1 **a) Title:** Survival estimates of Greater Crested Terns (*Thalasseus bergii*) in

2 southern Africa

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21

22

b) Abstract

The nominate race of the Greater Crested Tern (*Thalasseus bergii*) only breeds along the Benguela coast of southern Africa, where its population is increasing, in contrast to the other breeding seabirds in the region that depend on forage fish. Although this population's trends are well known, its demographic parameters remain obscure. We use multi-event capture-recapture-recovery modelling to provide the first survival estimates: survival of birds older than two years was 0.93 (0.91–0.95); second year survival was 0.93 (0.90–0.95) and first year survival 0.80 (0.73–0.85). A resighting of a 34-year old bird is a new longevity record for the species. Population growth rates estimated using a Leslie matrix model including our survival estimates were very similar to estimates from annual counts of the breeding population (7–8% y^{-1}), suggesting that the survival estimates adequately describe the species' demography. High survival rates have contributed to the species recent population increase.

2

48   **c) Text**

49   Introduction

50   Adequate data on the components of demographic change are vital for

51   management of wild populations (Nichols & Williams, 2006). An important

52   parameter is survival, and resulting longevity, as survival has an important

53   influence on population dynamics in K-selected species (Sæther & Bakke, 2000)

54   and, in turn, on our understanding of their capacity to cope with environmental

55   changes (Payo-Payo et al. 2016).

56

57   Seabirds are useful indicators of ecological change (Cury et al., 2011) and are

58   more threatened than other comparable groups of birds (Croxall et al., 2012).

59   They are also generally long-lived, with life histories that include delayed

60   maturation, intermittent breeding and strong dispersal capabilities (Schreiber &

61   Burger, 2001). As a consequence, getting robust demographic data can be

62   difficult; adult survival estimates are available for only ~20% of all seabird species

63   and juvenile survival estimates for < 2% (Lewison et al., 2012).

64

65   The Greater Crested or Swift Tern (*Thalasseus bergii*) is a small, colonial-

66   breeding seabird widely distributed from the southeast Atlantic Ocean east to the

67   west-central Pacific Ocean. The nominate subspecies *T. b. bergii* is endemic to

68   southern Africa, where it breeds from central Namibia to South Africa's Eastern

69   Cape (Cooper et al., 1990). Here they feed predominately on Anchovy *Engraulis*

70   *encrasicolus* (~65% of the diet) and other small, schooling pelagic fish (hereafter

71   forage fish) including Sardine *Sardinops sagax*, Redeye Round-herring *Etrumeus*

72   *whiteheadi* and Horse Mackerel *Trachurus capensis* (Gaglio et al., 2017, Gaglio,

2017). In the late 1980s and early 1990s, numbers breeding in the Western Cape

Province of South Africa, fluctuated between 1,500 and 4,700 pairs (Crawford &

Dyer, 1995). Over the last few decades, while the region's populations of other

seabirds that rely on forage fish have decreased, Greater Crested Tern numbers

have increased (Crawford et al., 2015). In less than 30 years the breeding

population has tripled, with ~14,000 pairs breeding in the Western Cape in 2015

(Department of Environmental Affairs, unpubl. data). This increase has been

attributed to the species' ability to adapt to a recent eastward shift in the

distribution of its main forage fish prey in South Africa (Crawford, 2009). In

particular, Greater Crested Terns have responded by shifting their main breeding

locations from islands in the vicinity of Saldanha Bay south and east to Robben

and Dyer Islands (Crawford, 2009; Crawford et al., 2015). Even though the

species' population trends in the Benguela region are fairly well documented, no

survival estimates exist for this species (Crawford & Dyer, 1995; Crawford, 2009),

hindering our understanding of the underlying ecological drivers of its population

change. We use 45 years of data on marked individuals to estimate survival of

Greater Crested Terns marked in southern Africa breeding colonies.

Material and methods

During 1968–2016, 17,081 pre-fledging Greater Crested Tern chicks were

marked using metal bands along Namibian and South African coast (see Figure

1) of which 67 individuals were resighted in southern Africa during the breeding

season (April–July) and 287 were recovered dead (SAFRING database). In

addition, since 1970 most cohorts were tagged with a year-specific colour band,

allowing estimates of longevity.

4

The goodness-of-fit test (GOF) of the Jolly Movement model for multistate data

was calculated using U-CARE 2.3.2 (Choquet et al. 2009a). GOF allows sources

of heterogeneity in recapture and/or survival (e.g. trap-dependence or transience;

Pradel et al. 2005) to be detected. We detected a significant 'trap-dependence'

effect – unequal probabilities of being re-encountered given the previous

encountered/non-encountered state (Pradel and Sanz-Aguilar 2012). To account

for this effect, we modelled recapture conditional on survival and on the previous

encounter state of the individual (i.e., recapture probabilities differ between birds

encountered and not encountered on the previous occasion, which accounts for

heterogeneity in resighting probabilities of birds settling in areas with different

observer effort). After accounting for trap-dependence, an acceptable variance

inflation factor was obtained ($\hat{c}$ = 1.01, Table 1) and we applied this to all models

constructed using E-SURGE software (Choquet et al., 2009).

Models were constructed in a multi-event, capture-mark-recapture-recovery

frequentist framework (CMRR), which relates the true state of the individual to

the observed event via a series of conditional probabilities (Pradel, 2005). This

modelling framework allowed us to account for trap-awareness and related

phenomena whereby successive capture events are not independent (Pradel &

Sanz-Aguilar, 2012).

Multi-event models use three different kinds of parameters: initial state

probabilities (Π, matrix 1; here all birds were ringed as chicks with a probability

1), transition between states probabilities (Ψ, matrix 2), and event probabilities

(B, matrix 3). We decomposed the transition probabilities into two consecutive

steps: the first (Ψ_1) represents survival probabilities (φ) and the second (Ψ_2)

recapture probabilities (p); event probabilities correspond to the recovery

probability (b). We built a model with four states and three events. The states

were as follows: alive and captured in the previous occasion (Aa), alive and non-

captured in previous occasion (Au), recently dead, i.e. during the previous year

(Dr), and long dead (Dl). Events were: not seen (0), seen alive (1) and recovered

freshly dead (2).

$$\Pi = (1 \quad 0 \quad 0 \quad 0) \tag{1}$$

$$\Psi = \Psi_1 {}_* \Psi_2 = \begin{array}{c} \\ Aa \\ Au \\ Dr \\ Dl \end{array} \overset{\begin{array}{cccc} Aa & Au & Dr & Dl \end{array}}{\begin{pmatrix} \varphi & 0 & 1-\varphi & 0 \\ 0 & \varphi & 1-\varphi & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{pmatrix}} * \begin{array}{c} \\ Aa \\ Au \\ Dr \\ Dl \end{array} \overset{\begin{array}{cccc} Aa & Au & Dr & Dl \end{array}}{\begin{pmatrix} p_{Aa} & 1-p_{Aa} & 0 & 0 \\ p_{Au} & 1-p_{Au} & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}} \tag{2}$$

$$B = \begin{array}{c} \\ Aa \\ Au \\ Dr \\ Dl \end{array} \overset{\begin{array}{ccc} 0 & 1 & 2 \end{array}}{\begin{pmatrix} 0 & 1 & 0 \\ 1 & 0 & 0 \\ 1-b & 0 & b \\ 1 & 0 & 0 \end{pmatrix}} \tag{3}$$

We included a trap-dependence effect in the recapture modelling (differential

recapture probabilities for individuals observed and not observed in the previous

occasion, as indicated by GOF tests). Recruitment age is unknown for Greater

Crested Terns in southern Africa but in Australia they usually recruit between 2

and 3 years old (Del Hoyo et al., 1996; Road et al., 1996). Our initial model

considered 3 age classes (i.e. differences between first year, second year and

adult individuals) assuming that Greater Crested Terns breeding in southern

Africa may recruit at age 3; second year individuals might prospect at colonies

146 and first year individuals should not visit breeding colonies (Langham & Hulsman,

147 1986; Crawford et al., 2002). We tested alternative models considering different

148 age structures and temporal effects. For recovery, we tested whether or not there

149 were any temporal effects. Once the best recapture and recovery structure was

150 found, we examined differences in survival among age classes: first year, second

151 year and older individuals.

152

153 We performed model selection using the second-order Akaike's information

154 criterion corrected for over-dispersion and small sample size (QAICc; Burnham

155 and Anderson, 2002). For each model j, we calculated the Akaike weight, w_j, as

156 an index of its relative plausibility (Burnham & Anderson 2002). Estimates were

157 obtained by model averaging where models contributed to the final estimate

158 according to their w_j (Burnham & Anderson 2002).

159

160 We used ULM-software to construct a Leslie matrix age-structured population

161 model and to examine whether our survival estimates were consistent with the

162 observed population increase (Legendre & Clobert, 1995). We parameterised a

163 simple 3 age-class Leslie matrix model using the survival estimates obtained from

164 the best model to calculate the southern Africa population's growth rate, $λ'$

165 (dominant eigenvalue of the Leslie matrix; Caswell, 2001). We assumed an equal

166 sex ratio at birth, breeding success of 0.5 chicks/pair/year (Gaglio, 2017) and

167 assumed recruitment at age 3.

168

169 The Western Cape breeding population represents around 90% of the southern

170 Africa population, so constitutes a good proxy of its population trend (Kemper,

171 2007; Makhado et al., 2013). Therefore, we used R (R Core Team, 2013) to

172 calculate the observed population growth rate in the Western Cape (λ) and its

173 confidence intervals by regressing the natural log (lm function) of the population

174 counts over a time interval against the amount of time elapsed (Morris & Doak,

175 2002).

176

177 Results

178 Survival probabilities were estimated by model averaging from the best ranked

179 models (M_0 and M_5, Table 2): first-year survival was 0.80 (95% CI: 0.73–0.85),

180 second year survival 0.93 (95% CI: 0.90–0.95) and adult survival 0.93 (95% CI:

181 0.91–0.95). The model with the lowest QAICc value (M_5, Table 2) included

182 survival differences for first year terns and older individuals, temporal, age and

183 trap-dependence effects in the recapture probabilities and a time-dependent

184 effect on recovery.

185

186 The predicted population growth rate was λ' = 1.08 (95% CI: 1.06-1.10), which

187 was similar to the observed population growth rate, λ = 1.07 (95% CI: 1.05–1.08),

188 from 1987 (3,314 pairs) to 2015 (13,904 pairs).

189

190 The oldest bird recorded from cohort colour banding was a 34-year-old tern

191 observed carrying a prey item at the breeding colony on Robben Island on 25

192 February 2013 (Figure 2). The bird was banded as a pre-fledging chick on Marcus

193 Island on 16 April 1979.

194

Discussion

Using long-term monitoring and multi-event CMRR modelling, we provide the first age-dependent estimates of survival for Greater Crested Terns. The first year of life is a critical period during an individual's life (Payo-Payo et al., 2016). As expected, juvenile (i.e. first year) Greater Crested Terns had lower survival probabilities than second year terns and adults, as reported for other tern species (Table 3). Our survival estimates are amongst the highest reported for terns, especially for adult survival estimates (Table 3). By using recovery data, our survival refers to real (not apparent) survival, which might explain why we obtained higher survival rates than many other studies of terns, but our values are similar to those for Royal Terns *Thalasseus maximus* (Collins and Doherty 2006, Table 3). The high adult survival estimate is consistent with the new longevity record for the Greater Crested Tern (although longevity estimates are highly sensitive to the numbers of individuals marked). Five other tern species have been reported to live ≥30 years: the Caspian Tern *Hydroprogne caspia*, the Sandwich Tern *Thalasseus sandvicensis*, the Sooty Tern *Onychoprion fuscatus*, the Common Tern *Sterna hirundo* and the Arctic Tern *Sterna paradisea* (Burger & Gochfeld, 2001; de Magalhães & Costa, 2009).

The high adult survival estimate for Greater Crested Terns in the southern Benguela is somewhat anomalous given the widespread changes that have occurred in this ecosystem in recent years (e.g. Crawford et al. 2015). Although we do not account for temporal effects on survival it is possible that survival was higher in the 1990s when fish abundance increased greatly, then fell post 2000 after changes in food abundance occurred. Other endemic seabird species, such as the African Penguin *Spheniscus demersus*, Cape Gannet *Morus capensis and*

220   Cape Cormorant *Phalacrocorax capensis,* which feed on similar forage fish

221   species as Greater Crested Terns, have experienced decreases in adult survival

222   over the last two-decades (Distiller et al., 2012; Sherley et al., 2014; Crawford et

223   al., 2016). In addition, first-year survival of African Penguins has generally been

224   low (<0.25) since the mid-2000s (Sherley et al., 2014) when large, adult forage

225   fish became scarce off western South Africa. It is possible that African Penguins,

226   Cape Gannets and Cape Cormorants are more dependent on anchovy and

227   sardine than Greater Crested Terns, which have a variety of feeding methods

228   (see Gaglio, 2017). Indeed, anchovy made up 84% (by mass) of the diet fed to

229   penguin chicks at Robben Island between 2001 and 2009 (Sherley et al., 2013)

230   versus 65% (by number) of the diet of Terns at the same locality between 2013

231   and 2015 (Gaglio, 2017). However, the diet of Cape Cormorants breeding in the

232   Western Cape between 1984 and 1992 was 64% anchovy (by mass; Cook et al.,

233   2012). Therefore, Terns may be less vulnerable to sudden changes in forage fish

234   availability (Futuyma & Moreno, 1988; Gaglio, 2017), but diet studies that overlap

235   in space and time would be needed to confirm this hypothesis.

236   Life-history theory predicts that adult survival should be the key parameter driving

237   population functioning. However, juvenile survival can be an important source of

238   variability in population dynamics (Votier et al., 2008; Sergio et al., 2011). Given

239   the low fecundity (maximum one chick per pair per year), high survival rates for

240   all age classes were necessary to maintain the growth of the Greater Crested

241   Tern population over the last two decades (Crawford, 2009). Although this

242   increase seems at odds with the large declines in other seabirds using the

243   Western Cape, the small body-size of the Greater Crested Tern may mean they

244   are able to sustain high adult and first-year survival on forage fish recruits (which

245 remain abundant off the west coast; Hutchings et al. 2009). This in turn makes

246 them less dependent on adult forage fish than larger penguins and gannets

247 appear to be (see above, Distiller et al. 2012, Sherley et al. 2014). Moreover, a

248 decrease in the numbers of migrant terns – especially Common Terns *Sterna*

249 *hirundo* – wintering in the southern Benguela might have reduced competition for

250 prey, therefore resulting in higher Greater Crested Tern fitness (Ryan 2013).

251 CMRR methods are vulnerable to low rates of recapture of marked animals

252 (Lebreton et al., 1992) and age-dependent recovery models may cause

253 parameter redundancy when only juveniles are marked (Lakhani & Newton,

254 1983). However, by combining recoveries and a few resightings we were able to

255 estimate survival. In fact, the population growth rates estimated from population

256 counts and estimates from a Leslie matrix with our survival and available breeding

257 success estimates were highly consistent. Robust estimates of demographic

258 parameters allow accurate diagnoses of the drivers of population change,

259 comparative studies, and targeted management action (Morris & Doak, 2002).

260 Although our results provide some insights into the mechanisms underlying the

261 recent increase in their population, future work linking demographic parameters

262 to the changing environmental conditions would shed further light on why Greater

263 Crested Terns appear to be one of the Benguela ecosystem's few seabird

264 winners.

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482   **e) Tables and tabulations**

483   **Table 1**. Goodness of fit (GOF) tests for a Jolly Movement model for Greater

484   Crested Terns breeding in southern Africa. χ^2=test value; df, degrees of

485   freedom; ĉ, variance inflation factor, i.e. χ^2/df. Test components are as in Pradel

486   et al. (2003). The GOF component 3G SR tests for the presence of transients,

487   i.e. individuals that are marked and are never recaptured or resighted; M.ITEC

component tests for the presence of trap-dependence; and "final $\hat{c}$" shows the
overdispersion coefficient after correcting for these trap-dependence and
transient effects in the starting models run in E-SURGE. 3G SM and LTEC have
no direct biological interpretation but this test components are as in (Pradel et
al., 2003).

Test	χ^2	p-value	df	$\hat{c}$
3G.SM	18.23	0.25	15.00	1.22
3G.SR	0.00	1.00	3.00	0.00
ITEC	120.24	0.00	30.00	4.01
LTEC	65.62	0.17	65.00	1.01
GLOBAL	204.4	0.00	113.00	1.81

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506 **Table 2.** Model selection for survival (Φ), recapture (p) and recovery probabilities

507 (b): w, trap-dependence; an, n age classes modelled; t, time; cst, constant; "+",

508 additive effect; NP, number of parameters; DEV, deviance; QAICc, second-order

509 corrected Akaike's information criterion; ΔQAICc, QAICc difference to the best

510 model; w_j: Akaike weight.

	Model formulation							
	Survival	Recapture	Recovery	NP	DEV	$QAIC_C$	$\Delta QAIC_C$	w_j
M_0	Φ_{a3}	p_{a3+w+t}	b_t	87	5513.67	5632.96	0.88	0.39
M_1	Φ_{a3}	p_{a3+w+t}	b_{cst}	50	5617.49	5662.16	30.08	0.00
M_2	Φ_{a3}	p_{a2+w+t}	b_t	85	5533.17	5649.23	17.15	0.00
M_3	Φ_{a3}	p_{w+t}	b_t	84	5536.56	5650.56	18.48	0.00
M_4	Φ_{a3}	p_w	b_t	48	5685.54	5725.52	93.44	0.00
M_5	Φ_{a2}	p_{a3+w+t}	b_t	86	5513.67	5632.08	0.00	0.61
M_6	Φ_{acst}	p_{a3+w+t}	b_t	85	5556.59	5672.42	40.34	0.00

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Table 3. Tern juvenile ($\Phi_{Juvenile}$) and adult survival (Φ_{Adult}) estimates with 95% confidence intervals (in brackets).

Species	Location	Years	$\Phi_{Juvenile}$		Φ_{Adult}		Reference
Thalasseus maximus	California, USA	1988-2004	0.86	(0.29-0.96)	0.95	(0.88-0.98)	(Collins & Doherty, 2006)
T. bergii	W Cape, South Africa	1968-2015	0.80	(0.73-0.85)	0.93	(0.91-0.95)	This study
T. sandvicensis					0.63-0.83		(Møller 1983)
Hydroprogne caspia					0.87-0.91		(Cuthbert & Wires, 1999)
Sterna hirundo	Cape Cod, USA	1940-1955	0.30-0.40		0.75		(Austin and Austin 1956)
	Bird Is., USA	1940-1956	0.60-0.10		0.89-0.93		(Nisbet, 1978)

		1970-1975	0.07-0.13				
	Bird Is., USA	1995-1997	Φ_{2-3} = 0.54	(0.24 -0.81)	Φ_{4-19} = 0.87	(0.72-0.94)	(Nisbet & Cam, 2002)
					$\Phi_{a>20}$ = 0.63	(0.15-0.94)	
	Great Gull Is., USA				0.92		(Dicostanzo, 1980)
	Wilhelmshaven, Germany	1992-1995	0.39	(0.22-0.48)	0.85-0.88[b]		(Becker & Wendeln, 1997)
	Wilhelmshaven		0.88-0.92		0.64-0.92		(Zhang et al., 2015)
S. dougallii	Falkner Is., USA	1993-2002			female 0.83	(0.78-0.88)	(Nichols et al., 2004)
					male 0.78	(0.73-0.84)	
	Falkner Is.	1988-1998	0.53-0.57		0.78-0.89		(Spendelow et al., 2002)
	Falkner Is.	1978-1980			0.74-0.75		(Spendelow, 1989)

	Falkner Is.	1979-1988		0.77		(Gould & Nichols, 1998)
	Buzzards Bay, USA	1988-1992		(0.74-0.84)		(Spendelow et al., 1995)
	Long Is., USA	1988-1998	0.37	0.83	(0.77-0.89)	(Lebreton et al., 2003)
	NW Europe	1992-2007	0.74	0.86		(Ratcliffe et al., 2008)
	USA	1988-2006		0.84	(0.83-0.85)	(Spendelow et al., 2008)
	Puerto Rico	1991-1994		0.71-0.80		(Shealer et al., 2005)
	Seychelles	2002-2007		0.81	(0.75-0.87)	(Monticelli et al., 2008)
S. paradisaea	Farne Is., UK	1966-1967		0.87	(0.83-0.91)	(Coulson & Horobin, 1976)
	Farne Is., UK	1952-1956		0.82		(Cullen, 1957)
	Gulf of Maine,	1999-2005		0.70-0.96		(Devlin et al., 2008)

Species	Location	Years	Survival	(CI)	Survival	(CI)	Reference
S. vittata bethunei	Snares Is., New Zealand	1967-2007	0.42	(0.26-0.58)	0.94	(0.88-0.99)	(Sagar et al., 2007)
Onychoprion fuscata	Seychelles	1993-1995			0.91	(0.89-0.93)	(Feare & Doherty, 2004)
O. anaethetus	W Australia				0.78-0.83		(Dunlop & Jenkins, 1994)
Sternula antillarum	Venice, USA	1978-1989	0.81	(0.72-0.87)	0.92	(0.88-0.95)	(Massey et al., 1992)
	Mississipi R.	1987-1992			0.85	(0.73-0.95)	(Renken & Smith, 1995)
	Camp Pendleton, USA	1994-1995			0.89 -0.92		(Collins et al., 1996)
S. balaenarum	Namibia	2000-2010	0.59	(0.48-0.68)	0.87	(0.73-0.96)	(Braby et al., 2011)
Anous minutus	Vatu-i-Ra, Fiji	1974-1982			0.75		(Tarburton, 1987) (Zhang et al., 2015)

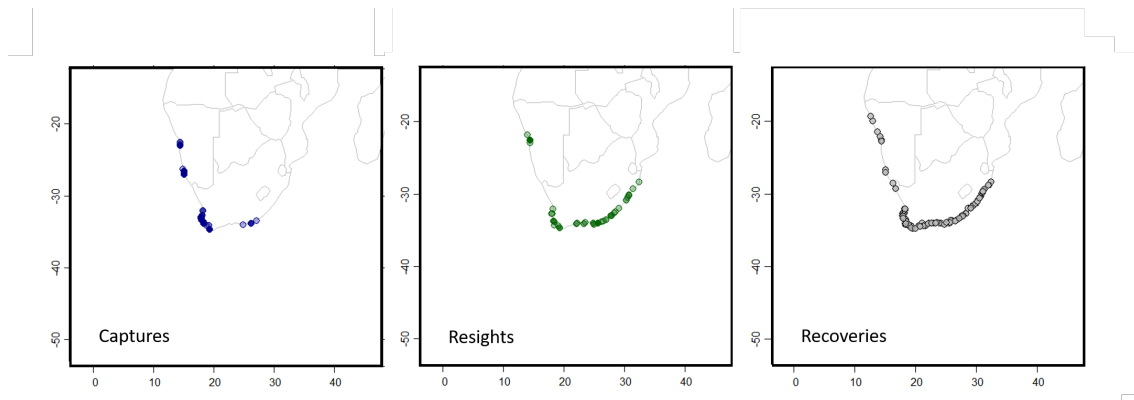|							
Chlidonias hybrida	New Zealand	1998-2001			0.80	(0.57-0.98)	(Keedwell, 2002)
					0.92	(0.58-0.99)	
	Poland	1993-2011	0.54	(0.49-0.59)	0.80	(0.70-0.90)	(Ledwoń et al., 2013)
C. niger	Netherlands	1993-1999	0.59		0.85		(Winden & Horssen, 2008)

g) Legends for figures

Figure 1. Distribution of Swift Tern captures (blue), resights (green) and recoveries (grey) in southern Africa.
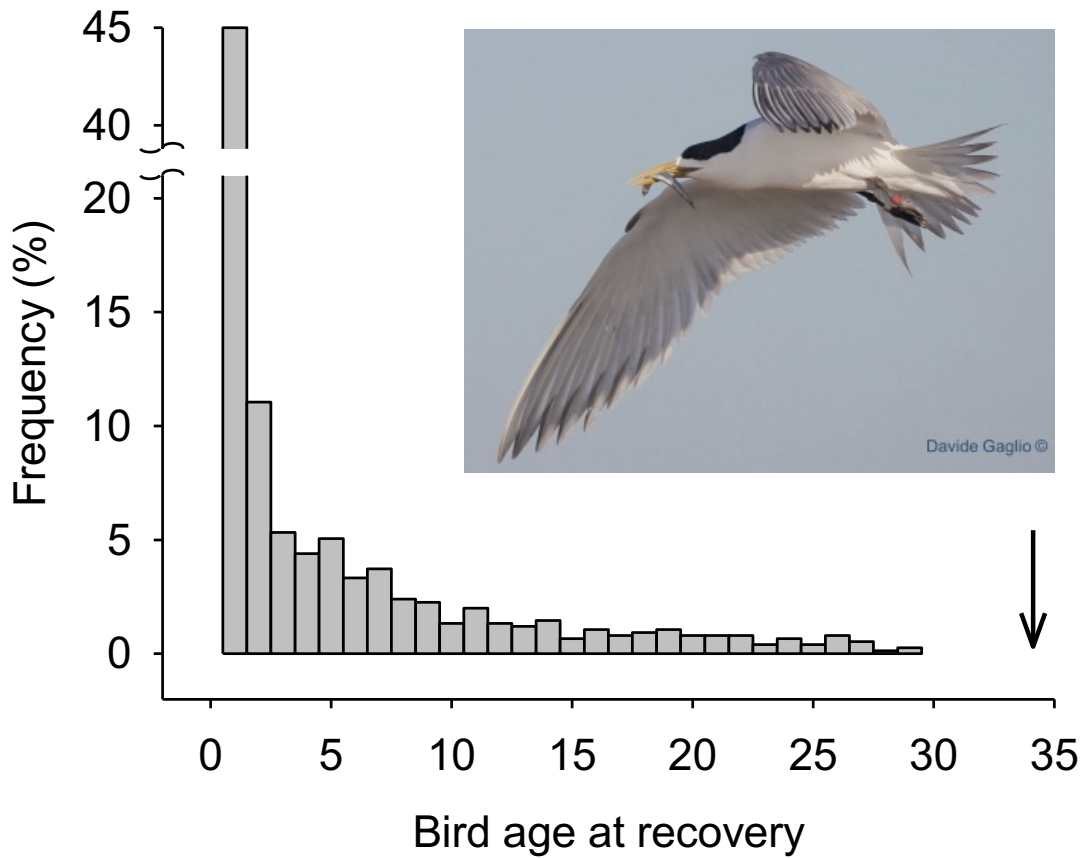
Figure 2: Frequency distribution (%) of recovery age of the Greater Crested Tern (*Thalasseus bergii*) in southern Africa. The arrow represents the resight of Greater Crested Tern banded as a chick on Marcus Island (33°02.6'S, 17°58.2'E) in April 1979 and re-sighted photographically at Robben Island (33°48.4'S 18°22.0'E) breeding colony in February 2013 (photo © Davide Gaglio).