and the end of October (Cramp and Simmons 1983). These two phases of migration involve different energy expenditure and this may have crucial influence on the speed of primary molt. Holmgren *et al.* (1993) and Serra *et al.* (1998) showed that migrating Dunlins (*Calidris alpina*) adjust their molt to maintain the wing area as large as possible, but later during residency time on molting grounds

Table 1. Comparison of linear measurements and body mass among adult and immature males and females of Black-headed Gull caught in Rewa between 27 July and 9 August in years 1992-1995. The mean, standard deviation and sample size is given. Values with the same superscript do not differ significantly according to post-hoc Tukey test at $P < 0.05$.

Measurement	Adults		Second-year birds		Results of ANOVA
	Males	Females	Males	Females	
Wing length	318.90 ^a	300.90 ^b	304.40 ^b	291.7 ^c	$F_{3,181} = 84.6$ $P < 0.0001$
	6.79	7.55	8.98	9.06	
	48	115	8	14	
Total head length	85.69 ^a	78.69 ^b	85.66 ^a	78.44 ^b	$F_{3,228} = 270.2$ $P < 0.0001$
	1.82	1.76	1.94	1.38	
	57	133	17	25	
Bill depth	8.64 ^a	7.71 ^b	8.54 ^a	7.60 ^b	$F_{3,227} = 125.3$ $P < 0.0001$
	0.37	0.33	0.23	0.36	
	57	132	17	25	
Body mass	295.36 ^a	249.91 ^b	283.47 ^a	238.56 ^b	$F_{3,224} = 69.3$ $P < 0.0001$
	24.62	20.83	17.08	25.77	
	56	132	15	25	

this species speed-up feather replacement and has much larger gaps in wing area.

Like in other gulls, adult Black-headed Gull starts primary replacement later than immatures (Harris 1971; Walters 1978; Coulson *et al.* 1983; Braune 1987; Smith 1988). Not all second-year Black-headed Gulls take part in breeding. In the eastern Baltic region about 23% of nesting birds were in their second year of life (Viksne 1968) and near Amsterdam their percent proportion was only 4.8% (Walters 1978). The rest of immatures spend the breeding season outside breeding colonies (Gluz von Blozheim and Bauer 1982). Later molt in adults was thought to be a result of breeding constraints and may be explained by much greater pressure on breeding birds, where energy needed for incubation and chick rearing is channeled away from molt resulting in delayed onset of primary replacement (Harris 1971; Smith 1988). Second-year Black-headed Gulls have much more abraded flight feathers than adults (Baker 1993) and this may be additional factor responsible for earlier initiation of molt. However, adults revealed a higher speed of molt during the two week study period and this suggests that the difference in molt score between both age classes probably become smaller toward the end of the molting period, like in Bonaparte's Gull (*Larus philadelphia*) (Braune 1987) and at least in some populations of Herring Gulls (*Larus argentatus*) and Yellow-legged Gull (*Larus michahellis*) (Vandenbulcke 1989). This contrasts with results obtained for Herring Gulls in Britain (Coulson *et al.* 1983), Kittiwakes (*Rissa tridactyla*) in Scotland (Smith 1988) and also for Black-headed Gulls near Amsterdam (Walters 1978), where primary molt of immatures started earlier and was more rapid than in adults. The majority of birds passing Puck Bay in July and August still had quite a long distance to cover to reach their wintering grounds (Gluz von Blozheim and Bauer 1982), while populations sampled near Amsterdam consisted of local breeders and migrants being not far from their final destination (Walters 1978; Gluz von Blozheim and Bauer 1982). It may have crucial influence on trade-offs be-

tween energy demands needed for molt and migration and adult Black-headed Gulls migrating through Puck Bay are forced to speed up primary molt before they start the next, faster migration phase. It is known at least for passerines that within a given species birds that start to molt later will molt more rapidly (Morton and Morton 1990; Hall and Fransson 2000). Black-headed Gulls, Herring Gulls and Kittiwakes in western Europe undergo short distance movements (Gluz von Blozheim and Bauer 1982; Wernham *et al.* 2002), and do not need to rush with primary replacement, especially as a consequence the quality of primaries growing at higher rate is reduced (Dawson *et al.* 2000; Serra 2001; Dawson 2004). Moreover, second year Black-headed Gulls migrate on an average further than adults (Michno 1986; Heldbjerg 2001) and it might be an additional reason of slower speed of primary replacement in immatures in Puck Bay.

Decrease of the gap size and the number of growing primaries with increasing molt score indicate that in Black-headed Gull the speed of molt is lower towards the end of feather replacement, like in many other species replacing primaries descendently (Newton 1967; Branson *et al.* 1979; Dawson 2003). In the studied period, immatures were more advanced in primary replacement than adults, this might be another reason for lower molt rate and smaller gap size in immatures.

The gap in wing area may have a detrimental effect on aerodynamic efficiency of the wing (Hedenström and Sunada 1999). Primary molt decreases wing area and usually birds lower their body mass accordingly to reduce the cost of flight (Swaddle and Witter 1997; Senar *et al.* 2002). Average body mass of Black-headed Gulls migrating through Puck Bay was similar to those recorded in other places in Europe at that time (Gluz von Blozheim and Bauer 1982) and only somewhat lower than in birds wintering in Spain and Dutch Waddensea (Gluz von Blozheim and Bauer 1982; Palomares *et al.* 1997). Hedenström (1998) and Hedenström and Sunada (1999) showed that the influence of molt gap on flight performance is rather small, which allows short and medium dis-

tance migrants to migrate with molting primaries regardless of increased energetic costs of flight and feather synthesis. Moreover, energetic cost of feather synthesis increases steeply with mass-specific metabolic rate (Lindström *et al.* 1993) and, in the case of Black-headed Gull, this cost is expected to be lower than in smaller species.

In adult Black-headed Gulls caught in Puck Bay larger gap in wing area accompanied higher energetic reserves. A similar tendency was found in Black Terns (*Chlidonias niger*) in Lagoon of Venice (Zenatello *et al.* 2002) and Dunlins in Ebro Delta (Figureola and Bertolero 1995). This might reflect higher flying costs of adults due to lower aerodynamic efficiency of the wing. It was suggested that birds try to buffer themselves against energetic stress, when much of energy has to be devoted to flight, feather synthesis and body temperature regulation during reduced insulation (Ginn and Melville 1983). Lower energetic reserves in immatures might also reflect disparity in feeding efficiency that occurred between adult and younger gulls (Burger 1987).

Differences in timing of molt between sexes would be expected if one of the parents is more involved in chick rearing. In Black-headed Gull both parents brood and provision chicks (Gluz von Blozheim and Bauer 1982). Although there is a suggestion that males depart from breeding colonies a little earlier than females (Makatch 1952), the difference is probably too small to have important influence on molt schedule. On the other hand, in the Puck Bay region gulls from different geographical populations stop-over during autumn migration (Gluz von Blozheim and Bauer 1982), thus possible small differences in advancement of primary molt between sexes can be blurred.

The primary molt in the Black-headed Gull takes about three months (Walters 1978; Ginn and Melville 1983) and the difference among seasons in the date of its completion is much smaller than in timing of other parts of annual cycle (Walters 1982). The studied period concerned only two weeks and obtained results cannot be representative for the whole primary molt cycle of this species.

Moreover, Black-headed Gulls from north-eastern Europe migrate numerously not only along southern Baltic, but also through inland towards Mediterranean (Gluz von Blozheim and Bauer 1982; Michno 1986). Birds migrating inland and along the sea-coasts encounter different ecological conditions and this may result in their different migration and molt strategies, because molt schedules are adapted to local selection pressures and they must fit adaptively in the annual cycle of a species (Verbeek 1979; Borrás *et al.* 2004; Summers *et al.* 2004). Thus more data are needed to assess geographical variation of molt schedule in Black-headed Gull, especially along inland migration route.

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LITERATURE CITED

- Alerstam, T. 1993. Bird Migration. Cambridge University Press, Cambridge.
- Ashmole, N. P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part I. General biology. *Ibis* 103: 235-273.
- Baker, K. 1993. Identification Guide to European Non-Passerines. Butler and Tanner, London.
- Borrás, A., T. Cabrera, J. Cabrera and J. C. Senar. 2004. Interlocality variation in speed of moult in the Citril Finch *Serinus citrinella*. *Ibis* 146: 14-17.
- Bosch, M. 1996. Sexual size dimorphism and determination of sex in Yellow-legged Gulls. *J. Field Ornithol.* 67: 534-541.
- Braune, B. M. 1987. Body morphometrics and molt of Bonaparte's Gulls in the Quoddy region, New Brunswick, Canada. *Condor* 89: 150-157.
- Branson, N. J. B., E. D. Ponting and C. D. T. Minton. 1979. Turnstone populations on the Wash. *Bird Study* 26: 47-54.
- Burger, J. 1987. Foraging efficiency in gulls: a congeneric comparison of age differences in efficiency and age of maturity. *Studies in Avian Biology* 10: 83-90.
- Coulson, J. C., P. Monaghan, J. Butterfield, N. Duncan, C. Thomas and C. Shedden. 1983. Seasonal changes in the Herring Gull in Britain: weight, moult and mortality. *Ardea* 71: 235-244.
- Cramp, S. and K. E. L. Simmons (Eds.). 1983. The Birds of Western Palearctic. Vol. III. Oxford University Press, Oxford.
- Dawson, A. 2003. A detailed analysis of primary feather moult in the Common Starling *Sturnus vulgaris* new feather mass increases at a constant rate. *Ibis* 145: E69-E76.

- Dawson, A. 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. Ibis 146: 493-500.
- Dawson, A., S. A. Hinsley, P. N. Ferns, R. H. C. Bonser and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society of London B 267: 2093-2098.
- Figureola, J. and A. Bertolero. 1995. Moulting strategies and body masses of migrating Dunlins through the Ebro Delta. Wader Study Group Bulletin 76: 20.
- Ginn, H. B. and D. S. Melville. 1983. Molt in Birds. British Trust for Ornithology, Herts.
- Gluz von Blozheim, U. N. and K. M. Bauer. 1982. Handbuch der Vögel Mitteleuropas. Band 8. Akademische Verlag, Wiesbaden.
- Hall, K. S. S. and T. Fransson. 2000. Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. Journal of Avian Biology 31: 583-587.
- Hanners, L. A. and S. R. Patton. 1985. Sexing Laughing Gulls using external measurements and discriminant analysis. Journal of Field Ornithology 56: 158-164.
- Harris, M. P. 1971. Ecological adaptations of moult in some British gulls. Bird Study 18: 113-118.
- Haukioja, E. 1971. Processing moult card data with reference to the Chaffinch *Fringilla coelebs*. Ornis Fennica 48: 25-32.
- Hedenström, A. 1998. The relationship between wing area and raggedness during moult in the Willow Warbler and other passerines. Journal of Field Ornithology 69: 103-108.
- Hedenström, A. and S. Sunada. 1999. On the aerodynamics of moult gaps in birds. Journal of Experimental Biology 202: 67-76.
- Heldbjerg, H. 2001. Migration and survival of Black-headed Gulls *Larus ridibundus* ringed as chicks in Denmark. Dansk Ornithologisk Forenings Tidsskrift 95: 28-35.
- Holmgren, N., H. Ellegren and J. Petterson. 1993. The adaptation of moult pattern in migratory Dunlins *Calidris alpina*. Ornis Scandinavica 24: 21-27.
- Ingolfsson, A. 1970. The moult of remiges and rectrices in Great Black-backed Gulls *Larus marinus* and Glaucous Gull *L. hyperboreus* in Iceland. Ibis 112: 83-92.
- Kjellén, N. 1994. Molt in relation to migration in birds—a review. Ornis Svecica 4: 1-24.
- Lindström, Å., G. H. Visser and S. Daan. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66: 490-510.
- Makatch, W. 1952. Die Lachmowe. Geest und Portig, Leipzig.
- Malling Olsen, K. 1993. Sträcket av måsar och tärnvor vid Falsterbo sommaren och hösten 1991 och 1992. Anser 32: 253-262.
- Malling Olsen, K. 2004. Gulls of Europe, Asia and North America. Christopher Helm, London.
- Meissner, W. 2002. Primary moult in the Kittiwake (*Rissa tridactyla*) on Bear Island (Bjørnøya). Ornis Norvegica 25: 49-51.
- Meissner, W. and S. Bzoma. 2005. Sexing of adult Black-headed Gulls *Larus ridibundus* in the breeding season based on biometric characters. Notatki Ornitológiczne 46: 35-40 (In Polish with English summary).
- Meltofte, H. 1993. The significance of the southern Baltic as a moulting area for gulls. Proceedings of the 6th Conference on the Study and Conservation of Migratory Birds of the Baltic Basin, Pruchten.
- Michno, B. 1986. The migration of Black-headed Gulls *Larus ridibundus* breeding in Poland. Vår Fågelvärld, Supplement 11: 141-146.
- Morton, G. A. and M. L. Morton. 1990. Dynamics of postnuptial molt in free-living mountain White-crowned Sparrows. Condor 92: 813-828.
- Newton, I. 1967. Feather growth and moult in some captive finches. Bird Study 14: 10-24.
- Palomares, L. E., B. E. Arroyo., J. Marchamalo, J. J. Sainz and B. Voslamber. 1997. Sex- and age-related biometric variation of Black-headed Gulls *Larus ridibundus* in Western European populations. Bird Study 44: 310-317.
- Senar, J. C., J. Domènech and F. Uribe. 2002. Great tits (*Parus major*) reduce body mass in response to wing area reduction: a field experiment. Behavioral Ecology 13: 725-727.
- Serra, L. 2001. Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*. Journal of Avian Biology 32: 377-380.
- Serra, L., N. Baccetti, G. Cherubini and M. Zenatello. 1998. Migration and moult of Dunlin *Calidris alpina* wintering in the central Mediterranean. Bird Study 45: 205-218.
- Smith, R. D. 1988. Age and sex-related differences in biometrics and moult of Kittiwakes. Ringing and Migration 9: 44-48.
- StatSoft, Inc. 2001. STATISTICA (data analysis software system), Version 6. www.statsoft.com.
- Stresemann, E. 1971. Über das Einsetzen der Handschwinger-Mauser bei Möwen und seine Auslösung. Vogelwarte 26: 227-232.
- Summers, R. W., L. G. Underhill, M. Nicoll, K-B. Strann and S. Ø. Nilsen. 2004. Timing and duration of moult in three populations of Purple Sandpipers *Calidris maritima* with different moult/migration patterns. Ibis 146: 394-403.
- Swaddle, J. P. and M. S. Witter. 1997. The effects of moult on the flight performance, body mass, and behavior of European Starlings (*Sturnus vulgaris*): an experimental approach. Canadian Journal of Zoology 75: 1135-1146.
- Torlaschi, C., P. Gandini, E. Frere and R. M. Peck. 2000. Predicting the sex of Kelp Gulls by External measurements. Waterbirds 23: 518-520.
- Vandenbulcke, P. 1989. *Larus argentatus* ssp. en *Larus cachinnans (michahellis)* aan de Belgische kust. Herkomst en verloop van de handpenruï. De Giervalk 79: 3-29.
- Verbeek, N. A. M. 1977. Timing of primary moult in adult Herring Gulls and Lesser Black-backed Gulls. Journal für Ornithologie 118: 87-92.
- Viksne, J. A. 1968. The structure of the nesting population of the Black-headed Gull in the coastal lakes of Latvia. Pages 207-228 in Ecology of waterfowl of Latvia. Ornithological Study 5 (H. A. Mihelsons and J. A. Viksne, Eds.).
- Walters, J. 1978. The primary moult in four gull species near Amsterdam. Ardea 66: 32-47.
- Walters, J. 1982. Completion of primary moult in the Black-headed Gull *Larus ridibundus*. Bird Study 29: 217-220.
- Wernham, C., M. Toms, J. Marchant, J. Clark, G. Siriwardena and S. Baillie (Eds.). 2002. The Migration Atlas: Movements of the Birds of Britain and Ireland. T.&A.D. Poyser, London.
- Zenatello, M., L. Serra, and N. Baccetti. 2002. Trade-offs among body mass and primary moult patterns in migrating Black Terns *Chlidonias niger*. Ardea 90: 411-420.