A proposed new method for obtaining penguin moult count estimates

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Abstract

A double Gaussian form is fit to annual moult count observations for both adult and juvenile penguins at Robben and Dassen Islands. While giving similar results for total moult numbers to the conventional linear interpolation approach in most cases, this new approach seems preferable for seasons where there are lengthly gaps between successive observations, and is accordingly proposed as a preferred approach. The approach is also used to provide coarse estimates of the precision of estimates of total moult numbers.

Introduction

African penguins moult annually (Randall and Randall 1981) and are known to habitually moult at their breeding colonies (Randall 1983). Counts of moulting penguins have been used as population abundance estimates. A census of the two largest African penguin colonies in the Western Cape has been taken annually since the 1988/1989 moult season at Robben Island, and since the 1994/1995 moult season at Dassen Island (Wolfaardt *et al*. 2009). The moult season was chosen to run from 1 July until 30 June the following year since most birds moult during the months of November to January at these colonies (Underhill and Crawford 1999). The census has been conducted by separately summing the counts taken at two-week intervals of adult birds and immature birds in the feather-shedding phase of moult (Randall *et al*. 1986). These tallies are thought to give slightly conservative estimates for the total numbers of adult and immature birds moulting at the islands (Crawford and Boonstra 1994), since the mean duration of the feather-shedding phase of moult has been observed to be 12.7 days (Randall 1983), slightly less than the count interval of two weeks.

African penguins at a particular colony are known to synchronize their moult, usually peaking in late November at Dassen Island and early December at Robben Island (Wolfaardt *et al*. 2009). The peak is sharper at Robben Island, where 60% of adult birds moult within an eight week period, compared to eleven weeks at Dassen Island (Wolfaardt *et al*. 2009). Interannual variability in moult phenology is thought to be influenced by factors such as the success or failure of the previous breeding season, food availability and major oil spills (Crawford *et al*. 2006).

The juvenile moult season is often characterized by two peak periods. The first peak occurs in late spring, coincident with the peak period of the adult moult, and the second peak occurs late in the summer (Underhill and Crawford 1999). Wolfaardt *et al*. (2009) suggest that the first peak may comprise birds which delay moulting into their adult plumage until their second summer when they moult with the majority of the colony (“skippers”), while birds which fledge early in the year may

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moult during late summer or autumn, soon after they reach 12 months of age ("squeezers") (Kemper and Roux 2005).

Methods

Counts are not made daily, so interpolation needs to be used to estimate the number of birds moulting on days between counts. The simplest method is linear interpolation which can be used to estimate the number of birds moulting on each day of the year. The total number of moulters is then calculated by dividing the sum of daily moulters by 12.7, the mean length of the feather-shedding phase (Underhill and Crawford 1999).

However, a concern with this linear interpolation approach is that counts are not always made every two weeks, and sometimes the intervals between counts can be quite lengthly, rendering linear interpolation a rather coarse approach. An alternative approach is to model the expected number of birds moulting on each day d as the sum of two Gaussian functions:

$$\hat{M}_d = \frac{1}{\sqrt{2\pi\sigma_1^2}} N_1 e^{-\frac{(d-\mu_1)^2}{2\sigma_1^2}} + \frac{1}{\sqrt{2\pi\sigma_2^2}} N_2 e^{-\frac{(d-\mu_2)^2}{2\sigma_2^2}} \quad (1)$$

where

$N_1 + N_2$ is the total number of moulting birds which would be counted if counts were made daily (if the moult season was "infinitely" long),

μ_1 and μ_2 are the days on which the two peaks of the moult season occur, and

σ_1 and σ_2 characterize the degree of synchrony of the moult.

The sum of two Gaussians was chosen because the juvenile penguin moult season is known to have two peaks, and the additional flexibility is useful as it can take account of asymmetric shapes of the overall distribution.

Values for the six parameters in equation (1) are obtained by minimizing the negative log-likelihood for the Poisson process of sighting moulting birds given the data:

$$-\ln L = \sum_{i=1}^{n} \left(\hat{M}_i - M_i^{\text{obs}} \ln \hat{M}_i \right) \quad (2)$$

where i indexes each moult count with a total of n such observations made during the season. This method may be more robust than the linear interpolation method, both in the case of noisy data and when the intervals between consecutive counts are several weeks or even months.

If σ_1 and/or σ_2 are large, the Gaussian functions have wide tails, resulting in values of $\hat{M}_d >> 0$ for days outside of the split year in question. This has been taken into account by subtracting the tails T_1 and T_2 of each of the Gaussian functions:

$$T_1 = N_1 \left(\text{erfc}\left(\frac{\mu_1 - d_1}{\sqrt{2}\sigma_1} \right) + \text{erfc}\left(\frac{d_{L+1} - \mu_1}{\sqrt{2}\sigma_1} \right) \right) \quad (3)$$

$$T_2 = N_2\left(\operatorname{erfc}\left(\frac{\mu_2 - d_1}{\sqrt{2}\sigma_2}\right) + \operatorname{erfc}\left(\frac{d_{L+1} - \mu_2}{\sqrt{2}\sigma_2}\right)\right) \tag{4}$$

where the subscripts 1 and L indicate the first and last days or the moult year (1 July and 30 June respectively) and the complementary error function is defined as:

$$\operatorname{erfc}(x) = \frac{1}{\sqrt{\pi}}\int_x^{\infty} e^{-t^2}\,dt \tag{5}$$

The total number of birds moulting in one year is then calculated as:

$$M = \left(N_1 + N_2 - T_1 - T_2\right)/12.7 \tag{6}$$

By using the optimization program ADMB to fit the double Gaussian curves to the annual moult counts, the Hessian-based CV s is readily obtainable for each estimate under the assumption that model errors are Poisson distributed. However, the actual errors are greater than this assumption suggests so that overdispersion must be accounted for when calculating realistic coefficients of variation. After grouping observations so that each $\hat{M}_i > 5$, the overdispersion for the each annual estimate is calculated as:

$$D = \sqrt{\frac{1}{n^* - p}\sum_{i=1}^{n^*}\left(M_i^{\text{obs}} - \hat{M}_i\right)^2 \Big/ \hat{M}_i} \tag{7}$$

where n^* is the number of observations in that year (after grouping) and p is the number of parameters estimated. CVs are then calculated as:

$$CV = s\tilde{D} \tag{8}$$

where $\tilde{D}$ is the median of all overdispersion parameters calculated for each series.

An alternative to the maximum likelihood approach is to use the Markov-Chain Monte Carlo method to obtain a Bayes posterior distribution for M. This was attempted for a few years and gave very similar results.

Results

Double Gaussian functions were fitted to all the available adult and juvenile moult count data for Robben Island and Dassen Island. The number of observations, the estimated parameters and the overdispersion coefficients are given in Table 1 to Table 4.

The columns in Table 5 to Table 8 list series of moult count estimates from the linear interpolation analysis of Wolfaardt *et al*. (2009), unpublished data supplied by Rob Crawford, our own linear interpolation analysis which attempts replication of the earlier results, and the results of the double Gaussian method described above with coefficients of variation.

The only notable differences between our linear interpolation and Wolfaardt *et al*.'s results are for the 2001/2002 season when no counts were made from July to October at Robben Island, or for nine weeks during September and October at Dassen Island.

In most cases the fitted double Gaussian results are very similar to the linear interpolation results, but there are a few exceptions: Robben Island (1996/1997 and 2001/2002) and Dassen Island (2002/2003). The reasons underlying these are detailed below.

According to Underhill and Crawford (1999), "The abnormal pattern in 1996/97 was a result of errors in the November and December counts, which were undertaken by an inexperienced observer." Consequently, three data points were excluded when fitting the double Gaussian function for this season (Figure 5). The result is a 30% larger estimate for adult moulters and a 7% larger estimate for juvenile moulters for 1996/1997.

The 2001/2002 estimate for Robben Island is unreliable since only nine counts were taken during that year, with none before November (Figure 6 and Figure 7). A decrease in moulters the year following the *Treasure* oil spill would perhaps be expected, as was the case in 1995/1996 following the sinking of the *Apollo Sea*. Compared to the linear interpolation estimates, the double Gaussian estimates given here are 21% and 27% lower for the adults and juveniles respectively.

At Dassen Island in 2002/2003, only one count was made between 8 October and 22 January, making it difficult to quantify the time or the extent of the peak of the moult season that year (Figure 8). The linear interpolation method would certainly underestimate the number of moulters, especially if the peak was in mid to late November as usual. The double Gaussian estimate for the adults is 13% higher.

The double Gaussian fit failed to converge satisfactorily in three cases: Dassen Island adults in 1994/1995, Dassen Island juveniles in 2008/2009, and Robben Island adults in 2009/2010. In the latter two cases, a single Gaussian was fitted instead. This was not feasible for the Dassen Island adults in 1994/1995 because of the absence of data for the first half of the season, so no revised estimate is provided in that case.

Discussion and conclusions

Results from deriving moult count estimates via the method of the fitted double Gaussian are in most cases similar to the results of linearly interpolating the count data. However, particularly in seasons where there are large gaps between some counts, the double Gaussian approach seems preferable. Accordingly it is proposed that the associated revised estimates be accepted for use for further modeling purposes.

The motivation for use of the double Gaussian was bimodality in the juvenile count distributions, and the corresponding μ_1 and μ_2 estimates in Table 3 and Table 4 are broadly consistent with a first peak in early summer and a second peak in late summer. The adult count fits (Table 1 and Table 2) do not show a similar pattern, and the justification of the use of two Gaussians there is more to provide greater overall shape flexibility. A more refined approach might consider fitting through the use of a Hermite polynomial series expansion, but this does not seem justified here as the double Gaussian approach achieves a sufficiently good fit to the data to provide estimates of reasonable accuracy for population modeling purposes.

The estimates of overdispersion in Tables 1 to 4 always exceed 1, but are also very variable and sometimes very large. The last category generally arises from instances where counts are relatively high at the very beginning and/or very end of the 12 month period considered, which are times when the double Gaussian predicts very low values. Although these differences are not large in the context of the overall count estimate M , they can influence the estimates of overdispersion D considerably. For this reason, CVs have been presented based on the median of the D estimates for each season. This is of course a somewhat coarse approach, but seems useful to provide some broad indication of the precision of the estimates obtained.

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Table 1: Estimated parameter values for equation (1) for adult penguins moulting at Robben Island. Symbols are defined in the text.

Robben adults	n	N_1	μ_1	σ_1	N_2	μ_2	σ_2	D
1988/1989	18	39248	13 Dec	19.264	4828.4	19 Jan	66.176	4.5
1989/1990	25	33982	13 Dec	16.304	9164	07 Jan	54.726	3.1
1990/1991	24	48582	12 Dec	19.056	11425	11 Jan	55.986	3.7
1991/1992	26	46954	12 Dec	20.39	15806	11 Jan	57.837	3.2
1992/1993	26	71918	10 Dec	16.986	11210	04 Jan	56.787	4.3
1993/1994	24	91001	12 Dec	21.921	9547.1	16 Jan	58.233	7.6
1994/1995	25	32469	12 Nov	13.494	68284	23 Dec	40.923	6.0
1995/1996	25	64385	08 Dec	19.448	20401	11 Jan	56.846	4.1
1996/1997	23	72095	17 Dec	22.931	20668	20 Jan	57.283	3.3
1997/1998	25	83273	05 Dec	22.436	25436	08 Jan	58.067	3.7
1998/1999	20	93079	16 Dec	36.279	27583	22 Dec	10.386	9.4
1999/2000	21	117280	06 Dec	18.587	31249	12 Jan	51.263	2.6
2000/2001	15	113540	22 Nov	17.07	50074	22 Dec	42.065	2.3
2001/2002	9	101810	27 Nov	19.55	55507	06 Jan	65.802	15.4
2002/2003	16	152490	04 Dec	24.226	31588	19 Jan	68.331	6.7
2003/2004	14	111400	30 Nov	18.165	104350	11 Dec	54.884	9.2
2004/2005	15	116200	30 Nov	20.192	41817	01 Jan	48.214	7.0
2005/2006	20	80941	01 Dec	28.934	16646	29 Dec	77.12	4.3
2006/2007	17	66480	29 Nov	31.114	15793	15 Dec	77.086	4.5
2007/2008	19	52628	04 Dec	22.448	13021	02 Jan	72.325	2.4
2008/2009	26	39798	11 Dec	28.674	7820.5	06 Jan	67.933	2.7
2009/2010*	26	56268	16 Dec	44.341	–	–	–	6.8

*Single Gaussian only fitted

Table 2: Estimated parameter values for equation (1) for adult penguins moulting at Dassen Island.

Dassen adults	n	N_1	μ_1	σ_1	N_2	μ_2	σ_2	D
1994/1995	32	–	–	–	–	–	–	–
1995/1996	46	74569	11 Dec	20.7	83645	18 Dec	72.5	4.9
1996/1997	46	115650	09 Dec	33.8	52007	12 Jan	96.8	3.3
1997/1998	47	160090	17 Dec	35.6	49142	31 Dec	101.5	3.4
1998/1999	38	236770	12 Dec	30.1	39748	26 Dec	103.3	4.5
1999/2000	21	212580	01 Dec	24.8	107320	23 Dec	58.2	4.0
2000/2001	24	206590	22 Nov	17.8	125940	28 Dec	54.8	7.9
2001/2002	14	153100	10 Nov	19.8	174200	16 Dec	48.8	3.7
2002/2003	16	191000	11 Nov	29.2	128960	29 Dec	58.1	3.4
2003/2004	13	99884	21 Nov	25.7	111710	12 Dec	56.8	6.7
2004/2005	14	155310	22 Nov	28.0	67374	27 Nov	76.5	7.4
2005/2006	26	129690	02 Dec	39.8	22384	02 Mar	180.0	11.3
2006/2007	27	97285	29 Nov	52.2	1565	10 Jul	19.7	3.8
2007/2008	12	22651	01 Dec	70.2	5140	23 Dec	5.9	3.3
2008/2009	27	4555	26 Nov	60.7	866	29 Apr	39.8	1.9
2009/2010	31	1001	08 Nov	13.2	3426	27 Dec	85.2	1.8

Table 3: Estimated parameter values for equation (1) for penguins in immature plumage moulting at Robben Island.

Robben immatures	n	N_1	μ_1	σ_1	N_2	μ_2	σ_2	D
1988/1989	18	6653.7	01 Dec	11.397	3516.1	23 Feb	42.084	2.7
1989/1990	25	7306.2	30 Nov	29.083	3618.1	11 Mar	27.788	4.8
1990/1991	24	7432.3	06 Dec	24.247	3985.5	21 Mar	32.822	2.2
1991/1992	26	17413	12 Dec	34.509	2422.3	29 Mar	25.246	7.1
1992/1993	26	8730	07 Dec	7.5553	12011	24 Dec	58.991	3.9
1993/1994	24	7689.8	28 Jan	58.923	12337	03 Dec	13.426	2.3
1994/1995	25	6711.3	28 Dec	13.961	10692	15 Jan	57.606	2.6
1995/1996	25	9058.8	28 Nov	32.168	8806.8	02 Mar	31.532	2.6
1996/1997	23	23047	19 Dec	22.949	5979.3	24 Mar	31.406	4.5
1997/1998	25	17602	25 Nov	25.31	12716	20 Jan	63.506	2.9
1998/1999	20	18893	28 Nov	26.224	15954	21 Jan	60.217	4.2
1999/2000	21	24849	30 Nov	20.834	10851	03 Mar	26.816	2.8
2000/2001	15	22735	15 Nov	27.734	8068.2	17 Mar	33.422	2.8
2001/2002	9	21905	26 Nov	12.387	12698	27 Feb	48.978	5.5
2002/2003	16	33711	03 Dec	23.522	11640	26 Mar	27.483	9.0
2003/2004	14	29882	25 Nov	26.849	12374	01 Mar	17.726	6.8
2004/2005	15	20585	02 Dec	17.468	11360	04 Jan	64.789	2.4
2005/2006	20	29868	28 Nov	24.744	4206.3	15 Mar	26.326	7.5
2006/2007	17	22349	13 Nov	47.549	2038	03 Apr	47.503	3.8
2007/2008	19	6238.2	06 Dec	13.25	11576	19 Dec	76.042	2.3
2008/2009	26	16314	04 Dec	30.565	6649.6	02 Mar	28.871	2.6
2009/2010	26	17413	29 Nov	28.318	4858.9	11 Mar	23.352	5.5

Table 4: Estimated parameter values for equation (1) for penguins in immature plumage moulting at Dassen Island.

Dassen immatures	n	N_1	μ_1	σ_1	N_2	μ_2	σ_2	D
1994/1995	32	9190	23 Dec	20.0	8571	10 Mar	37.1	3.2
1995/1996	46	15822	27 Dec	48.8	6632	20 Mar	33.0	3.3
1996/1997	46	33242	14 Dec	24.8	29510	15 Mar	32.2	5.4
1997/1998	47	5798	02 Dec	18.5	37212	20 Jan	60.9	3.0
1998/1999	38	48715	08 Dec	22.7	57059	16 Jan	52.9	3.7
1999/2000	21	75465	04 Dec	23.5	31201	01 Mar	24.8	5.0
2000/2001	24	60807	22 Nov	24.8	24543	16 Mar	30.7	4.1
2001/2002	14	72519	19 Nov	30.1	32959	12 Mar	24.2	3.2
2002/2003	16	48807	02 Dec	25.8	23324	25 Feb	32.0	5.5
2003/2004	13	25358	05 Dec	37.5	24364	03 Mar	23.7	6.5
2004/2005	14	44738	30 Nov	29.4	18833	10 Mar	28.7	7.9
2005/2006	26	15003	02 Dec	28.1	12757	11 Mar	31.3	1.9
2006/2007	27	4926	22 Nov	17.7	16935	06 Jan	58.7	1.6
2007/2008	12	6254	17 Dec	60.6	1617	26 Feb	15.8	0.6
2008/2009*	27	969	12 Jan	69.2	–	–	–	1.9
2009/2010	31	1053	16 Nov	28.6	517	03 Feb	33.6	2.4

*Single Gaussian only fitted.

Table 5: Estimates of the number of penguins in adult plumage moulting at Robben Island. The Double Gaussian estimates correspond to the parameters in Table 1.

Robben adults	Wolfaardt *et al*. (2009)	Crawford (unpub.)	Linear interpolation	Double Gaussian MLE	
Year	M	M	M	M	CV (%)
1988/1989	3459	3125	3562	3468	8.3
1989/1990	3392	3015	3391	3397	8.5
1990/1991	4730	4378	4725	4724	6.1
1991/1992	4915	4626	4917	4939	5.8
1992/1993	6538	5909	6535	6544	4.4
1993/1994	8002	7213	7998	7915	3.6
1994/1995	7948	7159	7948	7933	3.6
1995/1996	6563	6350	6568	6674	4.3
1996/1997	5608	5235	5607	7300	3.9
1997/1998	8696	8556	8695	8556	3.4
1998/1999	9397	9710	9395	9501	3.0
1999/2000	11765	10667	11768	11694	2.5
2000/2001	13362	12059	13187	12883	2.2
2001/2002	16439	11549	15646	12362	2.3
2002/2003	14737	12607	14627	14469	2.0
2003/2004	17424	15774	17419	16975	1.7
2004/2005	12871	12640	12852	12442	2.3
2005/2006	7769	7286	7749	7660	3.8
2006/2007		5138	6494	6453	4.5
2007/2008		5229	5197	5157	5.6
2008/2009		3378	3740	3745	7.7
2009/2010		3738	4309	4430	6.5

Table 6: Estimates of the number of penguins in adult plumage moulting at Dassen Island. The Double Gaussian estimates correspond to the parameters in Table 2.

Dassen adults	Wolfaardt *et al*. (2009)	Crawford (unpub.)	Linear interpolation	Double Gaussian MLE	
Year	M	M	M	M	CV (%)
1994/1995	12360	12360	12390	–	–
1995/1996	12222	12222	12243	12373	2.8
1996/1997	12953	12954	12943	12950	2.6
1997/1998	16296	16296	16223	16195	2.2
1998/1999	21438	21438	21375	21531	2.6
1999/2000	25074	25074	25098	25174	2.9
2000/2001	26095	26096	26008	26175	2.9
2001/2002	25619	25618	29605	25767	10.2
2002/2003	22511	22510	22373	25177	5.8
2003/2004	17592	17592	17605	16642	5.4
2004/2005	18298	18298	18298	17385	3.7
2005/2006	11345	11344	11345	11377	3.9
2006/2007		7159	7878	7729	4.1
2007/2008		1827	2319	2160	14.7
2008/2009		449	433	420	18.5
2009/2010			342	340	22.6

Table 7: Estimates of the number of penguins in immature plumage moulting at Robben Island. The Double Gaussian estimates correspond to the parameters in Table 3.

Robben immature	Wolfaardt *et al*. (2009)	Crawford (unpub.)	Linear interpolation	Double Gaussian MLE	
Year	M	M	M	M	CV (%)
1988/1989	842	759	807	800	19.7
1989/1990	866	752	866	860	18.4
1990/1991	911	827	914	899	17.6
1991/1992	1598	1481	1599	1562	10.1
1992/1993	1597	1447	1596	1631	9.7
1993/1994	1585	1425	1583	1574	10.0
1994/1995	1373	1198	1373	1369	11.5
1995/1996	1403	1279	1413	1407	11.2
1996/1997	2138	2006	2138	2285	6.9
1997/1998	2351	2289	2350	2381	6.6
1998/1999	2834	2824	2833	2739	5.8
1999/2000	2803	2484	2810	2811	5.6
2000/2001	2565	2236	2521	2425	6.5
2001/2002	3921	3141	3737	2719	5.8
2002/2003	3330	3051	3291	3571	4.4
2003/2004	3440	3104	3431	3327	4.7
2004/2005	2617	2615	2606	2511	6.3
2005/2006	2654	2740	2647	2683	5.9
2006/2007		1621	1927	1911	8.3
2007/2008		1377	1443	1387	11.4
2008/2009		1614	1804	1808	8.7
2009/2010		1304	1707	1754	9.0

Table 8: Estimates of the number of penguins in immature plumage moulting at Dassen Island. The Double Gaussian estimates correspond to the parameters in Table 4.

Dassen immature	Wolfaardt *et al*. (2009)	Crawford (unpub.)	Linear interpolation	Double Gaussian MLE	
Year	M	M	M	M	CV (%)
1994/1995	1578		1580	1398	6.7
1995/1996	1767		1776	1767	6.9
1996/1997	4823		4825	4940	6.1
1997/1998	3418		3414	3374	4.3
1998/1999	8380		8320	8324	3.6
1999/2000	8462		8406	8399	4.4
2000/2001	6683		6655	6720	4.8
2001/2002	8380		8934	8305	5.7
2002/2003	5409		5485	5680	8.5
2003/2004	3864		3899	3915	7.4
2004/2005	5134		5134	5006	7.1
2005/2006	2184		2213	2186	6.8
2006/2007			1698	1719	7.6
2007/2008			622	618	23.5
2008/2009			77	76	36.8
2009/2010			133	124	33.4

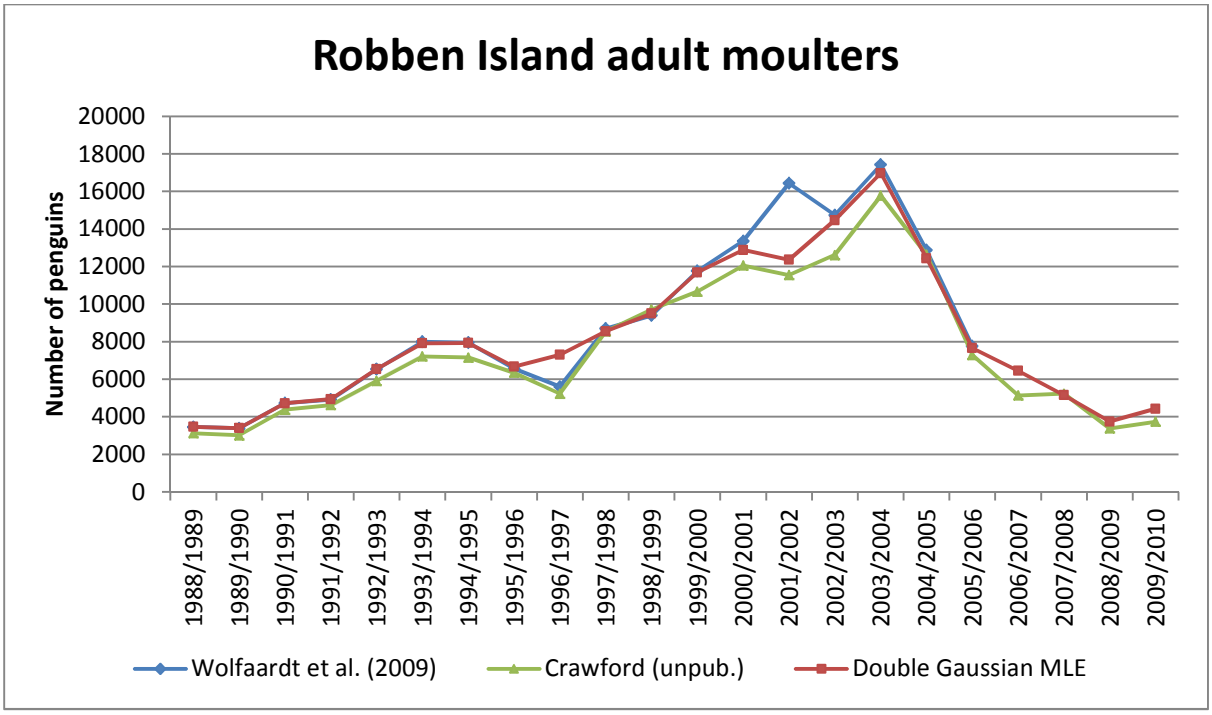

Figure 1: Comparison of previously derived moult count estimates with proposed revisions for Robben Island adult penguins.

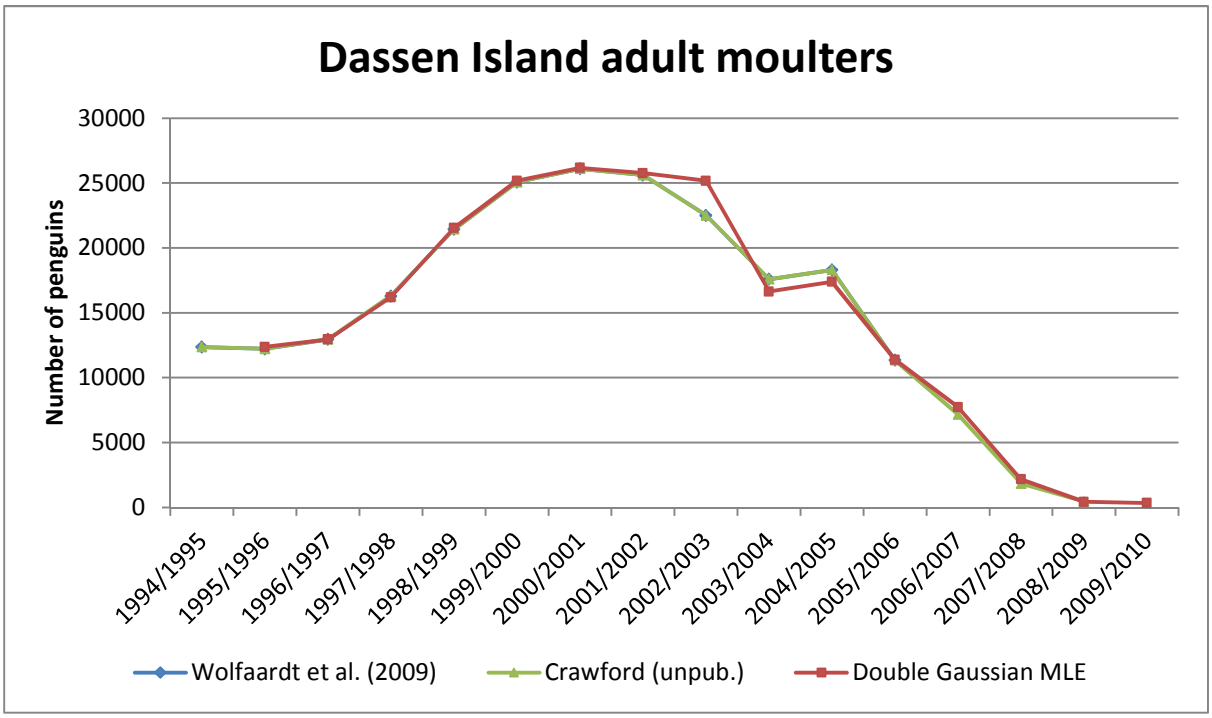

Figure 2: Comparison of previously derived moult count estimates with proposed revisions for Dassen Island adult penguins.

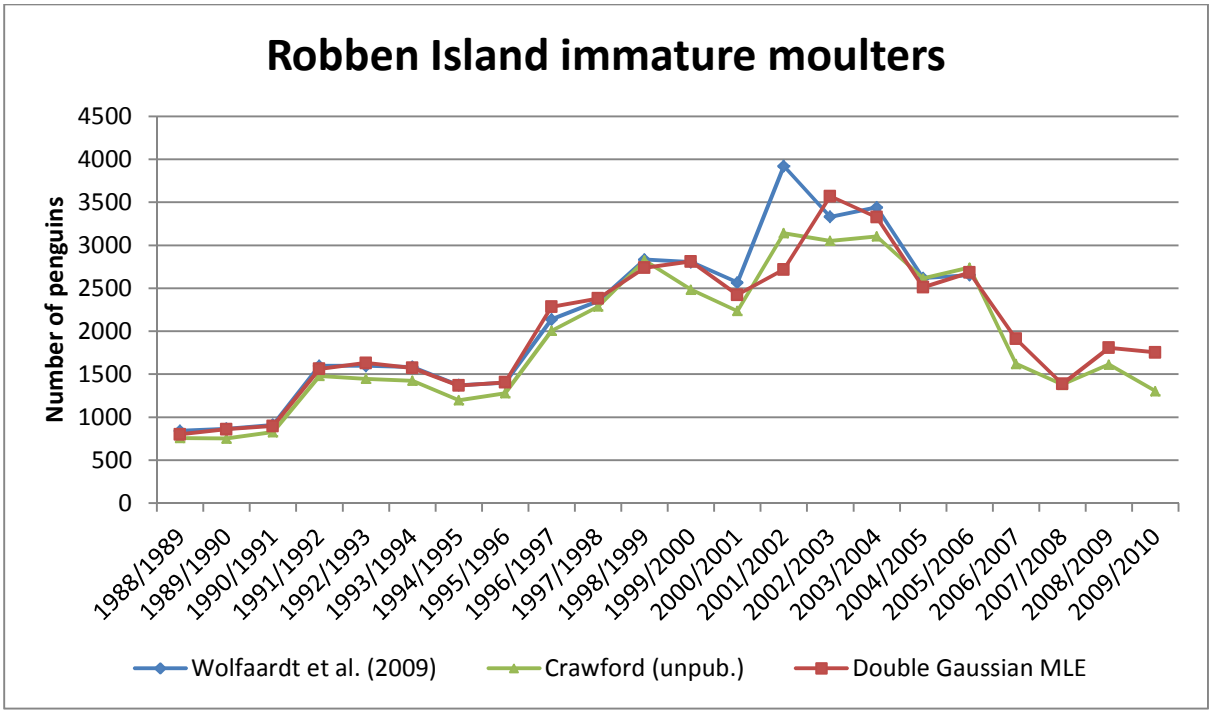

Figure 3: Comparison of previously derived moult count estimates with proposed revisions for Robben Island penguins in immature plumage.

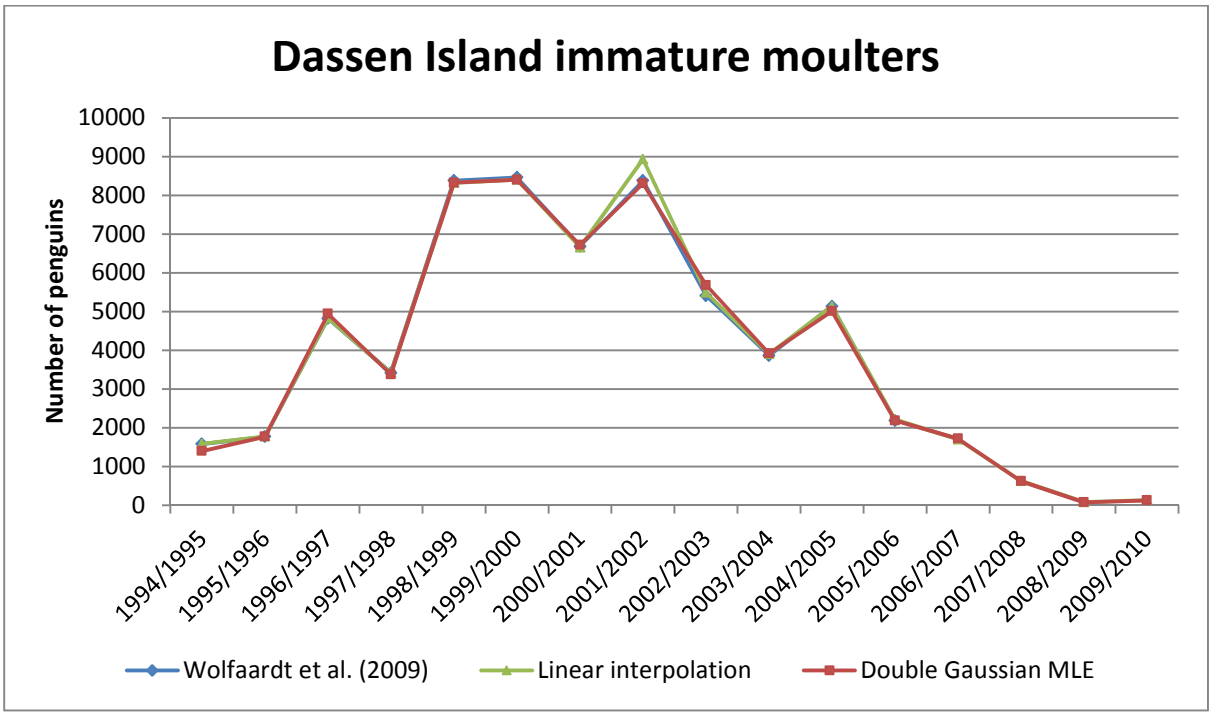

Figure 4: Comparison of previously derived moult count estimates with proposed revisions for Dassen Island penguins in immature plumage.

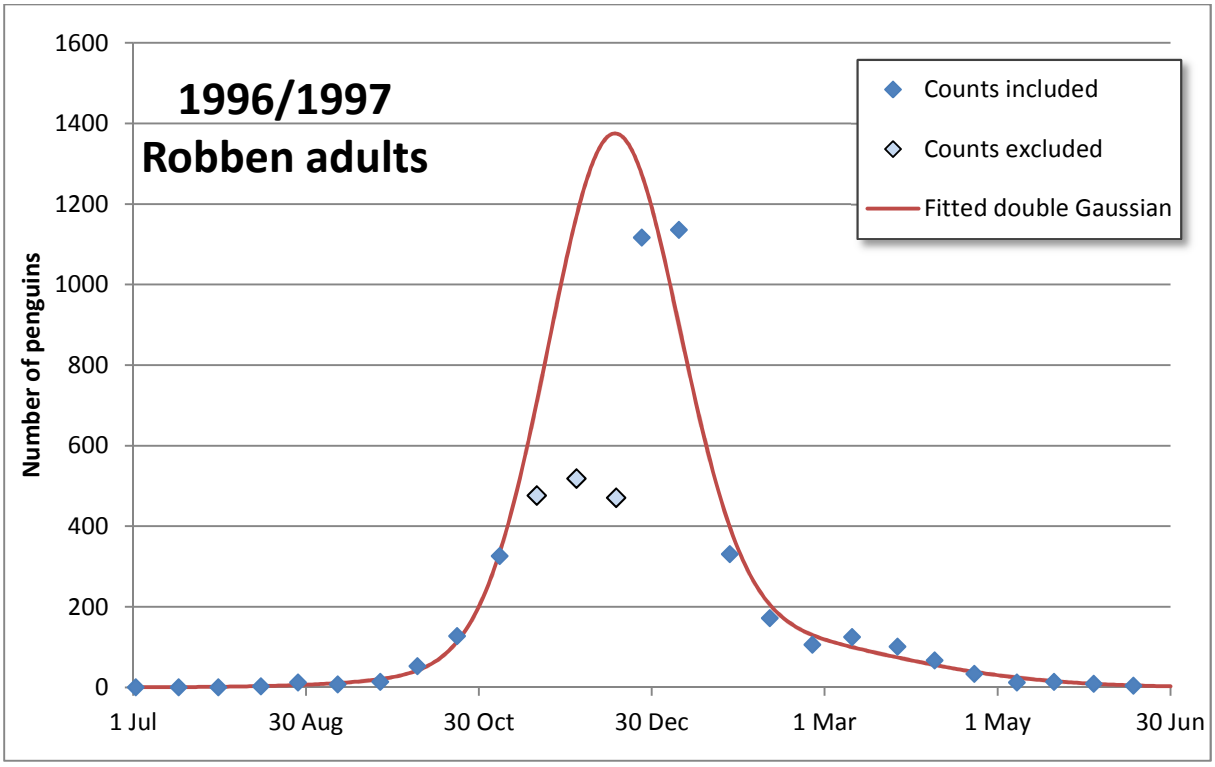

Figure 5: Counts of adult penguins at Robben Island in the 1996/1997 season, showing the double Gaussian curve fitted with the three indicated counts excluded.

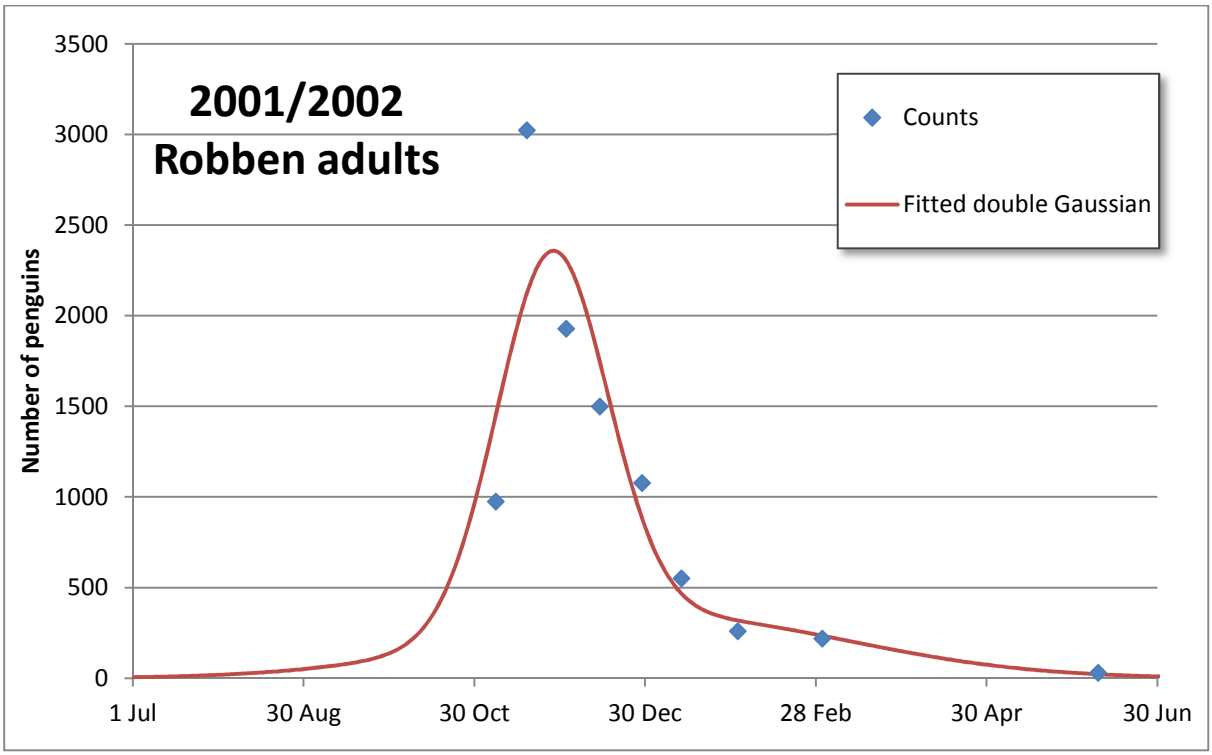

Figure 6: Counts of moulting adult penguins at Robben Island in the 2001/2002 season, showing the double Gaussian curve fitted.

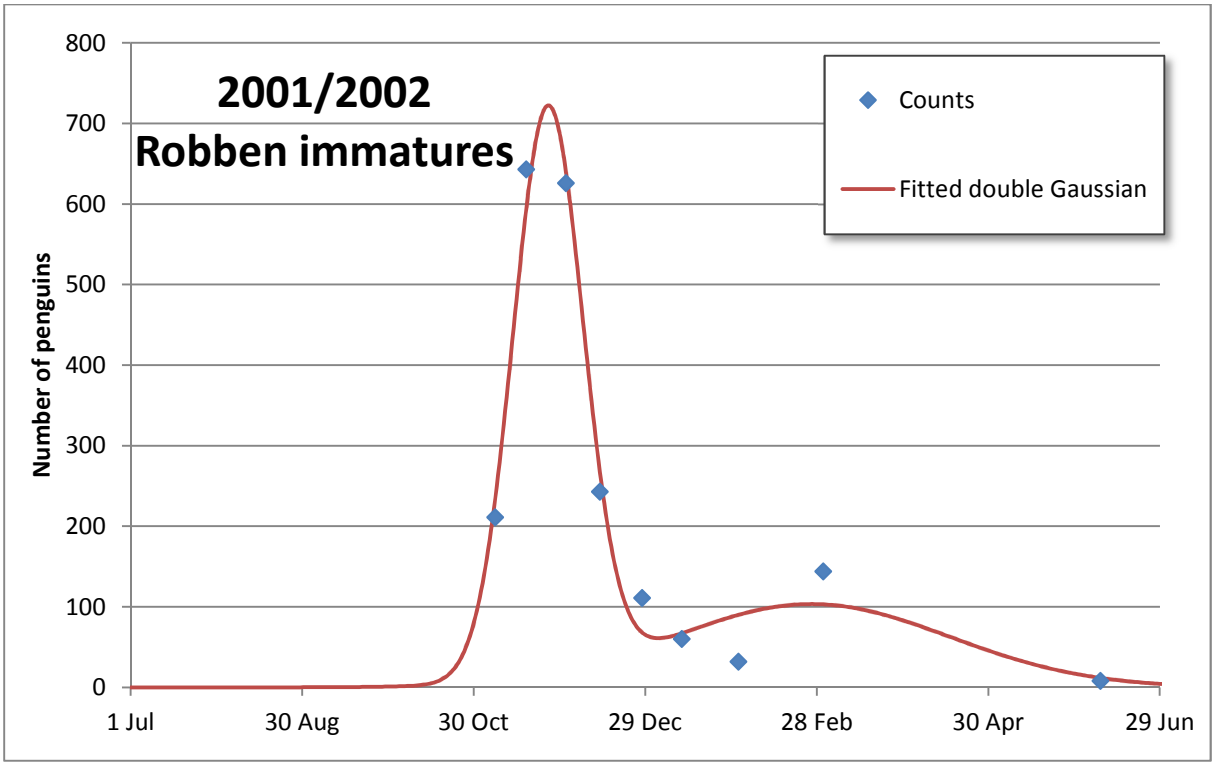

Figure 7: Counts of moulting penguins in immature plumage at Robben Island during the 2001/2002 season, showing the double Gaussian curve fitted.

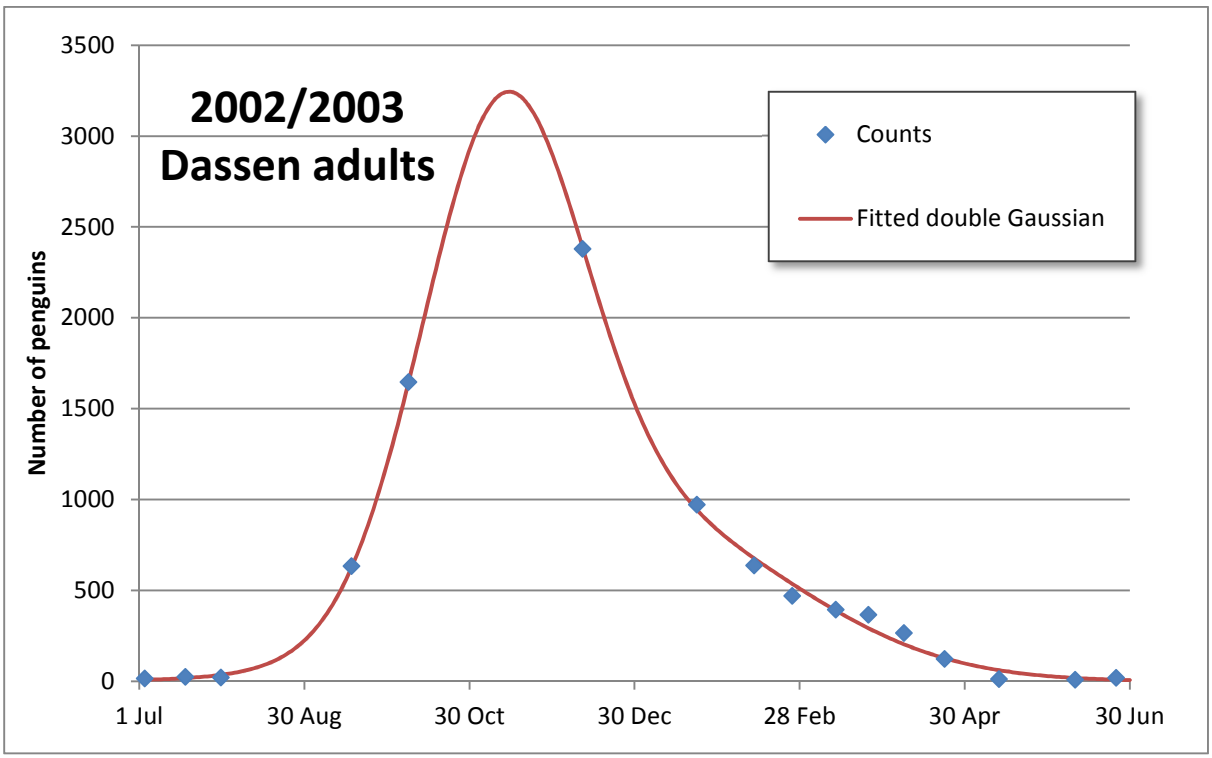

Figure 8: Counts of moulting adult penguins at Dassen Island during the 2002/2003 season, showing the double Gaussian curve fitted.