

Breeding durations as estimators of adult sex ratios and population size

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Received: 12 February 2010 / Accepted: 8 July 2010 / Published online: 29 July 2010
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Abstract Adult sex ratios (ASRs) and population size are two of the most fundamental parameters in population biology, as they are the main determinants of genetic and demographic viability, and vulnerability of a population to stochastic events. Underpinning the application of population viability analysis for predicting the extinction risk of populations is the need to accurately estimate parameters that determine the viability of populations (i.e. the ASR and population size). Here we demonstrate that a lack of temporal information can confound estimation of both parameters. Using acoustic telemetry, we compared differences in breeding durations of both sexes for a giant Australian cuttlefish *Sepia apama* breeding aggregation to the strongly male-biased operational sex ratio (4:1), in order to estimate the population ASR. The ratio of breeding durations between sexes was equal to the operational sex ratio, suggesting that the ASR is not strongly male-biased, but balanced. Furthermore, the short residence times of individuals at the breeding aggregation suggests that previous density-based abundance estimates have significantly underestimated population size. With the current wide application of population viability analysis for predicting the extinction risk of populations, tools to improve the accuracy of such predictions are vital. Here we provide a

new approach to estimating the fundamental ASR parameter, and call for temporal considerations when estimating population size.

Keywords Acoustic telemetry · Breeding aggregation · Operational sex ratio · *Sepia apama* · Viability analysis

Introduction

Simulation models are increasingly used in conservation biology to evaluate the extinction risk of populations, and to better understand the demographics of endangered species (Brook et al. 2000; Reed et al. 2002). Population viability analyses (PVA) are generally accurate predictors of population persistence (Brook et al. 2000), but rely on the accuracy of demographic parameters such as population size and adult sex ratios (ASRs). The population ASR is of critical importance for population viability, with the probability of persistence and population size shown to be significantly reduced with increased biases in the ASR (Vargas et al. 2007). The ASR will also influence the genetic viability of a population, whereby small populations with skewed sex ratios will have a lower genetic viability than unbiased populations of the same size (Gerber 2006).

Despite the significance of the ASR for viability analysis, and indeed its role in the evolution of sex roles (Cluttonbrock and Parker 1992; Kokko and Jennions 2008), there is a tendency to either ignore the influence of the ASR, or incorrectly equate it to the operational sex ratio (OSR; ratio of fertilizable females to sexually active males at the site and time of mating) (Kokko and Jennions 2008). Trivers (1972) urged researchers to investigate the influence of the ASR on the evolution of mating systems, but his plea has largely been ignored, and studies continue to

Communicated by Øyvind Fiksen.

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focus principally on the OSR (see review by Kokko and Jennions 2008).

Studies that calculate the OSR do so by quantifying the relative proportion of sexes ready to mate at a given time, or by using the concept of ‘time-in’ (the fraction of a reproductive cycle when an individual is ready to mate). With this method, the OSR is calculated as:

$$\text{OSR} = \frac{\text{mean male 'time-in'}}{\text{mean female 'time-in'}} \times \text{ASR}$$

(Cluttonbrock and Parker 1992; Kvarnemo and Ahnesjö 1996; Parker and Simmons 1996). Parker and Simmons (1996) demonstrated that calculating differences in time-in between sexes is sufficient to predict the direction of sexual selection provided that the ASR is unbiased. However, biased ASRs are common in nature (Kruuk et al. 1999), and measuring the parameter directly is often difficult. Although the above relationship is generally used to estimate the OSR (and therefore predict the direction and strength of sexual selection), it should be possible to estimate the ASR of a population if the OSR and time spent mating (time-in) between sexes are known. Here, we determine the relationship between time-in of each sex and a known OSR to estimate the ASR of a unique cephalopod breeding aggregation.

The giant Australian cuttlefish *Sepia apama* (Gray) is the largest cuttlefish species in the world and forms the only known cuttlefish breeding aggregation. From May to August each year, hundreds of thousands of mature individuals converge on a highly localised area of sub-tidal rocky reef (approximately 60 ha) at Point Lowly, northern Spencer Gulf, Australia, to breed. The mean OSR during the breeding season is skewed towards males by 4:1 (although it can reach 11:1 near the beginning of the season; Hall and Hanlon 2002) and the intense competition between males has led to the development of spectacular and complex mating strategies and displays (Norman et al. 1999; Hall and Hanlon 2002; Naud et al. 2004; Hanlon et al. 2005).

Like many other cephalopods, *S. apama* are short-lived (generally 12–24 months; Hall et al. 2007) and semelparous, spawning once at the end of their life cycle. Although processes of sexual selection during the aggregation are well studied in this iconic species (Hall and Hanlon 2002; Naud et al. 2004; Hanlon et al. 2005), little is known about sex ratios at birth, mortality throughout the life history, or adult sex ratios. *S. apama* therefore provides an excellent model to estimate the ASR using the known OSR and differences in time-in between sexes.

The aggregation site is devoid of cuttlefish outside of the 4-month breeding period (late April to early September), and given that all individuals present during the breeding period are reproductively mature, we make the assumption

that presence at the site during the breeding season indicates a readiness to mate—time-in. This assumption was made by Hall and Hanlon (2002), when calculating the OSR so we adopt this definition for consistency (although we acknowledge that debate exists on the most accurate way to measure population OSR; i.e. which animals are actually available to mate versus already committed to other parental activities). By quantifying residence time as a proxy of breeding durations, we can also obtain a measure of individual transience at the aggregation, and therefore have a greater confidence in estimates of population size. In other words, where mean residence times are significantly shorter than the overall breeding period (i.e. a high degree of transience), density-based abundance estimates will underestimate population size.

Acoustic telemetry is a central tool for the identification of fish home ranges and habitat use (Bellquist et al. 2008; Papastamatiou et al. 2009), activity patterns (Andrews et al. 2009; Blumenthal et al. 2009), and habitat connectivity (Pecl et al. 2006; Semmens et al. 2010). A range of approaches are employed, including the deployment of presence/absence receiver curtains (Pecl et al. 2006), high spatial resolution positioning systems (Jorgensen et al. 2006; Tolimieri et al. 2009) and the emerging accelerometry technique (Tsuda et al. 2006; Whitney et al. 2007). Several studies have used acoustic telemetry to examine cephalopod behaviour during spawning periods (Sauer et al. 1997; Pecl et al. 2006; Downey et al. 2010), but we are not aware of any published studies that have specifically examined gender differences in breeding durations. Using acoustic telemetry, we tested the hypothesis that individual residence times at the aggregation will be higher for males than females. If the ASR of the population is unbiased (1:1), then the ratio of time-in between males and females should correspond to the OSR of 4:1.

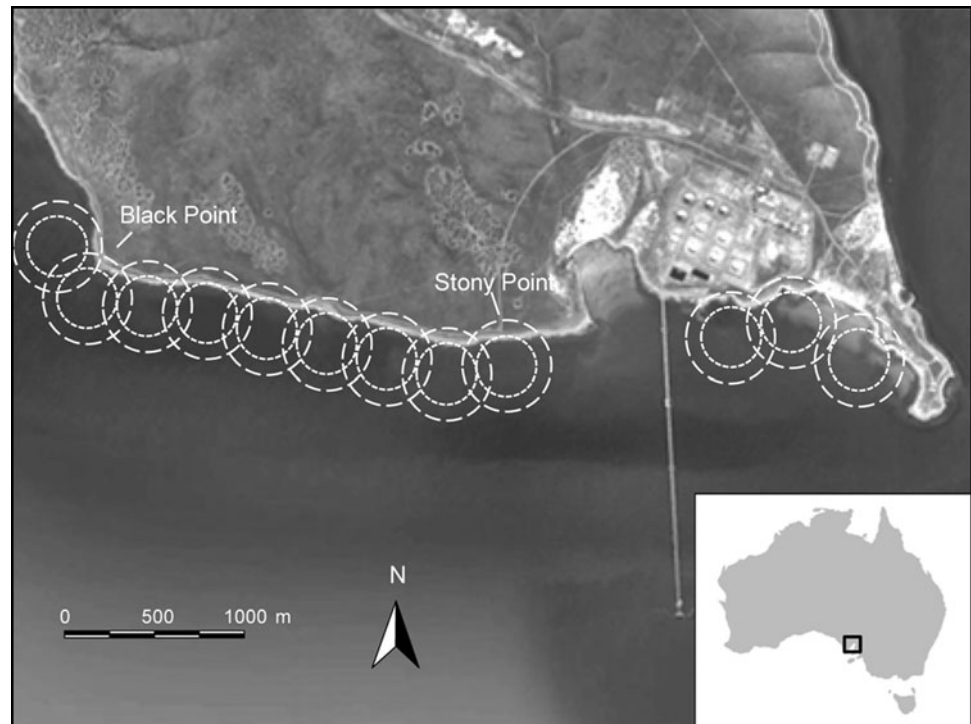
Materials and methods

Study site

The study was carried out at Point Lowly, northern Spencer Gulf (33°00'S, 137°44'E; Fig. 1), South Australia. Spencer Gulf is a relatively shallow (mean depth 22 m) inverse estuary, with salinities ranging from 36 g l⁻¹ at its entrance to an annual mean of 45 g l⁻¹ at its head (Corliss et al. 2003). In northern Spencer Gulf, water temperatures range from 12°C in mid-winter to 28°C in mid-summer (Nunes and Lennon 1986).

Sepia apama aggregate over a highly localised area (approximately 60 ha) of low relief rocky reef along the southern side of the Point Lowly peninsula, up to 150 m from shore. The highest densities of *S. apama* occur along

Fig. 1 Giant Australian cuttlefish *Sepia apama* aggregation site at Point Lowly, South Australia. *Isolines* indicate 47% (200 m; *short dash*) and 20% (300 m; *long dash*) detection probabilities around each receiver. The area of highest cuttlefish density is between Black Point and Stony Point. Image source: Google Earth mapping service



approximately 3 km of coastline between Black Point and Stony Point (Fig. 1) and can be as high as one individual per square metre (Hall and Hanlon 2002; Hall and Fowler 2003).

Acoustic receivers

Twelve Vemco (Halifax, Canada) VR2W acoustic receivers were deployed throughout the aggregation site. These single channel (69 kHz) receivers consist of an omnidirectional hydrophone that records the time, date and identity of digitally coded transmitters within range of the receiver. The effective detection range of receivers is variable, being influenced by environmental conditions such as wind speed, tidal movement, salinity, substrate type, and biological noise (Voegeli and Pincock 1996; Heupel et al. 2006; Simpfendorfer et al. 2008). Range tests were conducted at a variety of locations throughout the reef prior to the study, and indicated that with prevailing wind speeds of 5–10 knots (the seasonal average), detection efficiency for tags (transmitters used were V13-1H coded pingers) was 46.6% (± 15.3 SE) 200 m from receivers, and 19.5% (± 14.7 SE) 300 m from receivers. Nine receivers were moored equidistantly along the reef between Black Point and Stony Point, such that the space between consecutive receivers was 400 m (Fig. 1). A further three receivers were positioned on isolated patches of reef to the east of the main aggregation area (Fig. 1). Receivers were

moored 1.5 m from the seafloor, approximately 150 m from shore, in water depths ranging from 5 to 9 m. Given the overlap of detection ranges, and that breeding substrate occurs only to approximately 150 m from shore, we had a high level of confidence in the ability to detect tagged cuttlefish throughout this section of reef. Data were retrieved periodically throughout the monitoring period.

Acoustic transmitters and tagging

The acoustic transmitters used in this study were Vemco V13-1H coded pingers. Each transmitter (6 g in water, 10 mm diameter, 30 mm length) emits a unique sequence of acoustic pings at a frequency of 69 kHz throughout the battery life of the tag (approximately 360 days). This sequence is repeated after a pseudo-random delay of between 60 and 180 s, thereby minimising the probability of signal collision between tags.

Cuttlefish (15–33 cm mantle length) were caught via SCUBA and jigging and placed in 100-l holding tubs. Transmitters were secured to the interior of the mantle, ventro-laterally, by a hypodermic needle attached to the transmitter with two-part epoxy glue. The needle was pushed through the mantle and secured externally with a stainless steel crimp. Silicone washers were placed on either side of the mantle to minimise abrasion of the animal. Animals were typically released within 60 s of capture and were observed to jet strongly through the water column.

This tagging technique has previously been employed in a suite of cephalopod tagging studies (Aitken et al. 2005; Jackson et al. 2005; Stark et al. 2005; Pecl et al. 2006).

Nineteen animals were tagged, six of which were females (females are distinguishable by their shorter arms and distinctive skin patterns and postures). To capture potential differences throughout the breeding period, tagging occurred on two dates; ten animals (seven males and three females) were tagged on 22 May 2008 (as cuttlefish began to arrive at the aggregation), and nine (six males and three females) on 15 July 2008 (during the middle of the season). The initial tagging date of 22 May is somewhat later than the traditional start of the spawning season (late April; Hall and Fowler 2003); however, very few cuttlefish were present at the aggregation in late April/early May 2008, so tagging was delayed to account for this delayed onset of spawning in this year.

Data analyses

The residence time of an individual was defined as the number of days where greater than one detection per day was recorded from its transmitter throughout the array. We also calculated residence period (the number of days between the first and last day that the individual was detected), as a period of absence from the array could have resulted from either ‘time-out’ (i.e. a brief cessation of mating), or from mating in an area outside the detection range of receivers. Since we could not discriminate between these two models, we report both residence time and residence period. Data up to 12 h following release were excluded from analyses due to the possible influence of the tagging process on animal behaviour subsequent to release.

Unpaired *t*-tests were used to test null hypotheses that there were no differences in residence times or residence periods amongst sexes and tagging dates. Variances remained heterogeneous despite transformation, so heteroscedastic *t*-tests were performed to decrease the probability of type I error.

For a meaningful test of whether the estimated time-in ratios between sexes are equivalent to the OSR of 4:1 (and therefore that the ASR is unbiased) requires an estimate of variation in the sample ratios. To achieve this, we used a bootstrap approach, calculating the ratios of 5,000 random combinations of male:female residence times (and periods). The resulting positively skewed distribution was normalised by calculating the means of 500 samples (of $n = 19$) randomly taken from the bootstrap data. We then calculated the 95 and 70% confidence limits of the resulting normal distribution (by transforming the upper and lower boundaries of the standard normal distribution), and used these critical values to test the null hypothesis that the 4:1 OSR is indistinguishable from our generated mean

ratios. The 95% limits were chosen for convention, and the 70% limits were used to reduce the probability of false retention of the null hypothesis. If the OSR fell within the range of critical values, then the time-in ratios would be equivalent to the OSR of 4:1, thereby supporting the model that there are an equal number of males and females in the population (the ASR is unbiased).

Results

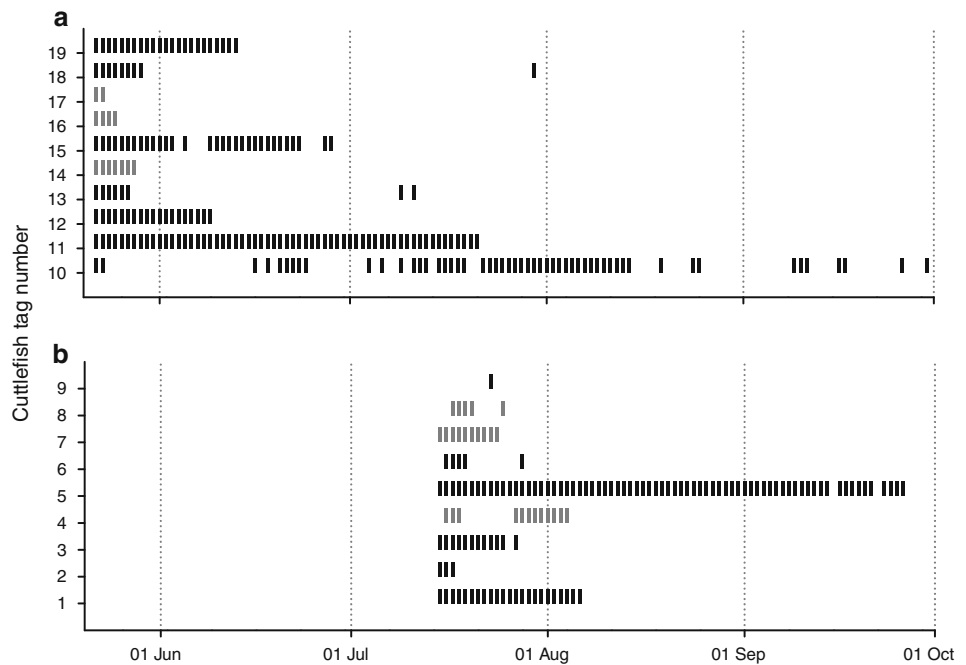
Residence times ranged from 1 to 72 days (mean 19.0 ± 4.8 SE), and residence period ranged from 1 to 132 days (mean 30.2 ± 7.8 SE; Fig. 2). The majority of cuttlefish were detected consistently throughout their residence period (residence times and periods were generally similar); however, there were some exceptions to this trend (Fig. 2). Male residence times (mean 24.69 ± 6.5 SE) were significantly longer than those of females (mean 6.67 ± 1.54 SE; unpaired *t*-test, $t = 2.70$, $P < 0.05$; Fig. 3a), such that the ratio of residence times between sexes was 3.7:1. Males also displayed significantly longer residence periods than females (40.07 ± 9.90 versus 8.67 ± 2.58 , respectively; unpaired *t*-test, $t = 2.97$, $P < 0.05$; Fig. 3b) with a ratio of residence periods between sexes of 4.6:1. Residence times and periods were similar for animals tagged on 22 May and those tagged on 15 July (unpaired *t*-tests, $t = 0.60$, $P > 0.05$ for residence time and $t = 1.47$, $P > 0.05$ for residence period; Fig. 3).

Bootstrapped data produced slightly higher mean time-in ratios for residence time (5.29 ± 0.07 SE) and period (7.73 ± 0.11 SE). However, at the 95% confidence level, the OSR falls within the confidence limits of the standard normal distribution of estimates for residence time (2.24–8.33%) and residence period (3.08–12.37%) so we retain the null hypothesis that the OSR is indistinguishable from both time-in ratios at this level. At the 70% level, the OSR falls within the confidence limits for residence time (3.67–6.9%), but outside for residence period (5.26–10.19%). We therefore have no evidence that the OSR is dissimilar to the residence time ratio, and would only reject the null hypothesis for residence period at the 70% confidence level.

Discussion

In a population with an ASR of 1:1, any bias in the OSR should correspond to a difference in male:female time-in of the same magnitude (Cluttonbrock and Parker 1992; Kvarnemo and Ahnesjö 1996; Prohl 2005). Given the striking congruence between the OSR (4:1) and gender differences in both time-in metrics (3.7:1 for residence

Fig. 2 Detection summary for *Sepia apama* tagged on **a** 22 May and **b** 15 July 2008. Individual ticks represent days where each tagged animal was present at the aggregation; grey ticks females, black ticks males



time and 4.6:1 for residence period, both of which were indistinguishable from the OSR at the 95% confidence level) for the *S. apama* breeding aggregation, we suggest that the ASR is indeed unbiased, and that the highly skewed OSR is a result of males displaying an extended breeding period relative to females. This is consistent with trawling by-catch data, which suggests the sex ratio of *S. apama* in northern Spencer Gulf outside of the spawning season is close to unity (Hall and Fowler 2003).

By determining the relationship between the OSR and gender differences in breeding durations, we provide a new method for indirectly estimating the ASR. This method requires the independent calculation of two parameters: the OSR, by estimating the ratio of fertilizable females to sexually active males at the site and time of mating; and the ratio of time-in between sexes. Clearly, using the ratio of time-in between sexes to estimate the OSR for our method would be inappropriate, as this requires the assumption of an unbiased ASR in the first place.

The mechanisms underlying the differences in time-in between sexes were not addressed in this study, but are likely to be a result of differences in reproductive investment. Where there is an unbiased ASR and no post-mating parental care, anisogamy (where females produce larger gametes than males) predicts that males, having a higher potential reproductive rate, will compete for limited females, and a male-biased OSR will result (Cluttonbrock and Vincent 1991; Cluttonbrock and Parker 1992; Kokko and Jennions 2008). This, in turn, leads to increased variance in male mating success, and the selection of male

competitive traits; such as the spectacular male displays that have evolved in the *S. apama* breeding aggregation.

Irrespective of sex, *S. apama* displayed lower than expected residence times (mean 19.0 ± 4.8 days) given the relatively long breeding period (approximately 4 months). Obviously individuals were present for an unknown period prior to tagging; however, animals of the initial cohort were tagged at the beginning of the season, and those of the second cohort had departed well before the end of the season, suggesting that individuals were indeed resident for only a fraction of the breeding season. Given the apparent transient nature of individuals within this aggregation, our results suggest that previous density-based biomass surveys may have significantly underestimated actual population size. As proposed by Hall and Fowler (2003), an ‘area under the curve’ approach (English et al. 1992; Hilborn et al. 1999), which accounts for individual residence times, may provide a more accurate estimate of actual population size.

The conclusions drawn from this study are underpinned by several important, but untested, assumptions, and these must be considered: first, that the relatively small sample sizes (13 males and six females) are representative of the exceedingly large (>200,000) population. The variance of residence times amongst both males and females were significant, and larger sampling effort would provide greater confidence in the accuracy of estimates of breeding durations for this species; second, that individuals were present for negligible periods of time prior to tagging. Staggering more sampling effort across a greater variety of

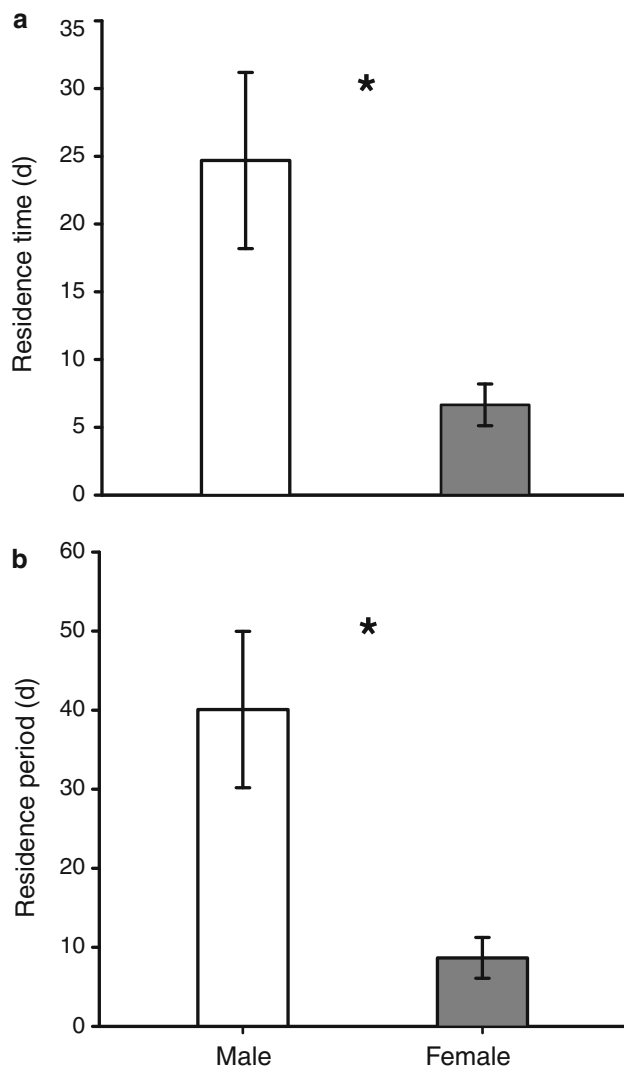


Fig. 3 Comparison of male ($n = 13$) and female ($n = 6$) **a** residence times and **b** residence periods (mean \pm SE) as metrics of ‘time-in’. Heteroscedastic t -tests were performed due to the heterogeneity of variances; * $\alpha = 0.05$. Note the variable scales on the y-axes

tagging dates, or tagging animals prior to arriving at the aggregation, would reduce the uncertainty in pre-tagged durations, and these approaches may be feasible in many other (particularly terrestrial) systems; third, that tagging does not have a sex-specific influence on behaviour. This assumption may be difficult to test for many species, but is likely to be particularly important for those displaying high degrees of sexual dimorphism, where tags are likely to have a disproportionate influence on the physiology of each sex; fourth, that female behaviour does not reduce the detectability of tags. Where mating behaviour differs between sexes, there must be minimal sexual bias in the method of observing breeding durations (which was acoustic telemetry in this case). Although female *S. apama*

are thought to spend more time sheltering in rock crevices than males (Hall and Fowler 2003), our protocol requires the successful decoding of just two detections (out of a mean maximum of 720 per day) to define an individual as resident on any given day. Where the calculation of breeding durations requires a temporal resolution greater than daily, a different observational approach may be required. Lastly, an extrapolation of the unbiased ASR to *S. apama* in greater northern Spencer Gulf would require the assumption that Point Lowly is the only source of recruits for the region. There is some suggestion that the northern Spencer Gulf population is genetically distinct from individuals throughout the rest of its range (and indeed southern Spencer Gulf; B. Gillanders, unpublished data), and trawling by-catch data support an unbiased ASR throughout northern Spencer Gulf. In the absence of information on recruitment and natal homing, however, we restrict our conclusion of an unbiased ASR to those individuals actually involved in the Point Lowly aggregation.

With the current reliance on PVA for predicting extinction risk, methods to increase the accuracy of estimating ASRs and population size are crucial. This study provides a new approach to indirectly estimating the population ASR, and highlights the importance of incorporating temporal information into estimates of population size.

Acknowledgments We thank Jim Mitchell (Santos Limited) for infrastructure support, and all volunteers for field assistance. Financial support was provided by The Field Naturalists Society of South Australia, Australian Geographic Society, Santos Limited., Mark Mitchell Foundation, and the ANZ Holsworth Foundation.

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