

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/8263081>

Reproductive success in presenescent common gulls (*Larus canus*): The importance of the last year of life

Article in *Proceedings of the Royal Society B: Biological Sciences* · November 2004

DOI: 10.1098/rspb.2004.2832 · Source: PubMed

CITATIONS

51

READS

31

1 author:



[Kalev Rattiste](#)

Estonian University of Life Sciences

16 PUBLICATIONS 283 CITATIONS

SEE PROFILE

Reproductive success in presenescent common gulls (*Larus canus*): the importance of the last year of life

Kalev Rattiste^{1,2}

¹*Institute of Zoology and Botany of the Estonian Agricultural University, Riia 181, Tartu 51014, Estonia (kratt@zbi.ee)*

²*Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE 752 36, Uppsala, Sweden (kalev.rattiste@ebc.uu.se)*

Survival selection against individuals of inferior quality (measured as breeding success) has been proposed to account for the increase in average reproductive success with advancing age in presenescent birds. This so-called selection hypothesis relies on quality-dependent survival. In the present breeding performance study of common gulls, *Larus canus*, this assumption was not verified. In particular, omitting the last breeding year from the analysis resulted in the disappearance of the correlation between breeding success and survival. A positive correlation in the full dataset was thus solely based on the poor breeding success of ultimate breeders. Indeed, presenescent individuals were shown to have a specifically low breeding success in their terminal breeding event. The poor success of ultimate breeders thus reflects an abruptly declined condition rather than the birds' overall quality. A comparison of the survival of poor and good performers, involving last-time breeders, thus needs not to be a proper test of the selection hypothesis. Longitudinal analysis revealed a steady increase of individual breeding success until the tenth breeding year. The results suggest that an increase of breeding success with age often found in cross-sectional analyses is primarily a result of age-related improvements of competence and/or increased reproductive effort.

Keywords: age-related reproductive success; survival; terminal breeding event; selection hypothesis; common gull; *Larus canus*

1. INTRODUCTION

The relationship between individual experience/age and reproductive success in birds is well documented (see reviews in Ryder 1981; Clutton-Brock 1988; Saether 1990). Generally, reproductive performance increases with age during the first reproductive years, stabilizes at middle age and sometimes declines in old age as an expression of senescence. A multitude of explanations have been proposed for the increase of mean reproductive success in young individuals. Forslund & Pärt (1995) classified these explanations in three major groups: (i) progressive appearance or disappearance of phenotypes (the selection and delayed breeding hypotheses); (ii) age-related improvements of competence (the breeding experience and constraint hypotheses); and (iii) optimization of reproductive effort (the restraint hypothesis). These hypotheses are not mutually exclusive and may act in concert to create an increase in reproductive performance with age (Wooller *et al.* 1990; Forslund & Pärt 1995).

The selection hypothesis (Curio 1983; Nol & Smith 1987; Newton 1989) ascribes the better performance of older individuals to an increased proportion of high quality birds in older age classes. This is a result of lower survival of inferior quality breeders. Thus, here the increase in performance is observable only within a cohort, and not attributable to individuals. The hypothesis assumes that individuals differ in phenotypic ('average lifelong') quality, which affects both their breeding success (and hence can be measured in terms of it) and their survival prospects. It is predicted that as a result of survival selection, birds of higher quality will have longer lifespans. In other words, the hypothesis states that, at any age, birds with a long

lifespan have better breeding success than birds with intermediate and short lifespans. If there is no selection, the annual breeding success of birds with different lifespans will not differ. These predictions hold, irrespective of whether individual breeding success is stable or changes with age.

Forslund & Pärt (1995) claim that the selection hypothesis can be confirmed by finding a positive relationship between reproductive performance and subsequent survival, or alternatively, by comparing the breeding success of birds surviving and not surviving to the next breeding season. Although several studies have shown differential survival for good and poor performers (e.g. Coulson & Porter 1985; Nol & Smith 1987; McCleery & Perrins 1988; Birkhead & Goodburn 1989; Wooller *et al.* 1990; Smith 1993; Laaksonen *et al.* 2002), the selection hypothesis is not supported in most species examined (Forslund & Pärt 1995; Martin 1995).

However, the proposed tests may suffer from a methodological problem. In particular, these tests necessarily rely on estimates of breeding success in the terminal breeding occasion for non-survivors. By contrast, the focal breeding occasion is not the ultimate one for survivors. If the breeding performance of last time breeders is reduced compared with previous breeding events, there is a risk of systematic error, because performance in the ultimate year of life may not reflect an individual's overall quality. For example, Coulson & Fairweather (2001) showed that kittiwakes (*Rissa tridactyla*), irrespective of the bird's age, achieved a lower breeding performance in their terminal breeding events. This suggests that there was a decline in their condition, which presumably led to, or contributed to, their

death after the breeding season. If this phenomenon is widespread, the conventionally used approach will examine the dependence between the individual's worsened condition and subsequent survival rather than reveal the actual relationship between the birds' overall quality and survival. To overcome this problem, the assessment of the selection hypothesis should not involve ultimate breeders. This would allow us to test whether individuals of inferior general quality (i.e. poor performers) have a lower probability of survival than birds of higher quality.

Using long-term performance and survival data on common gulls (*Larus canus*), I compare the breeding success of equally experienced birds in their ultimate and penultimate years of life, to show that presenescent individuals have a considerable decline in the breeding success in the terminal breeding event. I test the selection hypothesis by comparing survival of poor and good performers, and demonstrate that if the terminal breeding event is omitted from the dataset, there is no clear relationship between breeding success and survival. Furthermore, using a longitudinal analysis, I confirm the absence of survival selection against individuals of inferior quality, by showing that there is no difference in the annual breeding success in birds with different reproductive lifespans. This result holds only when the terminal breeding events are ignored in the analysis. Moreover, I point out that the breeding success of presenescent birds increases steadily until their last year of life. I conclude that the increase of breeding success with age, often found in cross-sectional analyses, is primarily a result of age-related improvements of individual competence and/or increased reproductive effort.

2. MATERIAL AND METHODS

(a) *Study species and breeding data*

Common gulls are monogamous colonial long-lived seabirds with a fixed clutch size of three eggs. Our previous studies have shown that they start to breed at the age of 3–4 years and only 10% of all eggs produce recruits (Rattiste & Lilleleht 1986, 1987). Typically, 50% of males and 10% of females return to breed in their natal colony. Breeders are highly faithful to their colony and less than 3% of them change colony between years, moving mostly to neighbouring colonies. On average, common gulls breed for 5–6 years, but oldest birds in the study area have bred for 26 years. Adult birds are considered presenescent until the eleventh breeding year because their breeding success does not start to decline until this age (figures 2 and 3). Annual survival of adult birds is 86–93% (Rattiste & Lilleleht 1995), 20% of common gulls breed for more than 10 years.

The main material of the present study was collected in 1968–1983 and 1986–2002 on three offshore islets in the Matsalu Nature Reserve, Estonia (58°46' N, 23°26' E). During this period, 235–423 pairs of common gulls bred in these colonies. To collect demographic data, adult birds were caught, sexed and individually marked both with metal and plastic rings at their first breeding attempt. This enabled their recognition without catching in later years. The possible effect of ring losses on the results is negligible as worn rings were replaced in time. On average, 94% of breeders were identified every year and nearly all chicks were ringed in their first day of life.

The analyses are based on birds breeding in 1968–1994 but not observed later. Their recruits were registered until 2002 to ensure complete data on breeding success. Birds known to have bred

previously outside the study area and permanent emigrants were excluded from the analysis. The risk of underestimation of a bird's experience and lifespan is thus greatly reduced. Experience was defined as number of breeding years since first breeding, and reproductive lifespan as total number of breeding years during the bird's lifetime. For illustration, birds were divided into five life-span categories: having bred only once, 2–3, 4–6, 7–11 and more than 11 years, respectively. Annual breeding success was assessed according to the number of recruits established either within the study area or outside it. Most of the successful breeders produced one recruit, and only 7.6% and 0.4% of them had two and three recruits, respectively. Hence, breeding success was considered a binomial variable, i.e. either successful or unsuccessful. Breeding years were classified into two types according to the values of the chicks' mortality: (i) favourable (mortality less than 14%; 1968–1970, 1973–1975, 1981, 1987–1989, 1992 and 1994); and (ii) unfavourable (mortality more than 14%; 1971, 1972, 1976–1980, 1982, 1983, 1986, 1990, 1991 and 1993).

(b) *Statistical analyses*

To examine whether individual condition, and hence breeding success, declines before a bird's death, the breeding success in the penultimate and ultimate years of life were compared. However, a direct comparison of an individual's breeding success in its ultimate and penultimate years of life may be misleading. In particular, if breeding success is year and age dependent, the comparison should involve years of similar favourableness and individuals of the same age. Hence, the breeding success of equally experienced individuals in the ultimate and penultimate breeding events (1604 and 1200 cases respectively), belonging to the same type of breeding year, was compared. Similarly, the breeding success in the penultimate year of life and in the year before it (980 cases) was compared. For this analysis, the SAS CATMOD procedure (Stokes *et al.* 1995) was used to fit the logistic regression model to relate breeding success to experience and its squared value (treated as continuous variable), breeding event (ultimate, penultimate, year before the penultimate one), sex and the type of year. The last three variables were considered categorical.

The dependence of survival on breeding success (unsuccessful versus successful) was examined both in the conventional and in the alternative way. The conventional approach compares the survival of poor and good performers to the next year. Here, the dataset (set A, figure 1 and table 1) involves three groups of breeders: (i) survivors in good condition (breeders a, b and c; figure 1); (ii) non-survivors in good condition during their ultimate breeding season (breeders d; figure 1); and (iii) non-survivors in poor condition during their ultimate season (breeders e; figure 1). In the alternative approach, the dataset was modified by omitting non-survivors to avoid the influence of the terminal breeding event. Thus, the new dataset (set B; figure 1 and table 1) included only individuals in good condition, all surviving to the next year (breeders a, b and c; figure 1). Therefore, in this dataset, the survival to the next year but one of successful and unsuccessful breeders was compared. A χ^2 test was used to compare survival of successful and unsuccessful performers. Tests were performed separately for each age class, because survival is age dependent (Rattiste & Lilleleht 1995).

The dependence of breeding success on individual experience and reproductive lifespan was studied in a longitudinal analysis. The SAS MIXED procedure and GLIMMIX macro (Litell *et al.* 1996) were used to fit a generalized linear mixed model of repeated measurements with binomial response. The factors sex, reproductive lifespan and experience were considered fixed, while the factor

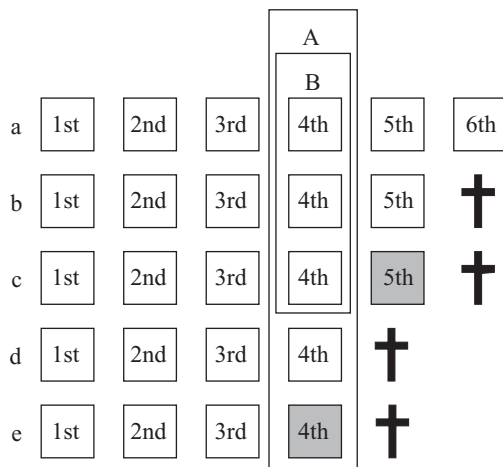


Figure 1. The two datasets for testing the survival selection hypothesis. Rows represent individual life histories, columns are breeding years. Crosses indicate death, shading points to premortal condition during the ultimate breeding season. A and B are the datasets used in the conventional and alternative tests, respectively.

individual was considered random. Both unstructured and autoregressive covariance types were used to model the covariance structure of breeding success within individuals. Breeding success was modelled as a quadratic function of experience to get smoothed trends over time. To examine the effect of the terminal breeding event, two datasets were used: (i) complete data including the terminal breeding events (8464 breeding occasions of 1794 individuals); and (ii) incomplete data with the terminal breeding events omitted from the life histories (6860 breeding occasions of 1443 individuals).

3. RESULTS

Breeding success of common gulls increased with experience until the tenth breeding year and started to decline thereafter (logistic regression; Wald test; experience: $\chi^2 = 22.25$, d.f. = 1, $p < 0.0001$; experience²: Wald $\chi^2 = 11.74$, d.f. = 1, $p = 0.0006$; figure 2). In addition, equally experienced individuals until their eighth breeding year had lower breeding success in the ultimate breeding event than in the penultimate one, whereas in older birds this difference disappeared (ultimate versus penultimate: Wald $\chi^2 = 10.44$, d.f. = 1, $p = 0.001$; experience \times breeding event interaction: Wald $\chi^2 = 4.07$, d.f. = 1, $p = 0.043$; figure 2). These effects did not differ between sexes (all two-factor interactions of sex non-significant). As expected, in favourable years the breeding success was higher than in unfavourable ones (type of year: Wald $\chi^2 = 28.94$, d.f. = 1, $p < 0.0001$), with no difference in the qualitative effects discussed above (two-factor interactions of the type of year non-significant; figure 2). However, the breeding success of equally experienced individuals in their penultimate year of life and in the year preceding it did not differ (both the effect of breeding event and its interaction with experience non-significant). Thus, the breeding success of presenescent common gulls declines drastically before their death, suggesting a comparatively sudden decline in their condition. So, the low reproductive success in the terminal breeding event reflects rather a specific premortal decline in condition than individual's overall quality.

Table 1. The survival of common gulls depending on their breeding success. (In dataset A, the terminal breeding events were included, but omitted in dataset B.)

reproductive age (years)	dataset A						dataset B					
	unsuccessful birds			successful birds			unsuccessful birds			successful birds		
	n	survival rate	χ^2_1	n	survival rate	p	n	survival rate	χ^2_1	n	survival rate	p
1	1191	0.772	5.27	53	0.906	0.022	919	0.852	0.13	48	0.833	n.s.
2	872	0.827	0.09	51	0.843	n.s.	721	0.849	2.04	43	0.767	n.s.
3	700	0.813	4.05	60	0.917	0.044	569	0.835	0.10	55	0.812	n.s.
4	606	0.828	0.27	66	0.803	n.s.	502	0.827	1.24	53	0.887	n.s.
5	540	0.822	2.45	61	0.902	n.s.	444	0.885	0.02	55	0.891	n.s.
6	460	0.876	4.68	76	0.961	0.030	403	0.779	0.99	73	0.726	n.s.
7	408	0.753	0.32	65	0.785	n.s.	307	0.772	0.53	51	0.726	n.s.
8	317	0.735	5.21	40	0.900	0.023	233	0.768	0.36	36	0.722	n.s.
9	243	0.716	0.33	26	0.769	n.s.	174	0.787	3.01	20	0.950	n.s.
10	185	0.773	0.86	27	0.852	n.s.	143	0.797	0.10	23	0.826	n.s.

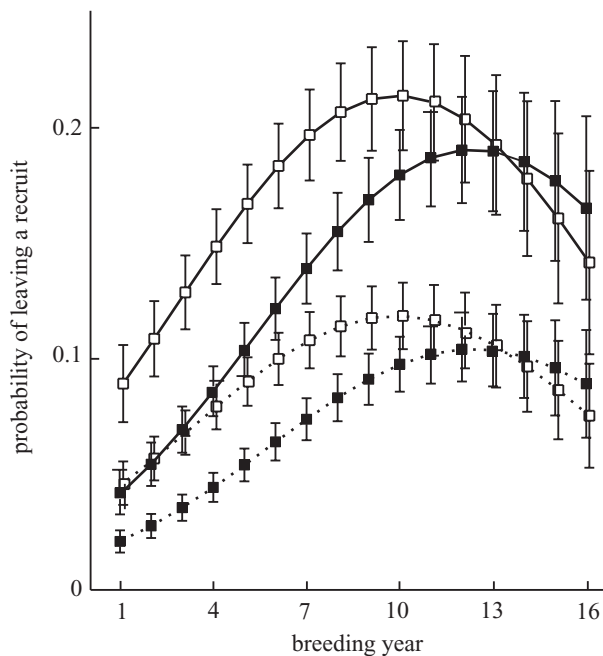


Figure 2. The breeding success of common gulls (predicted values from the model) in relation to bird's experience, type of breeding year (solid lines, favourable; dotted lines, unfavourable) and breeding event (filled squares, ultimate year of life; open squares, penultimate year of life). Error bars represent ± 1 s.e.m., sexes pooled.

There was a pronounced trend for successful breeders to enjoy a higher probability of survival to the next year in comparison with unsuccessful breeders, if the dataset includes terminal breeding events (table 1, dataset A). This difference was observed in 9 out of 10 age classes (binomial test: ratio 9 : 1 statistically different from 1 : 1, $p = 0.02$), being significant in four cases. When terminal breeding events were omitted, this trend disappeared (unsuccessful breeders had higher survival in six cases and successful breeders in four cases, all comparisons non-significant; table 1 dataset B). Hence, a positive correlation in the full dataset was solely based on the poor breeding success of terminal breeders and there is no convincing proof for differential survival among poor and good performers.

In the longitudinal analysis, the breeding success of common gulls increased until the tenth breeding year and started to decline thereafter (complete dataset; experience: $F_{1,6668} = 37.01$, $p < 0.0001$; experience²: $F_{1,6668} = 22.86$, $p < 0.0001$; figure 3a). Reproductive lifespan had a considerable effect on breeding success when the complete dataset was used ($F_{4,1789} = 2.72$, $p = 0.028$; figure 3a). Birds with longer lifespans had higher breeding success than short-lived individuals. However, this effect is mainly for to birds which bred only once during their life. When the terminal breeding events were omitted from the individuals' life histories, the effect of the reproductive lifespan on breeding success disappeared (incomplete dataset; reproductive lifespan: $F_{3,1439} = 0.03$, $p > 0.9$; figure 3b). In both analyses, the autoregressive covariance type was assumed as it had a better fit to the data than the unstructured covariance type (complete data: Akaike's Information Criterion (AIC) = 44 670 versus AIC = 44 797; incomplete data: AIC = 35 648 versus AIC = 35 700).

4. DISCUSSION

The assumptions of the selection hypothesis explaining the increase of mean reproductive performance with age could not be verified. In particular, common gulls with lower breeding success were shown not to have lower survival. There is thus no evidence of progressive elimination of poor breeders from the population. However, this result was obtained only when the terminal breeding events were omitted from the dataset. This discrepancy can be explained if one assumes that the low breeding success of premortal individuals is based on specific circumstances not associated with bird's overall quality. Moreover, one can expect that poor breeders have a lower burden of parental care and can therefore invest more into self-maintenance. This may, at least partly, explain the absence of survival selection on poor and good performers. An important implication of this is that lifespan itself could not be a good measure of individual's quality.

Longitudinal analysis led to qualitatively similar conclusions. Birds with different lifespans did not differ in their breeding success, when the terminal breeding event was omitted from their life histories. Thus, the increase in the average reproductive success with advancing age in pre-senescent common gulls cannot be explained by selection effects. Indeed, the longitudinal analysis revealed a steady increase in performance until the tenth breeding year, and consequently the increase in the average breeding success must be ascribed primarily to an age-related improvements of individual competence and/or increased reproductive effort. Life-history theory predicts increased reproductive effort (hence, increased breeding success) in long-lived animals when their residual reproductive value decreases (Williams 1966). As the mortality of common gulls starts to increase after the sixth breeding year, their residual reproductive value will decrease and they should allocate more resources to reproduction.

An important implication of the results of the present study is methodological. If the terminal breeding event is exceptional in terms of breeding success, it cannot be used to characterize an individual's general quality, because this low success reflects rather the individual's worsened condition than its quality. Thus, one may succeed in different conclusions about differential survival of poor and good quality individuals, depending on whether datasets do or do not include the terminal breeding events. More generally, this study emphasizes the advantage of longitudinal analyses over the cross-sectional ones.

The present study suggests that common gulls in good current condition do not differ in their prospects of subsequent survival depending on their breeding success (table 1, dataset B). However, one can expect that if a bird is already in a poor condition during the breeding season (ill, injured, starved), both its breeding success and survival probability will decrease. Clearly, in a conventional approach, the outcome of the test depends on the proportion of such birds among non-survivors. This can explain the inconsistent results of earlier studies (Forslund & Pärt 1995; Martin 1995). If the proportion of birds in poor condition during the breeding season is low, no substantial differences will be found. By contrast, if this proportion is considerable, the test will result in a significant positive relationship between breeding success and survival. A previous study (Rattiste & Lilleleht 1995)

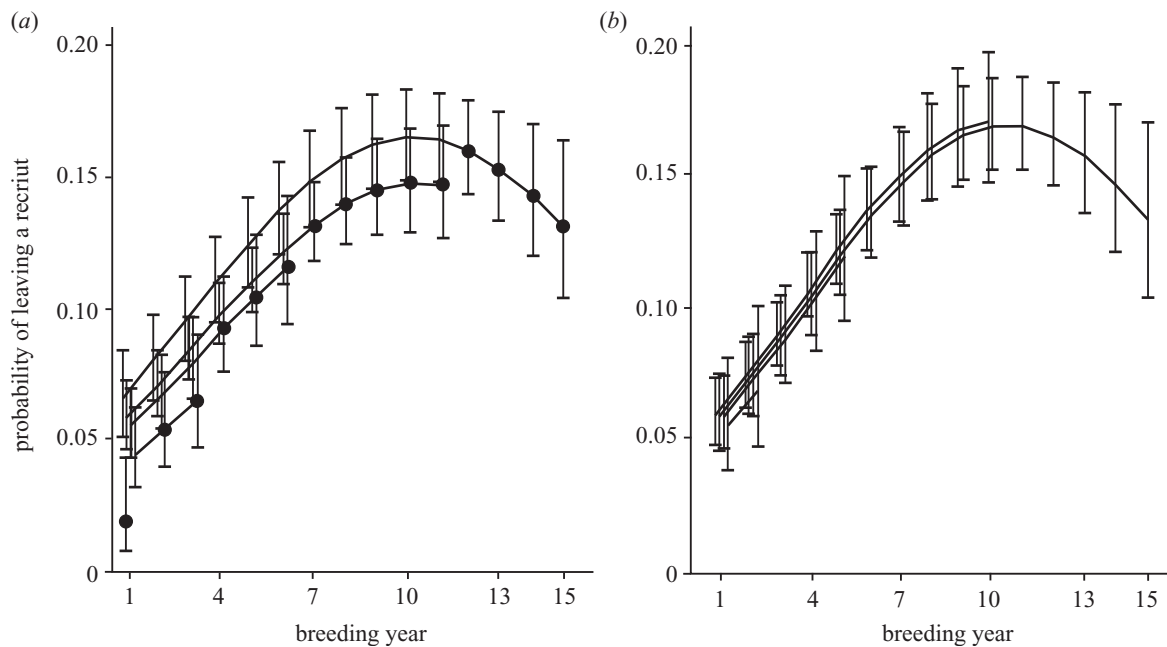


Figure 3. Breeding success of common gulls (predicted values from the model) in relation to the bird's prior breeding experience and reproductive lifespan according to whether life histories included terminal breeding events (a) or not (b). Curves represent the five lifespan categories (see § 2). Error bars indicate 95% confidence intervals, filled circles point to age groups containing the terminal breeding events, sexes pooled.

showed that the annual survival of common gulls depends mainly on winter severity. Thus, in years with a cold and normal winter, birds falling into poor condition after the breeding season make up a higher proportion of the non-survivors than in years with a rather mild winter. As a consequence, in the conventional approach, the results of the test to a great extent may depend on the winter climate during the study period.

In presenescent birds the reproductive success in the terminal breeding event was significantly reduced in comparison with the penultimate one, whereas senescent individuals did not suffer a sharp decline in performance (figure 2). This difference may be explained by a difference in the nature of premortal condition in birds of different age. Unfortunately, data are extremely scarce on causes of death (and hence, premortal condition) for natural bird populations. Ricklefs (1998, 2000) claimed that in presenescent birds externally induced death factors predominate such as predation, injuries, contagious disease, parasites, starvation and weather-related stress, whereas in senescent individuals internal death factors prevail, like physiological deterioration, vascular disease, cancer and autoimmune disease. Moreover, by comparing the mortality patterns of natural and captive bird populations, Ricklefs (2000) has concluded that birds in natural populations maintain a high level of physical fitness into old age and do not become more vulnerable to extrinsic mortality factors with increasing age. One may expect that the above mentioned external factors cause a noticeable decrease in a bird's physical condition, hence in its ability to defend its nesting territory and provide parental care. This may easily lead to complete reproductive failure. However, physiological deterioration, characteristic of senescent birds, presumably affects first of all the quality of offspring (smaller and lower-quality eggs/chicks), and to a lesser

extent adult bird's physical condition. As a result, senescent breeders should not suffer so often from complete breeding failure. These predictions can be tested by comparing predation rate, the quality of the eggs and prehatching mortality between these two age groups.

I am grateful to S. Onno for his pioneering work on common gulls, to the research team members and all the voluntary field assistants for their huge contribution in data gathering during all the years, to J. Brommer, H. van der Jeugd, T. Tammaru and S. Ulfstrand for discussions and helpful criticism on the manuscript, and to A. Vanatoa for technical assistance. K. T. Pedersen provided with plastic rings. Funding for this work was provided by target financing from the Ministry of Science and Education of Estonia.

REFERENCES

- Birkhead, T. R. & Goodburn, S. F. 1989 Magpie. In *Lifetime reproduction in birds* (ed. I. Newton), pp. 173–182. London: Academic.
- Clutton-Brock, T. H. (ed.) 1988 *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press.
- Coulson, J. C. & Fairweather, J. A. 2001 Reduced reproductive performance prior to death in the black-legged kittiwake: senescence or terminal illness? *J. Avian Biol.* **32**, 146–152.
- Coulson, J. C. & Porter, J. M. 1985 Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* **127**, 450–466.
- Curio, E. 1983 Why do young birds reproduce less well? *Ibis* **125**, 400–404.
- Forslund, P. & Pärt, T. 1995 Age and reproduction in birds: hypotheses and tests. *Trends Ecol. Evol.* **10**, 374–378.

- Laaksonen, T., Korpimäki, E. & Hakkarainen, H. 2002 Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. *J. Anim. Ecol.* **71**, 23–31.
- Litell, R. C., Milliken, G. A., Stroup, W. W. & Wolfinger, R. D. 1996 *SAS system for mixed models*. Cary, NC: SAS Institute Inc.
- McCleery, R. H. & Perrins, C. M. 1988 Lifetime reproductive success of the great tit, *Parus major*. In *Reproductive success: studies of individual variation in contrasting breeding systems* (ed. T. H. Clutton-Brock), pp. 136–153. University of Chicago Press.
- Martin, K. 1995 Patterns and mechanisms for age-dependent reproduction and survival in birds. *Am. Zool.* **35**, 340–348.
- Newton, I. 1989 Synthesis. In *Lifetime reproduction in birds* (ed. I. Newton), pp. 279–296. London: Academic.
- Nol, E. & Smith, J. N. M. 1987 Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *J. Anim. Ecol.* **56**, 301–313.
- Rattiste, K. & Lilleleht, V. 1986 Some aspects of the demography of the common gull *Larus canus* in Estonia. *Vår Fågelvärld* **11**(Suppl.), 179–186.
- Rattiste, K. & Lilleleht, V. 1987 Population ecology of the common gull *Larus canus* in Estonia. *Ornis Fennica* **64**, 25–26.
- Rattiste, K. & Lilleleht, V. 1995 Survival rates of breeding common gulls in Estonia. *J. Appl. Stat.* **22**, 1057–1062.
- Ricklefs, R. E. 1998 Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *Am. Nat.* **152**, 24–44.
- Ricklefs, R. E. 2000 Intrinsic aging-related mortality in birds. *J. Avian Biol.* **31**, 103–111.
- Ryder, J. P. 1981 The influence of age on the breeding biology of colonial nesting seabirds. In *Behavior of marine animals: current perspectives on research*, vol. 4 (ed. J. Burger, B. L. Olla & H. E. Winn), pp. 153–168. New York: Plenum.
- Saether, B. 1990 Age-specific variation in the reproductive performance of birds. In *Current ornithology*, vol. 7 (ed. D. M. Power), pp. 251–283. New York: Plenum.
- Smith, H. G. 1993 Parental age and reproduction in the marsh tit *Parus palustris*. *Ibis* **135**, 196–201.
- Stokes, M. E., Davis, C. S. & Koch, G. G. 1995 *Categorical data analysis using the SAS system*. Cary, NC: SAS Institute Inc.
- Williams, G. C. 1966 *Adaptation and natural selection: a critique of some evolutionary thought*. Princeton University Press.
- Wooller, R. D., Bradley, J. S., Skira, I. J. & Serventy, D. L. 1990 Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. *J. Anim. Ecol.* **59**, 161–170.