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Age-effects on breeding phenology and success of Common Guillemots *Uria aalge* at a North Sea colony

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Capsule Common Guillemots *Uria aalge* show delayed breeding and marked age-related changes in reproductive success consistent with improved performance with experience.

Aims To determine age of first breeding and age-related effects on breeding phenology and success of Common Guillemots.

Methods Resighting data from a long-term colour-ringing study of Common Guillemot chicks were combined with observations of breeding phenology and success to follow the recruitment process, breeding phenology and success of 62 birds at a major North Sea colony over a 30 year period.

Results The median age of first breeding of Common Guillemots was 6.6 years. There were no detectable costs of first breeding on return rates or the likelihood of breeding the next season but first time breeders bred later and less successfully. Age of first breeding and lifetime breeding success both varied among individuals but there was no clear optimal age of first breeding and early first breeding was not associated with higher lifetime breeding success.

Conclusions Common Guillemots in the Isle of May population delayed breeding for 3-4 years beyond physiological maturity. The marked increase in breeding success with age was consistent with improved performance with experience rather than selection for higher quality individuals. Findings from this study will inform population models by providing improved estimates of age of first breeding and age-related changes in reproductive performance.

Age of first breeding and subsequent decisions on whether or not to breed in a given season are key components of life-time reproductive success and can be influenced by both intrinsic and extrinsic factors (Newton 1989, Stearns 1992, Viallefont *et al.* 1995). Age of first breeding is also an essential prerequisite for the formulation of population models (Lebreton *et al.* 1992). However, the parameter is often underestimated, particularly in studies where the duration of data collection is short relative to the potential lifespan of the study species (Dillingham *et al.* 2012 and references therein). The best method of obtaining an accurate estimate of the age of first breeding is to follow cohorts of individually marked chicks until all surviving members have recruited into the breeding population. Seabirds are characterised by high survival rates (typically >90% in adults) and deferred maturity (typically 2 – 7 years, but >10 years in albatrosses and petrels) (Schreiber & Burger 2001). Thus age of first breeding and age-related breeding effects can potentially play a key role in seabird population dynamics (Pardo *et al.* 2013) but collecting the requisite data can be very time consuming.

The Common Guillemot *Uria aalge* (hereafter Guillemot) is one of the most numerous and well-studied seabirds in the North Atlantic and North Pacific (Cramp 1985, Gaston & Jones 1998, Ainley *et al.* 2002). Survival rates are high (90-94% per annum in adults; Meade *et al.* 2013, Lahoz-Monfort *et al.* 2014) and the age of first breeding is typically given as 5-7 years (Birkhead & Hudson 1977, Harris *et al.* 1994, Ainley *et al.* 2002). However, Guillemots have been recorded living up to over 42 years in the wild so there is plenty of scope for very protracted prebreeding periods (EURING 2014). To our knowledge, no previous study has investigated changes in Guillemot breeding performance in relation to age and breeding experience using known age birds. However, estimates based on birds ringed as breeding adults and using years since ringing or years prior to death as proxies for age, suggest that breeding success increases over the first 10 years and, along with survival, declines in the oldest individuals (Crespin *et al.* 2006, Reed *at al.* 2008). In the present study we used long-term data on individually marked Guillemot chicks at a North Sea colony to elucidate (1) the age of first breeding in this population, (2) the process of recruitment and (3) age and experience-related changes in the timing of breeding and breeding success. For a subsample of these birds where we had complete breeding histories from recruitment to death, we were also able to calculate the first estimates of lifetime breeding success for this species.

METHODS

Fieldwork was carried out between 1983 and 2015 on the Isle of May, Firth of Forth, southeast Scotland (56° 11’N, 2° 33’W). Over the study period the Guillemot breeding population varied between 10,-20,000 pairs. Each year between 1983 and 2012, an average of 246 ± se 10 chicks were marked with long-lasting hard metal rings on one leg and a colour-ring with a unique three digit alpha-numeric inscription on the other leg. Searches for these birds were made throughout the colony each subsequent summer up to and including 2015 to record when they were first seen back on the Isle of May and to follow the process of recruitment into the breeding population (see later). Concurrently, a detailed study was undertaken of c.700 pairs of Guillemots breeding in front of five permanent hides (details in Harris & Wanless 1988). Breeding sites were numbered on photographs and were checked at least three times a day during the laying period and at least once a day for the rest of the breeding season. All colour-ringed birds recorded in these areas were followed in detail so that for each individual that had been ringed as a chick and which subsequently recruited into these areas we knew: (a) the year of hatching, (b) when the bird was first seen anywhere on the Isle of May, (c) when it was first seen where it later bred, (d) its sex from observations of copulations (unknown for six individuals), (e) its age when it (or its mate) first laid an egg, (f) the date of laying of the single egg by the ringed bird (or its mate) relative to other pairs in the same study area (Wanless & Harris 1988; unknown for the few birds breeding at sites that were difficult to see clearly) and (g) whether or not it bred successfully (defined as the male parent accompanied by its chick aged >14 days leaving the site and not returning again that season (Varoujean *et al.* 1979)). Laying date and breeding success of these birds continued to be recorded either until they disappeared, presumably because they had died since Guillemots are extremely faithful to a very small area of the colony once they have bred (Harris *et al*. 1996), or until the study ended. The intensity of observations throughout the study meant that visits and/or breeding attempts by colour-ringed birds were very unlikely to have been missed. The high intensity of observations also enabled return rate of these known-age birds to be used to estimate survival rates from one season to the next.

Bird age was taken as the number of calendar years after ringing (e.g. a chick hatched in 1983 and found breeding in 1988 was five years old). Many of the most recent recruits and a few of the older birds were still alive at the end of the study resulting in records of breeding age and years breeding being right censored. To avoid the potential bias that long-lived birds have higher fitness, thereby leading to spurious positive correlations with age and experience, we used within-subject centring (van de Pol & Wright 2009) to separate within-subject effects (i.e. phenotypically plastic or facultative behavioural responses) from between-subject effects (i.e. evolutionarily fixed behavioural responses based on the individual).

Laying date was standardised (a) relative to the median date within each year for each study area, to allow for annual variation in timing of breeding, and (b) within individuals to their specific mean to allow for birds that bred consistently early or late. The relationship between relative laying date and the number of times that a bird had bred was analysed using a linear mixed model with individual fitted as a random effect.

Breeding success was analysed in relation to age and experience (defined as the number of years since an individual had first bred where 1 = year of first breeding) using a Generalized Linear Mixed Model (GLMM), where the dependent variable was binary (success or failure), individual and calendar year were random terms, and the fixed effects were either bird age or the number of years since first breeding. In 29 instances (5.8% of 502 records) involving 16 individuals, a bird was known to be alive but not definitely proved to have bred and in these cases the bird was scored as being unsuccessful in these years. To check that the right censored data did not bias the results, the analysis of the effect of age or the number of breeding events on breeding success was repeated after distinguishing three different ‘phenotypes’ of birds (a) last seen when 12 or less years old (the median age of birds when last seen that disappeared before the end of the study), (b) last seen at 13 years or older (median 15.5 years), and (c) still alive at the end of the study (median 15.5 years) regardless of when they had entered the data set. This last group inevitably includes many younger individuals. As previously, both individual and year were fitted as random effects. Models were fitted using GenStat version 17.

RESULTS

Age of first breeding and the recruitment process

Sixty-two colour-ringed birds recruited into in the study areas and all were paired with unringed and therefore unaged mates. The youngest bird bred for the first time at 4 years and the oldest at 11 years (Table 1). Overall, the modal age of first breeding was 6 years (35% of all birds) and the median was 6.6 years. The distribution of age of first breeding did not differ between the two sexes (χ^2 = 5.16, df = 6, *P* > 0.5 after pooling birds aged 10 and 11 years). At the end of the study eight colour-ringed birds were prospecting in the study areas. The oldest was 6 years old so it seems unlikely that there were any older birds still to recruit and thus that Guillemots in this population normally recruited by the time they were 12 years old. Restricting the data to the 1983-2003 cohorts (i.e. birds aged $\geq$12 years at the end of the study), gave a median age of first breeding of 6.7 years (Table 1).

All 62 birds were seen on the Isle of May for several years prior to recruiting into the study areas (Fig. 1). The median ages when they were first seen anywhere in the colony and where they later bred were 3.43 years (range 2-7) and 3.95 years (range 2-7), respectively. The earlier that an individual returned to the Isle of May, and to where it subsequently bred, the younger it was when it first bred (*r* = 0.31, *P* = 0.015 and *r* = 0.32, *P* = 0.010, respectively; both *n* = 62). Guillemots recruiting to a site that was not occupied in the previous year (39% of cases) did so when they were significantly younger than birds replacing birds at previously used sites (61% of cases; median age of recruitment at unoccupied sites = 6.0 years, previously occupied sites = 6.95 years, χ^2 = 7.54, df = 2, *P* = 0.023 after pooling birds aged 4 and 5 years, and 7 to 11 years). The type of site used was not associated with sex (71%, *n* = 28 males recruited to previously occupied sites compared to 57%, *n* = 28 females; χ^2 = 1.24, df = 1, *P* = 0.27).

Excluding the four birds that were first recorded breeding in 2015, 91.4% of birds returned in the season following their first breeding attempt, a value which did not differ significantly from values after subsequent breeding attempts (mean = 85.2%: 95% CI 78.3, 92.0). The frequency of nonbreeding by birds in the year following their first breeding attempt (37.8%, *n* = 53) was identical to the value for years after subsequent breeding events (37.8%, *n* = 424).

Changes in laying date and breeding success with age and experience

Laying date became progressively earlier over the first four breeding years (Exponential regression: $F_{2,435} = 14.78$, $P < 0.001$: Fig. 2) with the advance being most marked between the first and second years (3.4 days). There was no significant difference between the sexes in the advance in laying date with experience ($F_{1,420} = 0.2$, $P > 0.6$). After 12 years of breeding, individuals tended to breed later than in their prime (4-11 years of experience). There were no differences in the slopes of the 'within' individual effect and the 'between' individual effect (Table 2a: -0.995 ± se 1.2), so the effect of experience was not due to the early disappearance of some birds.

The median age of first successful breeding was 7.67 years (Fig. 1; range 6-15 years). Success of four- and five-year-olds was extremely low with only one of 12 attempts resulting in a fledged chick (Fig. 3a). There was no significant difference in the probability of success of the first breeding attempt of Guillemots that recruited to a previously occupied site (32%, *n* = 38) and those that recruited to a site that had been unoccupied the previous season (30%, *n* = 24; $\chi^2 = 0.04$, df = 1, $P = 0.84$).

After accounting for the random effects of individual and year, breeding success increased significantly with both age (Fig. 3a: Wald statistic, $\chi^2 = 11.08$, $P < 0.001$) and years since first breeding (Fig. 3b: Wald Statistic, $\chi^2 = 14.33$, $P < 0.001$). In neither case did the slope of the 'within' individual effect differ significantly from the 'between' individual effect (Table 2b & c: age = 0.0633 ± se 0.0525, years since first breeding = 0.0823 ± se 0.059). Thus there was no evidence that the increase in success with age/experience was due to 'poor quality' individuals dying when relatively young. This is illustrated graphically in Figure 3b which shows that there were no significant differences in the effect of experience between the three phenotype (those disappearing at 12 years or younger, those disappearing at 13 years or older and those still alive in 2015; slopes: Wald statistic 2.04, df = 2, $P > 0.3$; intercepts: Wald statistic 1.08, df = 2, $P > 0.5$).

Breeding success was also higher among individuals breeding earlier in the season, regardless of age and experience (Wald statistic = 15.89, $P < 0.001$). In general birds that were successful laid two days earlier than unsuccessful breeders ($F_{1,433} = 12.18$, $P < 0.001$).

Lifetime breeding success

The number of chicks fledged by the 34 birds that entered and left the population during the study showed considerable variation ranging from nine individuals (26%) failing to fledge any young to one male that fledged 19 chicks from 21 attempts (Fig. 4). The median number of chicks fledged was 3.09. There was no overall relationship between age of first breeding and lifetime breeding success ($r = -0.016$, $P = 0.52$, Fig. 5). The number of chicks fledged by the 28 individuals still alive at the end of the study period ranged 0 – 12 (median 5.5).

DISCUSSION

Compared to breeding success and adult survival, age of first breeding has received much less attention in studies of marine birds and as a consequence minimum rather than mean or median age often has to be used in analyses (Weimerskirch 2002). The pattern of recruitment we recorded over a 30 year period on the Isle of May accorded closely with previous shorter studies at this colony and those elsewhere in the breeding range, with individuals first seen back when they were 2-3 years old, becoming attached to a specific part of the colony when they were 3-5 years old and typically making their first breeding attempt when they were 6-7 years old (Birkhead & Hudson 1977, Halley *et al.* 1995, Lee *et al.* 2008). Only three Guillemots (one male, one female and one unknown sex) were recorded breeding when they were 4 years old. However, in captivity Guillemots have bred (although not successfully) when they were 3 years old (Swennen 1977). Scattered records in the literature suggest that birds in the wild have bred at 3 years but in all these cases there is uncertainty about the validity of the record, e.g. the possibility of allo-parenting by neighbours, and thus definite conformation of free-living Guillemots breeding at 3 years of age is lacking (Wanless & Harris 1985, Harris *et al.* 1994, Lee *et al.* 2008). Our results, therefore, indicate that Guillemots have a delayed onset of reproduction several years beyond the age of physiological maturity.

There appears to be little information on sex-related differences in age of first breeding in seabirds. Among the auks, Gaston and Jones (1998) found that, on average, female Brünnich's Guillemots *U. lomvia* bred when they were one year younger than males. In Common Guillemots the process of recruitment was remarkably similar in the two sexes with no significant differences in the age of first return to the island, the age at which birds moved into the area where they subsequently bred or the age at which breeding first occurred and was first successful. However, the recruitment process was influenced by the type of site a bird recruited to with Guillemots using a site that had not been occupied in the previous season breeding a year earlier than those which first bred at a site that had previously been occupied. To our knowledge this effect does not seem to have been recorded previously in Guillemots. It suggests some sort of social constraint whereby birds need additional time and/or experience to recruit to a site that has recently been bred at by other birds, presumably associated with replacing a bird that had died or evicting the previous owner. Although competition for the best breeding sites in Guillemot colonies is intense (Birkhead 1978), suitable sites on the Isle of May do not appear to be limited since even when the population was declining in the 2000s, new sites continued to be occupied and the colony boundary expanded (Harris *et al.* 1997, personal observations). Given the availability of sites, it is unclear why some Guillemots apparently delay the age of first breeding by recruiting to a previously occupied site rather than using a new one, particularly since there is no difference in breeding success of the first breeding attempt in the two types of site.

Guillemots typically breed annually but individuals sometimes skip a year's breeding (Reed *et al.* 2015). However, in contrast to the situation in the closely related Brünnich's Guillemot and several other species of seabird, the frequency of skipping in Guillemots was not significantly higher the year after first breeding compared to subsequent years (Wooller & Coulson 1977, Ollason & Dunnet 1988, Viallefont *et al.* 1995, Gaston & Hipfner 2000). Similarly, we also found no significant difference in return rates of first time and experienced breeders. Taken together these results suggest that during the study period, costs of the first breeding attempt were not sufficient to reduce subsequent overwinter survival or the likelihood of breeding the following season.

We did, however, find some marked differences in two key components of breeding performance (laying date and breeding success). Thus, first time breeders bred significantly later in the season than those with breeding experience and were less successful. However, in contrast to Brünnich's Guillemots in which breeding became progressively earlier over the first 8 seasons (Hipfner 1997), in Common Guillemots breeding advanced by 3-4 days between the first and second attempt and by a further day in birds breeding 4-11 times. Most Guillemots breeding for the first time failed to rear a chick but thereafter success increased steadily reaching 66% by the 10th attempt and 75% by the 15th attempt. Thus whilst low success in the first year could potentially have been due to poorer environmental conditions later in the season, subsequent improvements in success in the absence of changes in laying date are indicative of intrinsic effects. Experimental studies in European Shags *Phalacrocorax aristotelis* concluded that intrinsic effects were the main reason for lower breeding success in first time breeders (Daunt *et al.* 1999) but this approach would be challenging to carry out on Guillemots and would likely result in many eggs being lost.

In long-lived birds breeding success typically shows an inverse U-shaped relationship with age, increasing during the first few years, then plateauing before declining in the oldest age classes (Newton 1989, Forslund & Pärt 1995). An earlier study of Guillemots on the Isle of May based on birds individually marked as adults and using years since ringing as a proxy for age, found that success improved over the first 9-13 years and then remained stable for the next 6-10 years, before declining after 19 years of breeding (about 25 years of age; Crespin *et al.* 2006). In our smaller sample of known age birds there was no detectable decrease in success in the oldest birds, though some of these were still alive and may not yet have reached senescence since only seven were older than 21 years. Distinguishing whether the improvement with experience is directly due to age-related improvements in breeding performance or is a consequence of lower quality (i.e. less successful birds) having higher mortality and thus disappearing from the population, can be difficult with observational studies. However, the method recently proposed by van de Pol & Wright (2009) provides a powerful way of distinguishing between the two competing hypotheses by comparing 'within' and 'between' individual effects. In the case of Guillemots it indicates that the data are consistent with genuine age-related improvements in performance rather than the selection hypothesis, a conclusion supported by the simpler analysis classifying individuals into three phenotypes.

Estimates of lifetime breeding success in seabirds are rare and we are aware of only one other published value for an auk. Results from the study of Cassin's Auklet *Ptychoramphus aleuticus* by Pyle *et al.* (2001) with a mean value of 3.7 chicks fledged and a range of 0-34 chicks are similar to those for Guillemots. Both studies were carried out when the populations were declining for all or part of the study period and the low values for lifetime breeding success probably reflect that breeding conditions were poor (Harris *et al.* 2015). More recent estimates from the Isle of May when the breeding population has been increasing, suggest that lifetime fledging success has also increased with a median value of at least 5.5 chicks for individuals still alive at the end of the study.

Life history theory predicts that the timing of reproductive events during an individual's life will affect its fitness (Caswell 1982). Starting to breed early can increase the number of reproductive events over an individual's lifetime and thus potentially increase lifetime breeding success, particularly in species with a clutch size of one such as the Guillemot. Although our study was based on a relatively small number of individuals, the intensity of observations gives us confidence that the ages of first breeding and breeding performances recorded reflect the individual variation associated with this population. Whilst the majority of Guillemots first bred when they were 6 or 7 years, overall timing of first reproduction varied from 4 to 11 years. In species where age of first breeding is variable certain ages can be associated with a high reproductive success (Newton 1989). However, although lifetime breeding success in Guillemots showed considerable individual variation there was no clear optimal age of first breeding, no evidence that success was higher in birds recruiting at the median age and no relationship between age of first breeding and lifetime breeding success. A recent study exploring the relationship between age of first breeding and lifetime reproductive success across 34 species of birds, including a few seabirds, concluded that a delayed onset of reproduction beyond maturity is an optimal strategy that is explained by a long lifespan and costs of early reproduction (Mourocq *et al.* 2016). In our population the age when an individual started to breed had no effect on lifetime breeding success hence delaying breeding was no more optimal than earlier breeding.

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APPENDIX

Table 1. Sample sizes for plots shown in Figures 2 and 3

x-value	Figure 2	Figure 3a	Figure 3b		
			12 years or less	More than 12 years	Still alive
1	54		17	17	28
2	50		12	17	25
3	46		8	17	25
4	42	3	5	17	21
5	38	9	4	17	22
6	35	31	3	16	19
7	33	35		16	18
8	29	41		14	18
9	25	42		12	17
10	21	43		11	13
11	13	41		6	8
12	12	38		6	8
13	11	37		4	8
14	11	32		4	8
15	11	30		4	8
16	6	21		4	5
17	3	20		2	4
18		17		1	1
19		15			
20		12			
21		10			
22		7			
23		4			
24		3			
25		1			
26		1			
27		1			
28		1			
29		1			

Figure 1. Age distribution at key stages in the recruitment process of 62 known-age Common Guillemots. (a) Age (years) first seen on the Isle of May, (b) age first seen in study areas, (c) age of first breeding attempt and (d) age of first successful breeding. (Twelve birds had not fledged a chick by the end of the study.)

Figure 2. The mean relative laying date (± se) of Common Guillemots plotted against the number of breeding years. The asymptotic regression (Relative lay date = -0.957+17.3*(0.263**Number of breeding years) is fitted through all the 440 records. Sample sizes are given in the appendix.

Figure 3. Breeding success (chicks fledged/breeding attempt) of Common Guillemots in relation to (a) age and (b) years since breeding started. The regression lines are fitted to the observed binomial data rather than the mean breeding success shown by the points. In (b) three ‘phenotypes’ are distinguished, birds that disappeared when they were 12 years or younger (circles), those that were older than 12 years when they disappeared (diamonds), and those that were still alive in 2015 (crosses). Sample sizes are given in the appendix. In (a) squares indicate sample size <10 and in (b) small symbols indicate sample size < 5. A common regression line is fitted since there were no significant differences in slopes between phenotypes or differences in intercepts (see text).

Figure 4. Frequency distributions of (a) Lifetime breeding success (total number of chicks fledged during a Common Guillemot’s lifetime; $n = 34$) and (b) numbers of chicks fledged by birds still alive at the end of the study ($n = 28$).

Figure 5. Lifetime breeding success in relation to their age of first breeding of 34 Common Guillemots. Some points are slightly offset for clarity.

Table 1. Frequency distribution of ages of first recorded breeding of Common Guillemots on the Isle of May.

		Age at first breeding (years)								
	n	4	5	6	7	8	9	10	11	Median
Male	28	1	5	10	3	3	5	0	1	6.46
Female	28	1	2	10	8	4	2	1	0	6.67
All including unknown sex	62	3	7	22	12	9	7	1	1	6.59
Chicks from 1983-2003 cohorts	55	2	6	19	10	9	7	1	1	6.69

Table 2. Separating the within-individual effects from the between-individual effects on (a) relative laying date in relation to years of breeding experience (because of the exponential relationship, see Fig. 2, years of breeding experience was $\log_e$+1), (b) breeding success in relation to age, and (c) breeding success in relation to years of breeding experience. In all cases there was no significant difference in the slopes of the relationships comparing within individuals and between individuals.

	Coefficient	se	*P* - value
(a) Relative laying date			
Intercept	0.728	0.418	
Within individual effect	-2.55	0.552	< 0.001
Between individual effect	-1.563	1.064	0.140
Difference in effects	-0.995	1.200	n.s.
	Variance component		
Random individual effects	3.98	1.74	
(b) Age			
Intercept	0.2364	0.2003	
Within individual effect	0.0727	0.0318	0.023
Between individual effect	0.1360	0.0450	0.004
Difference in effects	0.0633	0.0525	n.s.
	Variance component		
Random individual effects	0.374	0.154	
Random year effects	0.485	0.216	
(b) Years breeding experience			
Intercept	0.2333	0.1987	
Within individual effect	0.0697	0.0318	0.029
Between individual effect	0.1520	0.0505	0.004
Difference in effects	0.0823	0.0590	n.s.
	Variance component		
Random individual effects	0.344	0.175	
Random year effects	0.487	0.218	

Figure 1. Age distribution at key stages in the recruitment process of 62 known-age Common Guillemots. (a) Age (years) first seen on the Isle of May, (b) Age first seen in study areas, (c) Age of first breeding attempt and (d) Age of first successful breeding. (Twelve birds had not fledged a chick by the end of the study.)

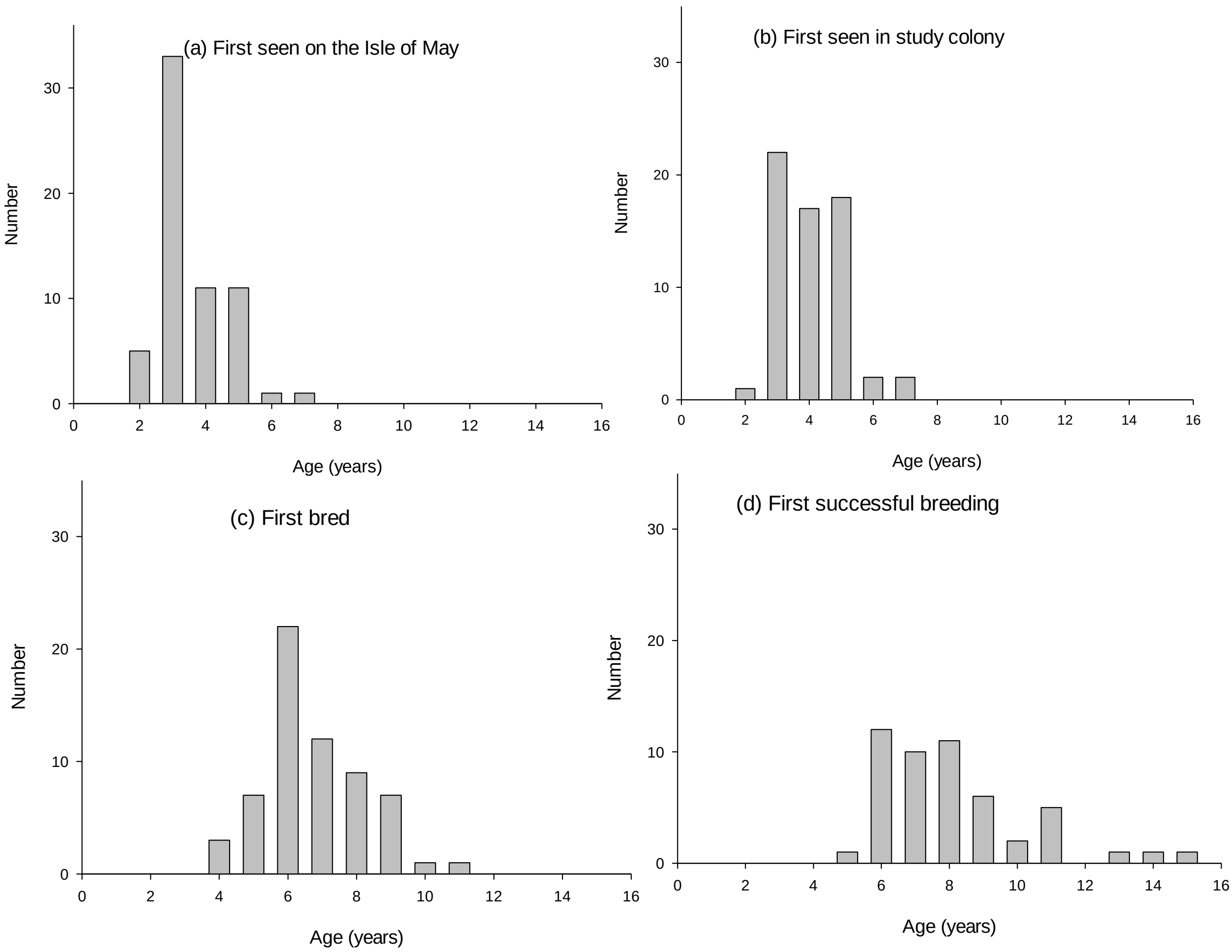

Figure 2. The mean relative laying date (±SE) of Common Guillemots plotted against the number of breeding years. The asymptotic regression (Relative lay date = $-0.957+17.3*(0.263^{\text{Number of breeding years}})$ is fitted through all the 440 records. Sample-sizes are given in the appendix.

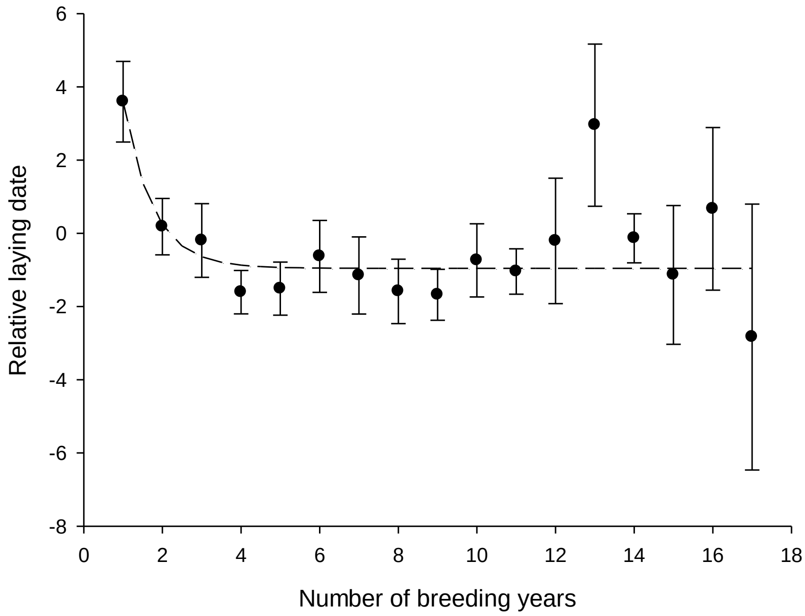

Figure 3. Breeding success (chicks fledged/breeding attempt) of Common Guillemots in relation to (a) age and (b) years since breeding started. The regression lines are fitted to the observed binomial data rather than the mean breeding success shown by the points. In (b) three ‘phenotypes’ are distinguished, birds that disappeared when they were younger than 12 years (circles), those that were older than 12 years when they disappeared (diamonds), and those that were still alive in 2015 (crosses). Sample sizes are given in the appendix. In (a) squares indicate sample size <10 and in (b) small symbols indicate sample size < 5. A common regression line is fitted since there were no significant differences in slopes between phenotypes or differences in intercepts (see text).

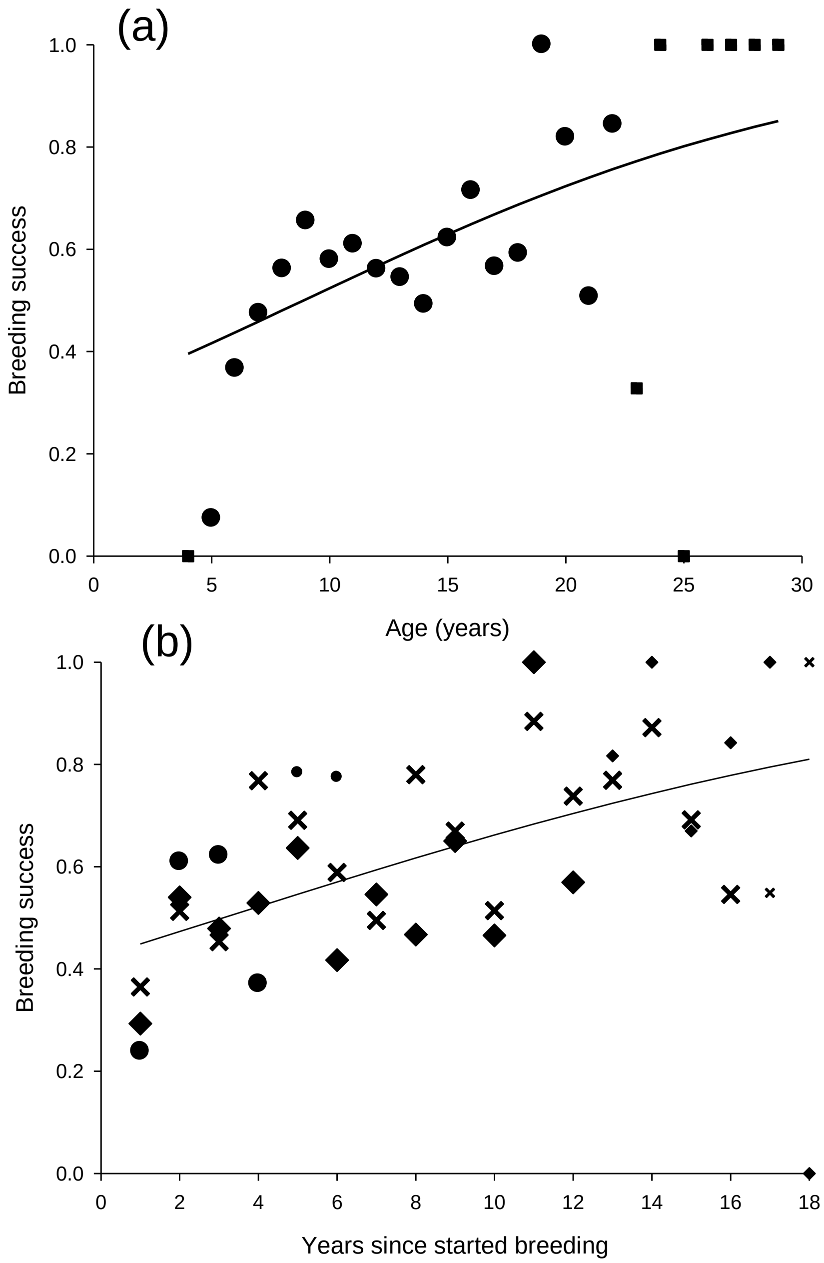

Figure 4. Frequency distributions of (a) Lifetime breeding success (total number of chicks fledged during a Common Guillemot's lifetime; n = 34) and (b) numbers of chicks fledged by birds still alive at the end of the study (n = 28).

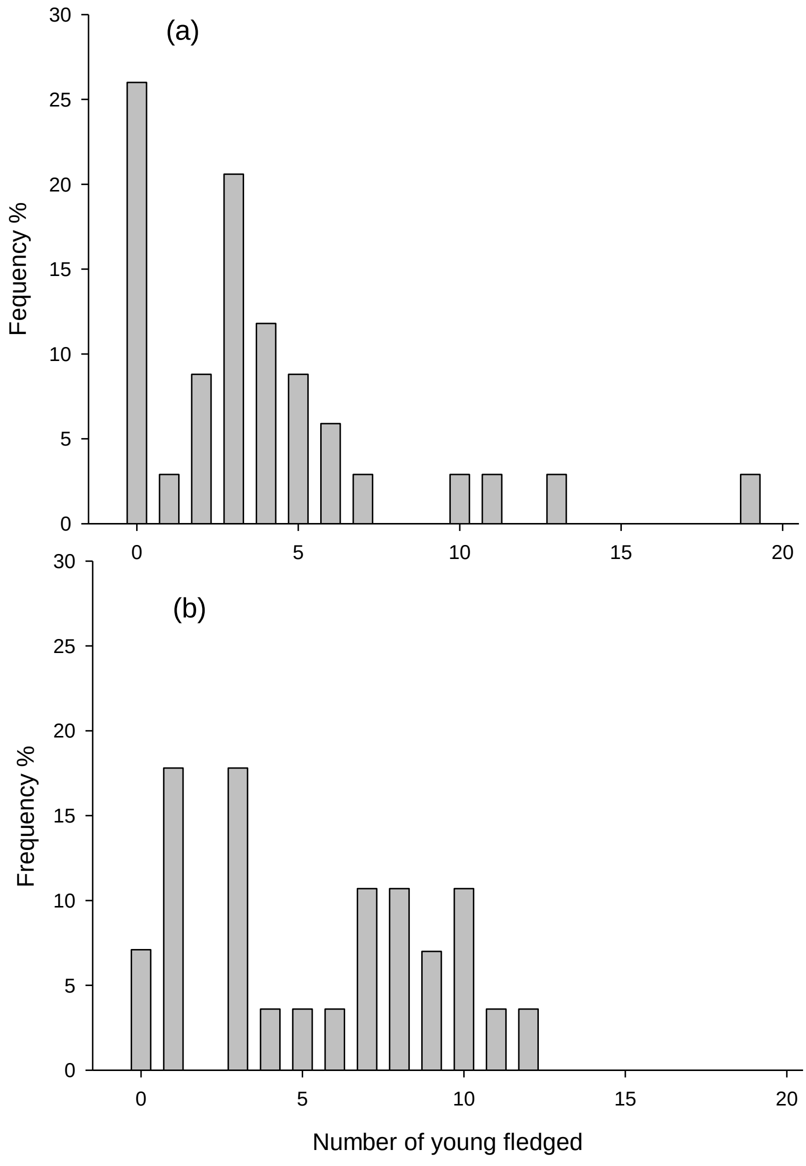

Figure 5. Lifetime breeding success in relation to their age of first breeding of Common Guillemots. Some points are slightly offset for clarity.