Survival estimates of Northern Gannets *Morus bassanus* in Alderney: big data but low confidence

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Survival estimates of Northern Gannets *Morus bassanus* in Alderney: big data but low confidence

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ABSTRACT

Capsule: There has been a linear increase in the survival rates for both adult and juvenile Northern Gannets *Morus bassanus* breeding on Alderney in the English Channel. However, given large confidence intervals, improved monitoring is required to better evaluate threats to this population.

Aims: To estimate the age-specific survival and reporting rate from an internationally important population of Northern Gannets *M. bassanus* breeding at one of the southernmost colonies for this species.

Methods: We use 28 years of ringing and recovery data in order to estimate age-specific survival and reporting rates.

Results: Adult and juvenile survival rates differ, and both survival and reporting rates are considerably lower in first-year birds than older birds. Additionally there is an increasing linear trend in survival rates over time, and a decreasing trend in reporting rates.

Conclusion: Threats to Gannets from anthropogenic disturbance are likely to be age and population specific. While these rates point towards continued growth of this population, the confidence intervals around our estimates are large, highlighting the need for improved resighting efforts in long-term studies of this nature.

Seabirds are threatened by anthropogenic changes to the marine environment (Croxall *et al.* 2012). To assess the past, current and future impacts of these threats, it is essential to understand the age-specific demographic rates of seabirds, and the temporal trends associated with them. Furthermore, since different populations of the same species face different threats and demographic rates can show divergent trends (Crawford *et al.* 2008, Pettex *et al.* 2015), it is important to study multiple populations from across each species range as well as individuals or groups (e.g. age and sex) within a population. However, demographic studies of long-lived birds such as seabirds require long-term data sets, which by their nature are challenging and resource intensive to accumulate. As a result, there are relatively few ongoing studies which consistently gather sufficient data (usually through ringing and resighting birds) to allow for meaningful analysis, thus all studies which do generate sufficient data are valuable.

Northern Gannets *Morus bassanus* (hereafter Gannets) breed in large colonies in the North Atlantic, with 75% of the worldwide population breeding in Europe (Wanless *et al.* 2005). The population of Gannets breeding on Alderney in the English Channel inhabits the offshore stacks of Ortac and Les Etacs (Figure 1). Although relatively small in comparison to some nearby UK populations, the size of the colony has increased rapidly since the first recorded nest on Ortac in 1940 (Nelson 1978). In 1967, Alderney supported 3000 breeding pairs but by 2011 the population had reached 7885 breeding pairs (Bohan 2012), having increased at an average of 3.6% per year. However, increasing colony size does not necessarily signify a population with highly profitable foraging conditions, and may be a result of birds working hard to forage during the breeding season (Gremillet *et al.* 2006) and/or the immigration of new breeders from other colonies (Siorat & Rocamora 1995).

Despite the healthy rate of population growth throughout the British and Irish colonies (Wanless *et al.* 2006), Gannets may be threatened by anthropogenic impacts, such as the installation of offshore wind farms, over-fishing, fishing gear-induced mortality, decreases in fisheries discards and climate change (Grecian *et al.* 2012). As with
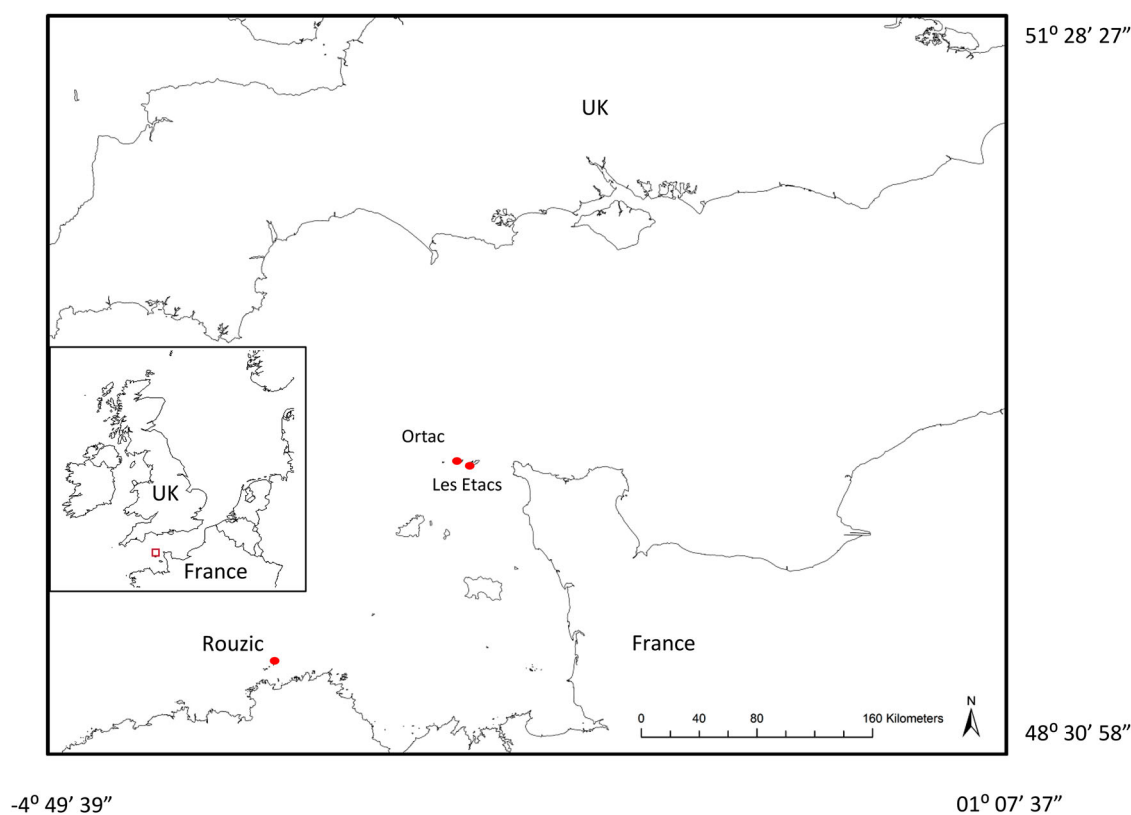
Figure 1. The Alderney population of Gannets on Ortac and Les Etacs. Rouzic is the southern boundary for breeding Gannets in Europe.

Gannets breeding at nearby Rouzic (Figure 1) which are thought to be operating at their energetic limits (Gremillet *et al.* 2006), Alderney's population may be particularly vulnerable due to its position near the southern limit of the species range (Brown *et al.* 1996). Furthermore this population's breeding seasons foraging areas overlap with nine sites proposed for the development of marine renewable energy installations (Soanes *et al.* 2013, Warwick-Evans *et al.* 2016). Variation in the behaviour of Gannets throughout their life cycle will result in different threats between the age classes. For example, many of Alderney's Gannets migrate to West Africa soon after fledging where they remain for the first year or two of life (Veron & Lawlor 2009), thus first-year survival is likely to be impacted by the industrial fishing practices occurring off West Africa (Gremillet *et al.* 2015). Conversely, Alderney's adult Gannets overwinter from the North Sea to the Bay of Biscay and North Africa (Veron & Lawlor 2009), alongside birds from neighbouring colonies which also overwinter off West Africa (Fort *et al.* 2012), returning to the English Channel during the breeding season. Hence adult survival will be impacted by environmental conditions and fishing practices in any or all of these areas (Gremillet *et al.* 2006).

Given the different threats to Gannets in different locations and that these threats will change throughout their life cycle, a robust approach to monitor colony-specific survival rates must be developed in order to determine which stages of each population are likely to be impacted by changes in local conditions and to what extent (Furness & Wanless 2014). We use 28 years of ringing data to calculate the age-specific survival rates for the Alderney population of Gannets.

Materials and methods

Ringing of Gannets in Alderney, Channel Islands, (49°42′50″N 2°12′18″E) by ringers operating under the Channel Island Bird Ringing Scheme began in 1947, however, there were many years where birds were not ringed. Regular annual ringing began in 1983, with only one year missing between 1983 and 2010. For this reason, the analysis was conducted using the 19732 individual birds ringed as chicks in Alderney during this period. Recoveries of birds found dead were used in order to calculate age-specific survival and reporting estimates. All birds recovered dead in the colony were removed from the analysis to avoid bias in the estimation of reporting rate (Frederiksen *et al.* 2008),

resulting in a total of 530 recoveries of birds ringed in Alderney and recovered dead outside the colony.

Most of the birds ringed in Alderney were ringed as nestlings (>99%), which creates a problem when calculating the independent estimate of reporting rates in adult birds necessary for dead recovery analysis (Francis 1995). Indeed, Furness & Wanless (2014) highlight the shortcomings in current demographic analysis of Gannets whereby a high proportion of birds ringed are nestlings, and very few adult birds are ringed. Therefore to enable the calculation of survival rates for Alderney's Gannets, we adopted a method previously used by Wanless et al. (2006) whereby the birds ringed as nestlings in Alderney were combined with data from birds ringed as adults in the UK in the same time period (a total of 1731 ringed, of which 94 were recovered), allowing the calculation of age-specific survival estimates for juvenile birds specific to Alderney, and adult survival rates as a combination of Alderney and UK birds. Kubetzki et al. (2009) show that Gannets from the Bass Rock colony overwinter in areas ranging from the North Sea down to West Africa. Rings recovered from Alderney's population show a similar overwintering distribution (Veron & Lawlor 2009), and Fort et al. (2012) found that Gannets from colonies neighbouring Alderney also showed a similar overwintering distribution. This suggests that reporting rates would be similar for UK and Alderney adult Gannets, thus supporting this approach.

Analysis

Dead recovery analysis was carried out using Seber models (1970) in order to estimate survival rate (S) and reporting probability (r) using Program MARK software (White & Burnham 1999) combined with the RMark package (Laake 2013) in statistical software R (R Core Team 2013).

Initially we fitted a range of age-dependent models, ranging from 0 to 5+ years for both the survival and reporting parameters before considering time-dependent factors (Table 1). These preliminary

models suggested that it was necessary to cap the number of age classes for the reporting rate to 2 in order for the algorithms to converge, and the models to run. The model which best fitted the data was that with 4 age classes in the survival parameter (i.e. variation between each of the first three years preceding adulthood), and 2 age classes for the reporting rate, thus all further models were structured using these age classes. A median c-hat goodness-of-fit test was carried out on the full *age* and *time* dependent model ($S_{age4*time}$, $r_{age2*time}$) in MARK and the variance inflation factor was calculated (c-hat = 2.66). All subsequent models were adjusted to account for this and the best model was identified using quasi-Akaike's Information Criteria corrected for small sample sizes ($QAIC_C$). Models with all combinations of *age* (as an additive effect), *time* (where all years have an individual parameter estimate) and *Time* (a linear trend in change over time) and with both an additive effect of time and a multiplicative effect of time for both survival and reporting rate were run and ranked by QAICc (Appendix Table A1). This resulted in a total of 25 models. Weighted mean estimates and 95% confidence intervals of annual survival were calculated for each age class using the *weighted.mean* function in R.

Results

The model with the lowest QAICc value was the one in which survival rates were dependent on *age* and *Time* (as a linear trend), where *Time* had an additive effect on *age* such that the trend ran parallel between the age classes ($S_{age+Time}$ r_{age}). Reporting rate was dependent on *age*. There was not a large difference in QAICc values for the top models (Table 2), therefore model averaging was used to obtain final parameter estimates. Overall there was a gradual increasing linear trend in estimated survival from 1983 to 2010 (Figure 2). This trend was more pronounced in first-year birds (from 0.43 to 0.69) than in older age classes (Figure 2). Gannets in their second year or older all had high estimates of

Table 1. Comparison of model performance in relation to the number of age classes in models to calculate the survival rate of Alderney's population of Gannets.

Number of age classes	AICc
1	8659.9
2	8630.9
3	8632.1
4	8628.9
5	8630.5
6+	8631.2

Table 2. The top 6 models comprising 99% of the weighting of all models averaged in order to calculate survival rates between 1983 and 2010 for the Alderney population of Gannets.

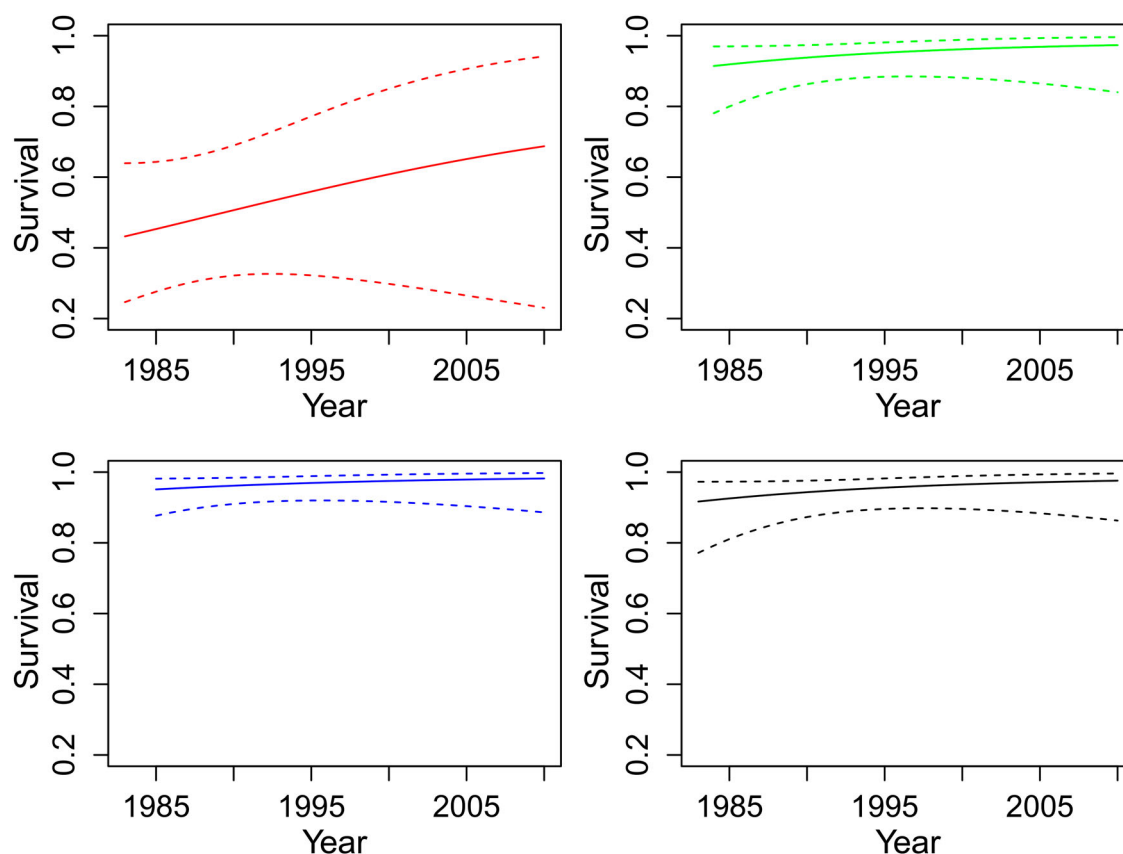| Model	DeltaQAICc	Number of parameters	Weight
$S_{age+Time}$, r_{age}	0	7	0.50
S_{age}, $r_{age+Time}$	1.44	7	0.24
$S_{age+Time}$, $r_{age*Time}$	3.24	9	0.1
$S_{age*Time}$, r_{age}	3.84	10	0.07
$S_{age*Time}$ $r_{age*Time}$	4.24	12	0.06
$S_{age*Time}$, $r_{age+Time}$	5.82	11	0.03

Figure 2. Estimates of survival rates (with 95% confidence intervals) for the Alderney Gannet population with age classes: (a) nestlings (red), (b) 2nd year (green), (c) 3rd year (blue) and (d) 4+years (black). Estimates are based on weighted averages from all models.

survival rates ranging from 0.91 to 0.98 (Figure 2). Mean estimates of annual survival were considerably lower for first-year birds than those in older age classes (Table 3). Overall there was a decreasing trend in reporting rate during the study period, with reporting rate for first-year birds considerably lower than for older birds (Figure 3).

Discussion

The high mean adult survival rate for Alderney's Gannet population (0.95) is consistent with high survival rates estimated for the UK and Ireland populations (0.92, Wanless *et al.* 2006). High adult survival rates are expected in seabirds, as they are generally long lived and slow to reach maturity (Bell 1980), traits which

Table 3. Mean estimates (and 95% confidence intervals) of survival rates for Alderney's Gannet population from 1983–2010.

Age class	Survival rate
1st year	0.57 (0.29–0.79)
2nd year	0.95 (0.86–0.91)
3rd year	0.97 (0.91–0.99)
4+ year	0.95 (0.87–0.98)

result in prioritizing survival over reproduction in years when environmental conditions are poor (Pichegru *et al.* 2010).

Although the model which most parsimoniously fitted the data was structured with 4 age classes for survival, survival rates for second- and third-year birds were very close to those of adult birds (Figure 2), and only first-year birds showed a considerably lower rate of survival. This lower rate of first-year survival is consistent with previous studies of Gannets (Nelson
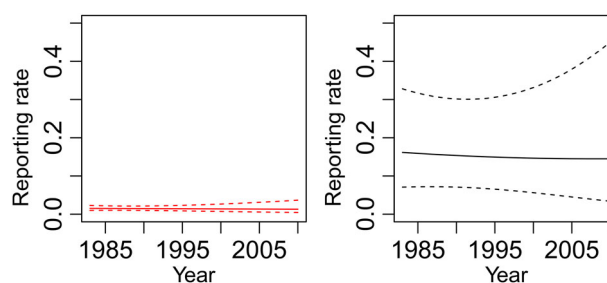

Figure 3. Estimates of reporting rates (with 95% confidence intervals) for the Alderney Gannet population with age classes: (a) first year (red), b) 2+ year (black). Estimates are based on weighted averages from all models.

2002, Wanless *et al.* 2006) and is possibly due to problems faced by juvenile Gannets when learning how to feed themselves (Hamer 2002). A linear increase in survival rate over time was found for all age groups, and coincides with recent increases in Alderney's Gannet population (Bohan 2012), although this trend could also be driven by increasing productivity rates. Thus despite being near the southern limit for the range of the Gannet, the population is continuing to grow, consistent with the global increase in populations of this species (BirdLife-International 2015). This suggests conditions for Gannets are improving, which is likely to be due to their propensity to feed on fisheries discards (Votier *et al.* 2013), or may be a result of increased abundances of larger, energy dense prey, such as mackerel (Davies *et al.* 2013).

However, seabirds are threatened by many anthropogenic activities (Croxall *et al.* 2012) such as climate change, offshore development, fishing, and changes to the fisheries discarding policy (Grecian *et al.* 2012, Bicknell *et al.* 2013), and threats will change throughout the life cycle of the bird. For example, juvenile Gannets residing in West Africa, or adults overwintering in this area, are likely to be impacted by the industrial fisheries occurring in this region (Gremillet *et al.* 2015). Adult birds are also likely to be affected by conditions further north and in the English Channel, where they return annually to breed (Gremillet *et al.* 2006). Alderney's Gannets forage in areas which overlap with nine sites proposed for the development of marine renewable energy installations (Soanes *et al.* 2013), which may result in increased mortality for adult birds (Furness & Wanless 2014). Populations of long-lived seabirds with high survival rates are especially impacted by increased adult mortality (Sæther & Bakke 2000) and minor declines in survival can result in major changes to population growth rate (Wanless *et al.* 2006). Alderney's population of Gannets may be particularly vulnerable to climate change due to their location towards the southern extent of the range for this species. It is predicted that northern hemisphere populations of any species which reside near their southern boundaries will be more strongly effected by climate change (Brown *et al.* 1996), as the environmental conditions for themselves and their prey become unsuitable. Nelson (1978) suggests that the southern limits of the breeding range for Gannets may be fixed by the abundance of principal prey items, although Hamer *et al.* (2007) suggest that the ability of Gannets to consume a wide variety of prey may overcome this potential impact. However, Montevecchi (2012) observed starving Gannet chicks

in Newfoundland after sea temperatures were 4°C higher than average and suggested the fish were distributed in deeper waters than usual and at depths which were unavailable to diving Gannets. These pressures on seabirds can operate across all life-history stages and may vary between locations, which again highlights the need to estimate age-specific demographic rates for as many populations as possible.

Dead recovery analysis of seabirds can be problematic if the majority of birds are ringed as nestlings, because this may create problems when estimating the reporting rate for adult birds (Francis 1995). In this instance, we were able to partially overcome this by combining birds ringed in the UK as adults with nestlings ringed on Alderney, although by using this method we do not know Alderney-specific reporting rates for adult birds, which could introduce a source of error. Reporting rates were lower for first-year birds than older birds and Gannets do not reach maturity until their fifth year, until this time they spend long periods at sea (Nelson 1978). For example, first-year birds from Alderney migrate south towards the Mediterranean and Africa (Veron 1988) often remaining in these areas into their second year in order to take advantage of the calmer waters and more easily handled prey (Nelson 2002). Second- and third-year birds disperse widely throughout the breeding season, potentially prospecting at other colonies as has been seen in other populations (Votier *et al.* 2011). Fewer recoveries are expected from these areas with low human population density (Veron & Lawlor 2009), and the combination of this, and longer periods at sea are likely to explain the lower reporting rate for first-year birds, which is supported by previous findings for UK and Irish Gannets (Wanless *et al.* 2006). On top of this limitation, reporting rates for Alderney's Gannets have declined in recent years which is also consistent with findings from the UK and Ireland (Wanless *et al.* 2006).

The declining trend in reporting rates for both juvenile and adult birds results in challenges when estimating the impacts of anthropogenically induced changes in the marine environment. Therefore it is imperative that a robust system is developed in order to obtain precise colony-specific estimates of demographic rates for Northern Gannets, particularly for adults. Currently the high levels of uncertainty surrounding the survival estimates for recent years due to lower rates of recovery (Wanless *et al.* 2006) results in demographic analysis of ringing data that may not necessarily reflect current conditions in their environment. This is because the time lag between

real-time changes in demographic rates and results from population modelling may result in the detection of changes years after they occur in the population (Beissinger & Westphal 1998). Wanless *et al.* (2006) conclude that it is necessary to ring more adult Gannets in order to gain more accurate, colony-specific survival estimates, and Furness & Wanless (2014) recommend a large-scale colour-ringing programme be initiated immediately in order to thoroughly assess the impacts to Gannet populations from offshore wind farms. The lack of adult data from our study supports this move. Not only will this overcome the problem when calculating reporting rates for adult birds, but colour-ringing adults will increase the precision of estimates for more recent years, reducing the lag phase, and enable combined live–dead survival analysis.

Our study is the first to provide any demographic parameters for Alderney's population of Northern Gannets. If both adult and immature survival rates are maintained then the population is likely to continue to grow. However, despite the considerable efforts in both ringing and recovery, estimates of survival have large confidence intervals thus there are limitations surrounding our understanding of adult survival. Further data are required in order to investigate threats to Gannets throughout their life cycle, predict population trajectories in the presence of wind farms, or under different environmental conditions, and implement successful management strategies. Our study demonstrates that even substantial data sets such as this one require increased resightings data, particularly of birds ringed or resighted as adults. This can be achieved relatively easily by the instigation of large-scale colour-ringing schemes of adult birds.

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Appendix

Table A1. All models that were averaged in order to calculate survival rates between 1983 and 2010 for the Alderney population of Gannets.

Model	QAICc	No. parameters	Weight
$S_{age+Time}, r_{age}$	0	7	0.50
$S_{age}, r_{age+Time}$	1.44	7	0.24
$S_{age+Time}, r_{age*Time}$	3.24	9	0.1
$S_{age*Time}, r_{age}$	3.84	10	0.07
$S_{age*Time}, r_{age*Time}$	4.24	12	0.06
$S_{age*Time}, r_{age+Time}$	5.82	11	0.03
$S_{age+Time}, r_{age+Time}$	13.51	8	<0.01
$S_{age}, r_{age*Time}$	13.89	8	<0.01
S_{age}, r_{age}	15.40	6	<0.01
$S_{age+time}, r_{age}$	31.32	33	<0.01
$S_{age+time}, r_{age*Time}$	35.08	35	<0.01
$S_{age+Time}, r_{age+time}$	45.75	34	<0.01
$S_{age}, r_{age+time}$	46.77	33	<0.01
$S_{age*Time}, r_{age+time}$	49.10	37	<0.01
$S_{age+time}, r_{age+time}$	49.51	34	<0.01
$S_{age+time}, r_{age+time}$	76.21	60	<0.01
$S_{age+Time}, r_{age*time}$	79.89	61	<0.01
$S_{age*Time}, r_{age*time}$	86.07	64	<0.01
$S_{age}, r_{age*time}$	94.53	60	<0.01
$S_{age+time}, r_{age*time}$	128.74	87	<0.01
$S_{age*time}, r_{age*Time}$	149.94	115	<0.01
$S_{age*time}, r_{age}$	150.98	113	<0.01
$S_{age*time}, r_{age+Time}$	155.60	114	<0.01
$S_{age*time}, r_{age+time}$	207.47	140	<0.01
$S_{age*time}, r_{age*time}$	247.35	167	<0.01