

SHORT COMMUNICATION

Preliminary survival and movement data for a declining population of Flesh-footed Shearwater (*Ardenna carneipes*) in Western Australia provides insights into marine threats

JENNIFER L. LAVERS, SIMEON LISOVSKI and ALEXANDER L. BOND

Summary

Seabirds face diverse threats on their breeding islands and while at sea. Human activities have been linked to the decline of seabird populations, yet over-wintering areas typically receive little or no protection. Adult survival rates, a crucial parameter for population persistence in long-lived species, tend to be spatially or temporally restricted for many seabird species, limiting our understanding of factors driving population trends at some sites. We used bio-loggers to study the migration of Western Australian Flesh-footed Shearwaters (*Ardenna carneipes carneipes*) and estimated adult survival over five years. Western Australia is home to around 35% of the world's breeding Flesh-footed Shearwaters, a population which was up-listed to Vulnerable in 2015. During the austral winter, shearwaters migrated across the central Indian Ocean to their non-breeding grounds off western Sri Lanka. Low site fidelity on breeding islands, mortality of adult birds at sea (e.g., fisheries bycatch), and low annual breeding frequency likely contributed to the low estimated annual adult survival (2011-2015: $\phi = 0.634-0.835$).

Keywords: annual adult survival; at-sea threats; over-wintering grounds

Running head: Shearwater survival and movement

Introduction

Many seabird populations are declining, particularly the tubenoses (Procellariiformes; Croxall et al. 2012). Marine-based threats are often implicated in these declines, as negative interactions (e.g., bycatch in fisheries) contribute to mortality of adults and juveniles at-sea (Lewison and Crowder 2003; Lewison et al. 2004). The movements of seabirds originally inferred from banding studies and shipboard surveys have been refined through data from

miniaturized tracking devices (e.g., Brothers et al. 1997; Hedd et al. 2012). Understanding the
35 complete annual cycle, including non-breeding distributions, where migration corridors exist,
migratory connectivity, and foraging behaviours is key to predicting how populations will
respond to changing climate or prey stocks (Grémillet and Boulinier 2009; Marra et al. 2015),
and anthropogenic activities (Lewison and Crowder 2003; Anderson et al. 2011). Knowledge
40 of the physical and biological processes that influence seabird habitat selection may also
assist with identifying significant areas as targets for marine conservation (Lavers et al.
2014b).

Despite its large size and ship-following habits, the Flesh-footed Shearwater (*Ardenna*
carneipes) has been one of the least studied seabirds in Australia (Powell 2009). They breed
on islands in southern Australia (Lavers 2015) and northern New Zealand (Waugh et al.
45 2013), with many populations known or suspected to be declining (Reid et al. 2013a; Waugh
et al. 2013; Lavers 2015). Mitigation of some threats, such as cessation of harvesting and
reductions in fisheries bycatch off the east coast of Australia, has not reversed population
declines on some islands (Gaze 2000; Reid et al. 2013a). Increasing awareness of the
diversity of pressures faced by Flesh-footed Shearwaters throughout their breeding range, and
50 evidence of a decline at their largest breeding colony on Lord Howe Island (Priddel et al.
2006), led to the New South Wales population (~16,500 breeding pairs; Reid et al. 2013a)
being listed as Vulnerable in 2000 (Lunney et al. 2000). More recently, Flesh-footed
Shearwaters breeding in New Zealand and Western Australia (combined total of ~45,000
pairs accounting for ~60% of the world's population; Waugh et al. 2013; Lavers 2015) have
55 also been up-listed to Vulnerable (Robertson et al. 2013; DPaW 2015). Owing to recent
population declines, the species was up-listed to Near Threatened on the IUCN Red List in
2017 (BirdLife International 2017).

Significant numbers of Flesh-footed Shearwaters are taken as bycatch in the Tasman
Sea (Waugh et al. 2012; Lavers et al. 2013; Richard & Abraham 2013) and North Pacific
60 Ocean (DeGange and Day 1991; Tuck et al. 2003; Ogi 2008; Artukhin et al. 2010) where
birds from New Zealand and Lord Howe Island forage and over-winter (Rayner et al. 2011;
Lavers et al. 2013; Reid et al. 2013b). Bycatch of Flesh-footed Shearwaters in Western
Australia is also a significant issue, with >500 birds (mostly breeding adults) killed per year
(Dunlop 2007; Lavers 2015). A lack of information on demographics, the timing of
65 migration, routes, and location of wintering grounds for Western Australian Flesh-footed
Shearwaters limits our ability to identify additional areas of overlap with marine threats that
may influence population trends at the breeding colonies. To inform conservation efforts

more effectively, we report preliminary annual survival estimates, and non-breeding movements determined by light-level geolocators, for adult Flesh-footed Shearwaters from Western Australia.

METHODS

Study site and capture methods. Shelter (or Muttonbird) Island is 130 m offshore of Torbay, Western Australia (35°03'S, 117°41'E), where ~200 pairs of Flesh-footed Shearwaters breed (Lavers 2015). Breeding shearwaters were captured from burrows over a two-week period in mid- to late-incubation in 2011-2015. A uniquely numbered band was placed on the right leg. Sex was determined using measurements of head-bill length and minimum bill-depth from both members of breeding pairs (Thalman et al. 2007).

Tag deployment and analysis. Star-Oddi light-level geolocators (mass of tag and attachment: 3 g) were attached to the left leg of 10 adult birds (mean body mass: 599 g) on 22 January 2012. Maximum light measurements were recorded in every 20-minute period as well as water temperature after 20 minutes when the tag was wet, which acted as auxiliary environmental data for estimating location. Prior to deployment, tags were placed in an open area at the deployment location for five days to produce light recordings from which solar elevation estimates could be calculated. After retrieval, raw archived tag data were downloaded, and adjusted for internal clock drift.

At-sea locations were estimated from light intensity recordings using a threshold method: estimation of locations based on sunrise and sunset events and a threshold of 2.5 units (Lisovski *et al.* 2012). The corresponding sun elevation angle was estimated using sunrise and sunset times recorded after the deployment of the loggers and when the birds were known to be at the breeding sites. To refine location estimates, we used recorded sea-surface temperature, a spatial mask, and a movement model in a Bayesian framework implemented in the R package 'SGAT' (Sumner, Wotherspoon & Hindell 2009; Wotherspoon, Sumner & Lisovski 2013). The twilight model allows us to estimate locations for a single sunrise/sunset with an expected error distribution. The discrepancy between observed and expected times of twilight was assumed to follow a log-normal distribution. For sunrise, positive values corresponded to an observed sunrise occurring after the expected time of sunrise, whereas positive values for sunset corresponded to an observed sunset before the expected time of sunset. We chose a conservative prior (log-normal distribution: meanlog = 1.5, sdlog = 0.8) since error in twilight detection could vary over the annual cycle. The land

mask was based on the premise that birds only utilise marine environments (probability of 0 for positions on land). The probability on sea was further refined for each individual and each day separately, using remotely sensed sea-surface temperatures (weekly means on a 0.25×0.25 degree resolution: www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html) and the 60% and 95% quartiles of the temperature profiles experienced by the birds. A probability of 1 was assigned to areas with surface temperatures falling within the 60% percentile of the recorded temperature profile. Areas with surface temperatures within the 95% and 100% of the recorded temperature quartiles were assigned with probabilities of 0.5 and 0.1 respectively. The potential flight speeds were modelled following a gamma distribution (shape = 1.3, rate = 0.1). For each individual, we used these parameters to run the Markov chain Monte Carlo simulation. The first 10,000 iterations were used for burn-in and tuning. A further 40,000 samples were drawn to evaluate chain convergence before drawing another 5,000 samples to describe the posterior distribution.

115

Adult survival analysis. We captured and banded 114 adult birds from their burrows in November 2012, December 2013, January 2015, and December 2015, and coded breeding seasons by the year in which they began (2011-2012 is denoted as “2011”), resulting in four periods over which to estimate survival (2011-2012 through 2015-2016 breeding seasons). We estimated apparent adult survival (ϕ) and encounter probabilities (p) following Lebreton et al. (1992) in Program MARK (White and Burnham 1999). Given the relatively small number of marked individuals, we did not formally consider emigration (Pradel et al. 1997; Prévot-Julliard et al. 1998), but searched for marked birds in a 10 m buffer around three small, well-defined sub-colonies (see Discussion and Figure S1). We also did not consider models including breeding propensity, but enumerated birds with encounter histories that suggested skipped breeding (i.e., birds not present for 1-2 years between encounters). Birds that had not been seen in the last two encounter periods could not be assigned confidently.

We constructed four models with time-varying and time-invariant estimates of ϕ and p (Table S1). Models were ranked using Akaike’s Information Criteria adjusted for small sample size (AIC_c; Akaike 1974; Burnham and Anderson 2002). We tested for goodness-of-fit using 100 parametric bootstraps to generate the mean deviance and overdispersion (Jones et al. 2002; Bond et al. 2013). The observed deviance and overdispersion were then divided by their respective bootstrap mean, and the higher of these two values was used to adjust for overdispersion and extrabinomial error (\hat{c}). This value of \hat{c} was used to adjust model likelihoods using quasi-AIC_c (QAIC_c). We generated parameter estimates and unconditional

135

standard errors (\widehat{SE}) weighted across all four models by Akaike weight (w_i ; Burnham and Anderson 2002), and examined mark-recapture model assumptions using TEST 2 and TEST 3 in U-CARE (Choquet et al. 2009).

140

RESULTS

Tracking data. Three geolocators were recovered from shearwaters on 27 November 2012 (two additional birds were recaptured, but the tags were missing). The three recovered tags ceased operating after 110-130 days, providing data for a total of 373 days at sea (Table 1). Birds A (σ) and B (ϕ) reared chicks to fledging successfully while the chick of bird C (ϕ) died of an unknown cause. The post-breeding migration of successful breeders commenced between 2-16 May with bird A requiring 6.5 days to travel northwest ~5,900 km to the south coast of Sri Lanka (Figure 1a). Bird C remained in the southern Indian Ocean until ~8 April 2011 before heading north along the coast of Western Australia for approximately 23 days and then west towards Sri Lanka (Figure 1c; Table 1).

150

Adult survival. Of the 114 breeding adults banded during December and January 2012-2015, 38 were recaptured during 2012-2015. An additional 22 adults were banded in 2015-2016 (i.e., no opportunity for recapture).

There was no trap-dependence (TEST 2.CT: $\chi^2_2 = 1.782$, $p = 0.41$; TEST 2.CL: $\chi^2_1 = 0.936$, $p = 0.33$), and survival did not depend on when animals were marked or recaptured (TEST 3.SR: $\chi^2_3 = 1.467$, $p = 0.69$; TEST 3.SM: $\chi^2_2 = 0.000$; $p = 0.99$). The top-ranked model included variable survival and a constant encounter probability ($w_i = 0.46$), followed by a model in which survival was constant over time, but encounter probability varied ($w_i = 0.26$, $\Delta QAIC_c = 1.16$), and one where both survival and encounter probabilities were constant ($w_i = 0.23$, $\Delta QAIC_c = 1.40$). The model where survival and encounter probabilities varied over time received the least support (Table S1). Model-averaged parameter estimates gave annual apparent survival rates ($\pm \widehat{SE}$) between 0.634 ± 0.130 and 0.835 ± 0.164 , and encounter probabilities between 0.391 ± 0.086 and 0.486 ± 0.147 (Table 2). **Overall, the annual survival and encounter probabilities over the 2011-2015 study period were 0.731 ± 0.073 SE (95% CI: 0.567-0.849) and 0.428 ± 0.078 SE (95% CI: 0.286-0.584), respectively.**

160

Of the 114 marked individuals, we determined breeding propensity for 48: 12 (25%) were absent in one ($n = 7$) or two ($n = 5$) years of the study. Among marked individuals, 30% of birds bred in the next breeding season given that they bred in the current season, though

170 this included birds which were never encountered subsequently. Using only birds known to be alive, 50% of birds were breeding the following year.

DISCUSSION

We provide much needed insight into the movement and survival of a declining population of Flesh-footed Shearwaters from Western Australia. Based on at-sea observations, Gibson-Hill
175 (1953) and De Silva and Perera (1995) predicted that Western Australian Flesh-footed Shearwaters would overwinter in the northern Indian Ocean. The limited geolocator data from 2012 confirm at least a portion of the Western Australian Flesh-footed Shearwater population spends the non-breeding period in the Arabian Sea and Bay of Bengal (Figure 1). Incomplete tracking data (GPS devices ceased transmission in the central Indian Ocean) for
180 Flesh-footed Shearwaters from King George Sound, Western Australia, also indicated this migration route and over-wintering area (Powell 2009). This region is highly productive and a major upwelling region that attracts a diversity of marine predators (Prasad and Nair 1960; Ballance et al. 1996; Vinayachandran et al. 2004; Catry et al. 2009). Wintering Flesh-footed Shearwaters also appeared to exploit this area, being one of the most commonly recorded
185 seabirds in the region, and in the highly productive waters of the Gulf of Oman (Nezlin et al. 2007) during mid-April to August (Ballance et al. 1996; Campbell et al. 2017), suggesting the area is frequented by the Western Australian breeding population.

The timing of departure from the breeding colony varies by location and year, with the most tracked Flesh-footed Shearwaters from Lord Howe Island (2005-2008; Reid et al.
190 2012) and New Zealand (2006; Rayner et al. 2011) departing between 20-30 April. In Western Australia, our data indicate departures between 2-16 May 2012 (Table 1) while five adult shearwaters carrying GPS satellite tags in 2008 departed King George Sound as early as 23 March (Powell 2009). The overall timing of the breeding season does not differ among sites (Warham 1958; Powell et al. 2007). The eastern population of Flesh-footed Shearwaters
195 requires around 20 days to migrate 9,000 km to their wintering grounds in the Sea of Japan (Rayner et al. 2011; Reid et al. 2013b), while those from Western Australia reach their wintering grounds off Sri Lanka (~5,900 km; Table 1) in around six days. Seabird flight is strongly influenced by wind (Spear and Ainley 1997; Weimerskirch et al. 2012; Yonehara et al. 2016), with migration following low-cost “wind-highways” linking breeding and
200 wintering areas (Felicísimo et al. 2008). During May, Western Australian shearwaters completing their migration likely exploit the Southwest Monsoon Current which flows

northward, then curves east over the Arabian Sea and southeast towards India (Pocklington 1979; de Vos et al. 2013).

Our estimates of adult Flesh-footed Shearwater survival, while based on a small
205 sample, are low compared to other shearwaters (Table S2). Adult survival could be
influenced negatively by several factors, including disturbance from humans and feral species
(Lavers 2015), climate change and trophic decline (Bond and Lavers 2014), ingested plastic,
and contaminants (Lavers et al. 2014a). Western Australian Flesh-footed Shearwaters tracked
using GPS in 2015 (Lavers unpublished data) suggests adult birds forage in coastal waters
210 during the breeding season, only occasionally venturing beyond the continental shelf (Powell
2009). The cooler inshore waters around the mouth of King George Sound are spawning
grounds for Australian pilchards (*Sardinops sagax neopilchardus*) (Fletcher and Tregonning
1992), the shearwaters' key prey species (Lavers 2015). This reliance on pilchards, combined
with the species' gregarious and aggressive nature around fishing vessels (Wahl and
215 Heinemann 1969), brings Flesh-footed Shearwaters into regular contact with purse seiners
targeting pilchards in King George Sound (Dunlop 2007; Lavers 2015).

Flesh-footed Shearwaters breeding in New Zealand are exposed to many of these
same pressures (Waugh et al. 2008; Bond and Lavers 2011; Buxton et al. 2013), yet adult
survival is higher (75.6 to 94.0%; Barbraud et al. 2014) than in Western Australia (Table 2).
220 The low encounter rate at Shelter Island may explain this discrepancy, reflecting emigration
to nearby colonies or low breeding propensity. Breeding site fidelity is high in
Procellariiformes (Warham 1990; Brooke 2004), including some Flesh-footed Shearwater
populations (Barbraud et al. 2014). Low nest-site fidelity could result from human
disturbance (Carey 2011), and Shelter Island is visited often by the public. The low survival
225 estimates from Shelter Island could also indicate a lower rate of mate retention. Birds whose
mate did not survive (e.g., killed as bycatch) would need to find a new mate, which could
manifest in lower nest-site fidelity and therefore reduced probability of recapture (Mills and
Ryan 2005).

Some shearwaters, including Flesh-footed Shearwaters in New Zealand, may not
230 breed annually (Mougin et al. 1997; Waugh et al. 2014), similar to our findings. Many factors
influence whether individuals breed in a given year, including prior breeding success,
disturbance, and survival/return of a partner (Chastel 1995; Le Bohec et al. 2007; Finkelstein
et al. 2010). Of Flesh-footed Shearwaters encountered at least once after marking, half were
not encountered the year following a breeding attempt, suggesting a relatively low breeding
235 frequency relative to similar species (typically > 75%; Chastel 1995). The small number of

marked birds relative to the number of parameters in a multi-state model was too small to examine breeding propensity (Burnham and Anderson 2002).

240 Finally, heavy rainfall events can result in nest abandonment by burrowing seabirds (Thompson and Furness 1991; Tiller et al. 2013) and are implicated in the low site fidelity observed in December 2012 and 2015 when storms flooded burrows on Shelter Island (Lavers pers. obs.). To account for this movement, recapture effort was expanded to include unmarked burrows within a 10 m radius of each sub-colony. However, during subsequent breeding seasons, some banded birds were found breeding in new burrows up to 50 m away from their original capture location indicating a high degree of movement within the colony.
245 The survival estimate for Shelter Island is, therefore, conservative.

Factors influencing the survival of Flesh-footed Shearwaters on their overwintering grounds are poorly understood. Large-scale fishing fleets operate in the northern Indian Ocean, and data on seabird bycatch are extremely limited due to lack of reporting, however Flesh-footed Shearwaters have been observed following, and negatively interacting with, vessels in this area (Huang and Liu 2010; IOTC 2015). Small numbers are harvested and sold by local fishermen in southern India after the birds become hooked (Abdulali and Grubh 1982).
250

As sentinels of ocean health, seabirds, including those from Western Australia, tell a worrying story of increasing levels of marine pollution, changing oceanography and climate, and reductions in fish stocks (Bond and Lavers 2011; Chambers et al. 2011; Dunlop et al. 2013). Seabirds face pressures both on land and at sea, yet factors contributing to mortality and morbidity are often examined in isolation (Lavers 2007; Costello et al. 2010; Coll et al. 2012). Effective conservation requires targeted on-island management with concurrent protection of areas used by seabirds during breeding, migration, and over-wintering (Louzao et al. 2006; Lavers et al. 2014b). Enhanced protection of productive upwelling zones that form key staging grounds for Flesh-footed Shearwaters would provide much-needed protection for this declining species, as well as a suite of marine wildlife that also use these habitats.
260

265 **ACKNOWLEDGEMENTS**

BirdLife Tasmania, Trading Consultants Ltd, W.V. Scott Charitable Trust, and the Integrated Marine Observing System (IMOS) provided funding or equipment for this research. Special thanks to C. & G. Biddulph, P. Collins, A. Fidler, M. Hindell, C. McMahon, J. Pridham, P. Sharp, M. Stadler, S. Stuckenbrock, S. Toole, the Two Hands Project, and V. Wellington for

270 providing generous support. Discussions with A. Breton improved the survival analysis.
Research was undertaken with approval from the University of Tasmania animal ethics
committee (permit no. A12279 and A13598) and Western Australian Department of Parks
and Wildlife (permit no. CE004240 and SF010159). The manuscript benefited from
discussions with A. Kumar, R. Jeyabaskaran, M. Hindell, J. Praveen, and two anonymous
275 reviewers improved previous drafts.

LITERATURE CITED

- Abdulali, H. and Grubh, R. B. (1982) Pink-footed Shearwater [*Procellaria carneipes*
(Gould)] in India. *J Bombay Nat Hist Soc* 79:666-667.
- 280 Akaike, H. (1974) A new look at the statistical model identification. *IEEE Trans Automat
Contr* 19:716-723.
- Anderson, O. R. J., Small, C. J., Croxall, J. P., Dunn, E. K., Sullivan, B. J., Yates, O. and
Black, A. (2011) Global seabird bycatch in longline fisheries. *Endanger Species Res* 14:91-
106.
- 285 Artukhin, Y. B., Burkanov, V. N. and Nikulin, V. S. (2010) Прилов морских птиц и
млекопитающих на дрейфтерном промысле лососей в северо-западной части тихого
океана (Accidental bycatch of marine birds and mammals in the salmon gillnet fishery in the
northwestern Pacific Ocean). Moscow:Kamchatka Branch of the Pacific Geophysical
Institute, Russian Academy of Sciences.
- 290 Ballance, L. T., Pitman, R. L., Reilly, S. B. and Force, M. P. (1996) Report of a cetacean,
seabird, marine turtle and flying fish survey of the western tropical Indian Ocean aboard the
research vessel Malcolm Baldrige, March 21-July 26, 1995. (NOAA Technical
Memorandum).U.S. Department of Commerce.
- Barbraud, C., Booth, A., Taylor, G. A. and Waugh, S. M. (2014) Survivorship in Flesh-footed
295 Shearwater *Puffinus carneipes* at two sites in northern New Zealand. *Mar Ornithol* 42:91-97.
- BirdLife International. (2017) IUCN Red List for birds species factsheet: *Ardeenna carneipes*.
Downloaded from <http://www.birdlife.org> on 22/09/2017.
- Bond, A. L. and Lavers, J. L. (2011) Trace element concentrations in feathers of Flesh-footed
Shearwaters (*Puffinus carneipes*) from across their breeding range. *Arch Environ Contam*
300 *Toxicol* 61:318-326.
- Bond, A. L., Jones, I. L., Williams, J. C. and Byrd, G. V. (2013) Survival and reproductive
success of Crested Auklets (*Aethia cristatella*) in the presence of introduced Norway rats
(*Rattus norvegicus*). *Mar Ornithol* 41:41-47.
- Bond, A. L. and Lavers, J. L. (2014) Climate change alters the trophic niche of a declining
305 apex marine predator. *Global Change Biol* 20:2100-2107.
- Brooke, M. d. L. (2004) Albatrosses and petrels across the world. Oxford, U.K.:Oxford
University Press.
- Brothers, N. P., Reid, T. A. and Gales, R. P. (1997) At-sea distribution of Shy Albatrosses
Diomedea cauta cauta derived from records of band recoveries and colour-marked birds.
310 *Emu* 97:231-239.
- Burnham, K. P. and Anderson, D. R. (2002) Model selection and multi-model inference. New
York:Springer Science + Business Media.
- Buxton, R. T., Currey, C. A., Lyver, P. O. B. and Jones, C. J. (2013) Incidence of plastic
fragments among burrow-nesting seabird colonies on offshore islands in northern New
315 Zealand. *Mar Pollut Bull* 74:420-424.

- Campbell, O., Smiles, M., Roberts, H., Judas, J. and Pedersen, T. (2017) Gulf of Oman: analysis of seabird records of boat trips from the east coast of the United Arab Emirates 2010-2016. *Sandgrouse* 39:138-164.
- 320 Carey, M. J. (2011) Investigator disturbance reduces reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*. *Ibis* 153:363-372.
- Catry, T., Ramos, J. A., Le Corre, M. and Phillips, R. A. (2009) Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the Wedge-tailed Shearwater in the western Indian Ocean. *Mar Ecol Prog Ser* 391:231-242.
- 325 Chambers, L. E., Devney, C. A., Congdon, B. C., Dunlop, J. N., Woehler, E. J. and Dann, P. (2011) Observed and predicted effects of climate on Australian seabirds. *Emu* 111:235-251.
- Chastel, O. (1995) Influence of reproductive success on breeding frequency in four southern petrels. *Ibis* 137:360-363.
- 330 Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M. and Pradel, R. (2009) U-CARE: Utilities for performing goodness of fit tests and manipulating CAPture-REcapture data. *Ecography* 32:1071-1074.
- Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W. W. L., Christensen, V., Karpouzi, V. S., Guilhaumon, F., Mouillot, D., Paleczny, M., Palomares, M. L., Steenbeek, J., Trujillo, P., Watson, R. and Pauly, D. (2012) The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Global Ecol*
- 335 *Biogeogr* 21:465-480.
- Costello, M. J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H. and Miloslavich, P. (2010) A census of marine biodiversity knowledge, resources, and future challenges. *PLoS One* 5:e12110.
- 340 Croxall, J. P. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J. J., Sullivan, B. J. J., Symes, A. and Taylor, P. (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Cons Int* 22:1-34.
- De Silva, R. I. and Perera, L. (1995) Shearwater migration off the coast of Sri Lanka. *Loris* 20:97-100.
- 345 de Vos, A., Pattiaratchi, C. B. and Wijeratne, E. M. S. (2013) Surface circulation and upwelling patterns around Sri Lanka. *Biogeosci Discuss* 10:14953-14998.
- DeGange, A. R. and Day, R. H. (1991) Mortality of seabirds in the Japanese land-based gillnet fishery for salmon. *Condor* 93:251-258.
- DPaW. (2015) Wildlife conservation (specially protected fauna) notice 2015. (Government gazette of Western Australia). Perth:Department of Parks and Wildlife.
- 350 Dunlop, J. N. (2007) Protected species bycatch in Zone 1 of the South Coast Purse Seine Fishery 2010/11. Perth:Department of Environment and Conservation.
- Dunlop, J. N., McNeill, S. and Cannell, B. (2013) Seabird feathers as indicators of mercury & selenium contamination in the coastal waters of south Western Australia. Perth:Conservation Council of Western Australia.
- 355 Felicísimo, Á. M., Muñoz, J. and González-Solis, J. (2008) Ocean surface winds drive dynamics of transoceanic aerial movements. *PLoS One* 3:e2928.
- Finkelstein, M. E., Wolf, S., Goldman, M., Doak, D. F., Sievert, P. R., Balogh, G. and Hasegawa, H. (2010) The anatomy of a (potential) disaster: Volcanoes, behavior, and population viability of the Short-tailed Albatross (*Phoebastria albatrus*). *Biol Cons* 143:321-
- 360 331.
- Fletcher, W. J. and Tregonning, R. J. (1992) Distribution and timing of spawning by the Australian pilchard (*Sardinops sagax neopilchardus*) off Albany, Western Australia. *Mar Freshwater Res* 43:1437-1449.

- Gaze, P. (2000) The response of a colony of Sooty Shearwater (*Puffinus griseus*) and Flesh-footed Shearwater (*P. carneipes*) to the cessation of harvesting and the eradication of Norway rats (*Rattus norvegicus*). *New Zealand Journal of Zoology* 27:375-379.
- Gibson-Hill, C. A. (1953) Notes on the sea birds of the orders Procellariiformes and Pelecaniformes recorded as strays or visitors to the Ceylon coast. *Spolia Zeylanica* 27:83-201.
- Grémillet, D. and Boulinier, T. (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. *Mar Ecol Prog Ser* 391:121-137.
- Hedd, A., Montevecchi, W. A., Otley, H., Phillips, R. A. and Fifield, D. A. (2012) Trans-equatorial migration and habitat use by Sooty Shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. *Mar Ecol Prog Ser* 449:277-290.
- Huang, H.-W. and Liu, K.-M. (2010) Bycatch and discards by Taiwanese large-scale tuna longline fleets in the Indian Ocean. *Fish Res* 106:261-270.
- IOTC. (2015) Report of the 11th Session of the IOTC Working Party on Ecosystems and Bycatch, IOTC-2015-WPEB11-R[E]. Olhão, Portugal:Indian Ocean Tuna Commission.
- Jones, I. L., Hunter, F. M. and Robertson, G. J. (2002) Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. *Oecol* 133:38-44.
- Lavers, J. L. (2007) Cumulative mortality and population parameters for a vulnerable seabird. Chapter Seven: Populations under pressure. St. John's, Newfoundland:Memorial University of Newfoundland.
- Lavers, J. L., Bond, A. L., Van Wilgenburg, S. L. and Hobson, K. A. (2013) Linking at-sea mortality of a pelagic shearwater to breeding colonies of origin using biogeochemical markers. *Mar Ecol Prog Ser* 491:265-275.
- Lavers, J. L., Bond, A. L. and Hutton, I. (2014a) Plastic ingestion by Flesh-footed Shearwaters (*Puffinus carneipes*): Implications for chick body condition and the accumulation of plastic-derived chemicals. *Environ Pollut* 187:124-129.
- Lavers, J. L., Miller, M. G. R., Carter, M. J., Swann, G. and Clarke, R. H. (2014b) Predicting the spatial distribution of a seabird community to identify priority conservation areas in the Timor Sea. *Cons Biol* 28:1699-1709.
- Lavers, J. L. (2015) Population status and threats to Flesh-footed Shearwaters (*Puffinus carneipes*) in South and Western Australia. *ICES J Mar Sci* 72:316-327.
- Le Bohec, C., Gauthier-Clerc, M., Gremillet, D., Pradel, R., Bechet, A., Gendner, J. P. and Le Maho, Y. (2007) Population dynamics in a long-lived seabird: I. Impact of breeding activity on survival and breeding probability in unbanded King Penguins. *J Anim Ecol* 76:1149-1160.
- Lebreton, J. D., Burnham, K. P., Clobert, J. and Anderson, D. R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monograph* 62:67-118.
- Lewison, R. L. and Crowder, L. B. (2003) Estimating fishery bycatch and effects on a vulnerable seabird population. *Ecol App* 13:743-753.
- Lewison, R. L., Crowder, L. B., Read, A. J. and Freeman, S. A. (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol Evol* 19:598-604.
- Louzao, M., Hyrenbach, K. D., Arcos, J. M., Abelló, P., de Sola, L. G. and Oro, D. (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. *Ecol App* 16:1683-1695.
- Lunney, D., Curtin, A. L., Ayers, D., Cogger, H. G., Dickman, C. R., Maitz, W., Law, B. and Fisher, D. (2000) The threatened and non-threatened native vertebrate fauna of New South Wales: status and ecological attributes. Sydney:National Parks and Wildlife Service.
- Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E. and Tonra, C. M. (2015) A call for full annual cycle research in animal ecology. *Biol Lett* 11:20150552.

- 415 Mills, M. S. L. and Ryan, P. G. (2005) Modelling impacts of long-line fishing: what are the effects of pair-bond disruption and sex-biased mortality on albatross fecundity? *Anim Conserv* 8:359-367.
- Mougin, J. L., Jouanin, C. and Roux, F. (1997) Intermittent breeding in Cory's Shearwater *Calonectris diomedea* of Selvagem Grande, North Atlantic. *Ibis* 139:40-44.
- 420 Nezlin, N. P., Polikarpov, I. G. and Al-Yamani, F. (2007) Satellite-measured chlorophyll distribution in the Arabian Gulf: Spatial, seasonal and inter-annual variability. *International Journal of Oceans and Oceanology* 2:139-156.
- Ogi, H. (2008) International and national problems in fisheries seabird by-catch. *Journal of Disaster Research* 3:187-195.
- 425 Pocklington, R. (1979) An oceanographic interpretation of seabird distributions in the Indian Ocean. *Mar Biol* 51:9-21.
- Powell, C. D. L., Wooller, R. D. and Bradley, J. S. (2007) Breeding biology of the Flesh-footed Shearwater (*Puffinus carneipes*) on Woody Island, Western Australia. *Emu* 107:275-283.
- 430 Powell, C. D. L. (2009) Foraging movements and the migration trajectory of Flesh-footed Shearwaters *Puffinus carneipes* from the south coast of Western Australia. *Mar Ornithol* 37:115-120.
- Pradel, R., Rioux, N., Tamisier, A. and Lebreton, J. D. (1997) Individual turnover among wintering teal in Camargue: A mark-recapture study. *J Wildl Manage* 61:816-821.
- 435 Prasad, R. R. and Nair, P. V. R. (1960) A preliminary account of primary production and its relation to fisheries of the inshore waters of the Gulf of Mannar. *Indian Journal of Fisheries* 7:165-168.
- Prévot-Julliard, A. C., Lebreton, J. D. and Pradel, R. (1998) Re-evaluation of adult survival of Black-Headed Gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *The Auk* 115:85-95.
- 440 Priddel, D., Carlile, N., Fullagar, P., Hutton, I. and O'Neill, L. (2006) Decline in the distribution and abundance of Flesh-footed Shearwaters (*Puffinus carneipes*) on Lord Howe Island, Australia. *Biol Cons* 128:412-424.
- Rayner, M. J., Taylor, G. A., Thompson, D. R., Torres, L. G., Sagar, P. M. and Shaffer, S. A. (2011) Migration and diving activity in three non-breeding Flesh-footed Shearwaters *Puffinus carneipes*. *Journal of Avian Biology* 42:266-270.
- 445 Reid, T., Hindell, M. and Wilcox, C. (2012) Environmental determinants of the at-sea distribution of encounters between Flesh-footed Shearwaters *Puffinus carneipes* and fishing vessels. *Mar Ecol Prog Ser* 447:231-242.
- 450 Reid, T., Hindell, M., Lavers, J. L. and Wilcox, C. (2013a) Re-examining mortality sources and population trends in a declining seabird: using Bayesian methods to incorporate existing information and new data. *PLoS One* 8:e58230.
- Reid, T., Tuck, G. N., Hindell, M. A., Thalmann, S., Phillips, R. A. and Wilcox, C. (2013b) Nonbreeding distribution of Flesh-footed Shearwaters and the potential for overlap with North Pacific fisheries. *Biol Cons* 166:3-10.
- 455 Robertson, H. A., Dowding, J. E., Elliott, G. P., Hitchmough, R. A., Miskelly, C. M., O'Donnell, C. F. J., Powlesland, R. G., Sagar, P. M., Scofield, R. P. and Taylor, G. A. (2013) Conservation status of New Zealand birds, 2012. New Zealand Threat Classification Series 4. Wellington:Department of Conservation.
- 460 Spear, L. B. and Ainley, D. G. (1997) Flight speed of seabirds in relation to wind speed and direction. *Ibis* 139:234-251.
- Thompson, K. R. and Furness, R. W. (1991) The influence of rainfall and nest-site quality on the population dynamics of the Manx Shearwater *Puffinus puffinus* on Rhum. *J Zool* 225:427-437.

- 465 Tiller, C. J., Klomp, N. I., Fullagar P.C, P. J. and Heyligers. (2013) Catastrophic breeding failure in shearwaters caused by heavy rainfall. *Mar Ornithol* 41:97-99.
- Tuck, G. N. N., Polacheck, T. and Bulman, C. M. M. (2003) Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biol Cons* 114:1-27.
- 470 Vinayachandran, P. N., Chauhan, P., Mohan, M. and Nayak, S. (2004) Biological response of the sea around Sri Lanka to summer monsoon. *Geophys Res Lett* 31:L01302-L01302.
- Wahl, T. R. and Heinemann, D. (1969) Seabirds and fishing vessels: co-occurrence and attraction. *Condor* 81:390-396.
- Warham, J. (1958) The nesting of the shearwater *Puffinus carneipes*. *The Auk* 75:1-14.
- Warham, J. (1990) The petrels: their ecology and breeding systems. London:Academic Press.
- 475 Waugh, S. M., MacKenzie, D. I. and Fletcher, D. (2008) Seabird bycatch in New Zealand trawl and longline fisheries, 1998-2004. *Pap Proc R Soc Tas* 142:45-66.
- Waugh, S. M., Tennyson, A., Taylor, G. and Wilson, K.-J. (2013) Population sizes of shearwaters (*Puffinus* spp.) breeding in New Zealand, with recommendations for monitoring. *Tuhinga* 24:159-204.
- 480 Waugh, S. M., Jamieson, S. E., Stahl, J. C., Filippi, D. P., Taylor, G. A. and Booth, A. (2014) Flesh-footed Shearwater – population study and foraging areas (POP2011-02). Final report. Wellington, New Zealand.
- Weimerskirch, H., Louzao, M., de Grissac, S. and Delord, K. (2012) Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335:211-214.
- 485 White, G. C. and Burnham, K. P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120-S139.
- Yonehara, Y., Goto, Y., Yoda, K., Watanuki, Y., Young, L. C., Weimerskirch, H., Bost, C.-A. and Sato, K. (2016) Flight paths of seabirds soaring over the ocean surface enable measurement of fine-scale wind speed and direction. *Proc Nat Acad Sci* 113:9039-9044.

490

JENNIFER L. LAVERS*

Institute for Marine and Antarctic Studies, University of Tasmania, 20 Castray Esplanade, Battery Point, Tasmania 7004, Australia

495 SIMEON LISOVSKI

Deakin University, School of Life and Environmental Science, Centre for Integrative Ecology, Geelong, Victoria 3220, Australia

ALEXANDER L. BOND

500 *Bird Group, Department of Life Sciences, The Natural History Museum, Akeman Street, Tring, Hertfordshire, HP23 6AP, United Kingdom*

**Author for correspondence; email: jennifer.lavers@utas.edu.au*

505 Table 1. Sex and breeding status of adult Flesh-footed Shearwaters tracked using geolocation tags on Shelter Island, Western Australia.

Breeding status & sex	Tracking period	Departed Shelter Is.	Arrival “Laccadive Sea”
Successful male ^A	22/01/2012 – 07/06/2012	03/05/2012	09/05/2012
Successful female ^B	22/01/2012 – 26/05/2012	02/05/2012	Battery failed
Failed female ^C	22/01/2012 – 12/05/2012	16/02/2012	Battery failed

^{A,B,C}Indicates relevant panel for this bird presented in Figure 1.

510 Table 2. Model-averaged parameter estimates unconditional standard errors (\widehat{SE}), and 95% confidence intervals of apparent annual survival (ϕ) and encounter probability (p) of Flesh-footed Shearwaters. Survival intervals are presented based on the beginning of the breeding season such that “2011-2012” indicates survival from the 2011-2012 to 2012-2013 breeding season.

Interval	$\phi \pm \widehat{SE}$ (95% CI)	$p \pm \widehat{SE}$ (95% CI)
2011-2012	0.676 \pm 0.169 (0.314-0.905)	0.169 \pm 0.157 (0.205-0.752)
2012-2013	0.634 \pm 0.130 (0.367-0.838)	0.396 \pm 0.091 (0.236-0.581)
2013-2014	0.731 \pm 0.126 (0.436-0.905)	0.391 \pm 0.086 (0.240-0.567)
2014-2015	0.835 \pm 0.164 (0.330-0.981)	0.486 \pm 0.147 (0.230-0.750)

515

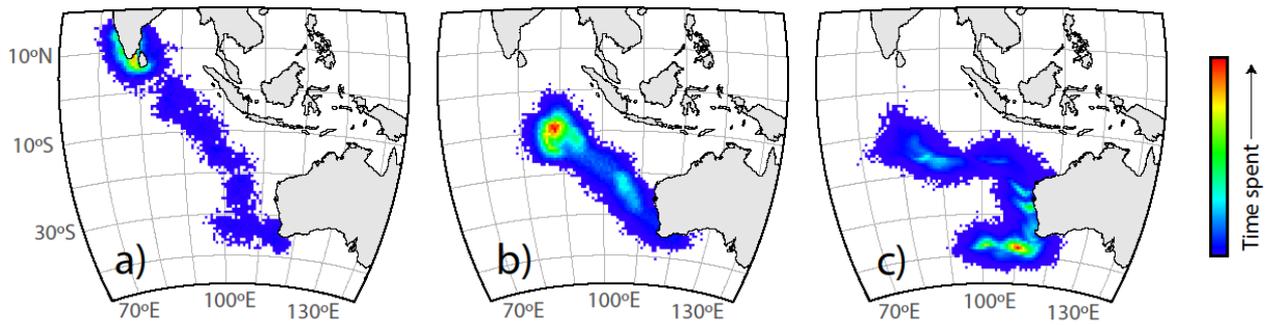


Figure 1. Map of relative time spent by migrating Flesh-footed Shearwaters carrying light-level geolocator tracking devices: A) successful breeding male, B) successful breeding female, and C) female whose chick died in early February. The density represents measures of relative time spent per area across the individual tracking period, incorporating the spatial uncertainty inherent in the model. Since individuals were tracked for different periods (36, 11.5, and 101 days), the scale of time spent is different for each individual. Bin size is 57 x 59 km.